Friends of the Bitterroot | WildEarth Guardians

April 12, 2019

Objection Reviewing Officer
USDA Forest Service, Northern Region
26 Fort Missoula Road
Missoula, MT 59804

Sent via Email: appeals-northern-regional-office@fs.fed.us

Re: Darby Lumber Lands Phase 2 Project Objection
Darby/Sula Ranger District Bitterroot National Forest
Responsible Official: Supervisor Matt Anderson

To the Objection Reviewing Officer,

Pursuant to 36 C.F.R. Part 218, Friends of the Bitterroot and WildEarth Guardians (collectively, "Objectors") file this Objection to the Draft Decision Notice and Finding of No Significant Impact ("FONSI") and 2019 Updated Environmental Assessment ("EA") issued by the Bitterroot National Forest (BNF).[1] All of the Objectors filed scoping comments on October 13, 2017 and comments on the Draft EA on November 19, 2018. Objectors have fully participated in the agency review of the project. As such they are proper Objectors under Part 218. Pursuant to 36 C.F.R. 218.8, the Objectors hereby state that the following content of this Objection demonstrates the connections between the comments noted above for all issues raised herein, unless the issue or statement in the FONSI and EA arose or was made apparent after the opportunity for comment closed.

WildEarth Guardians is a nonprofit conservation organization with offices in Montana and five other states. WildEarth Guardians has more than 200,000 members and supporters across the United States and the world. Guardians protects and restores wildlife, wild places, wild rivers, and the health of the American West. For many years, WildEarth Guardians has advocated that the Forest Service maintain a balance between access, risks and costs when addressing its road system. We submitted timely comments on the Forest Service's first EA.[2] Our comments advocated for thoughtful management of the agency's road system and its associated impacts to improve the health of watersheds and wildlife on the Bitterroot National Forest. We have

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[1] See https://www.fs.usda.gov/project/?project=49700

[2] November 20, 2018 Friends of the Bitterroot and WildEarth Guardians, Comments on Darby Lumbers Land – Phase II Project Environmental Assessment submitted to Darby District Ranger Eric Winthers.

organizational interests in the proper and lawful management of the forest road system and its associated impacts on the Bitterroot National Forest's wildlife and wild places.

Friends of the Bitterroot (FOB) is a non-profit, grass roots organization with over 200 members living in and around the Bitterroot. FOB has been monitoring the Bitterroot National Forest since 1988. The original members were disturbed by the unsustainable logging that was occuring in the Bitterroot and surrounding forests. Clear cutting, terracing and the building of thousands of miles of roads over many decades had taken a catastrophic toll on public lands. Forests, soils, fisheries, wildlife, and water quality had suffered appalling losses. For over 30 years, FOB has actively analyzed and commented on hundreds of projects, always making sure that the agency complies with environmental law and Forest Service rules and regulations. It is our goal to protect resources and preserve Montana's national heritage in the Bitterroot National Forest and to prevent unsustainable logging practices and the building of roads in an already overbuilt and underfunded forest road system.

As required by 36 C.F.R. § 218.8(d), we identify WildEarth Guardians as the lead objector. The lead objector's name, address, telephone number and email address are as follows:

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However, each Objector listed above are represented herein and all agency correspondence regarding this Objection should be directed to the Objectors' contacts as listed below.

I. Failure to prepare an environmental assessment that provides sufficient evidence and analysis of environmental impacts

A. The BNF improperly relied on internal project files and failed to prepare an EA useful to facilitate planning, decision making, and public disclosure.

CEQ's NEPA regulations directs that information used to inform NEPA analysis "must be of a high quality" and that "[a]ccurate scientific analysis . . . [is] essential to implementing NEPA." 40 C.F.R. § 1500.1(b). In order to ensure Forest Service officials meet this standard, agency regulations provide further direction for environmental assessments:

> **(3)** Environmental Impacts of the Proposed Action and Alternative(s). The EA:

> **(i)** Shall briefly provide sufficient evidence and analysis, including the environmental impacts of the proposed action and alternative(s), to determine whether to prepare either an EIS or a FONSI (40 CFR 1508.9);
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> **(ii)** Shall disclose the environmental effects of any adaptive management adjustments;
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> **(iii)** Shall describe the impacts of the proposed action and any alternatives in terms of context and intensity as described in the definition of "significantly" at 40 CFR 1508.27;
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> **(iv)** May discuss the direct, indirect, and cumulative impact(s) of the proposed action and any alternatives together in a comparative description or describe the impacts of each alternative separately; and
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> **(v)** May incorporate by reference data, inventories, other information and analyses.

36 C.F.R. § 220.7(b)(3)(i - v).

We acknowledge these regulations allow the agency to prepare an EA, "in any format useful to facilitate planning, decision making, and public disclosure as long as the requirements of paragraph (b) of this section are met. The EA may incorporate by reference information that is reasonably available to the public." [3] In the updated EA and FONSI, the BNF made numerous references to project files in order to support conclusory statements and respond to comments, for example:

- In responding to comments that dwarf mistletoe fulfills a natural ecological function and its presence does not justify even-aged harvest, the BNF responds, "[t]he forest recognizes mistletoe is a natural process. Project file document SILV-001 addresses the need to remove mistletoe infected trees within the treatment units."[4]
- In addressing the level of uncertainty from the proposed action, the BNF states, "[p]ast monitoring of similar actions and projects have not shown significant effects (PF-MONITOR-001-012)."[5]
- In justifying its focus on only sediment in the EA's aquatics analysis instead of using additional indicators such as temperature, passage barriers, habitat structure, etc., the BNF states, "[a] substantial body of scientific literature (Project File AQUATICS-003) as well as project monitoring carried out locally (Project File AQUATICS-003 and 025; USDA Forest Service, 2017) and regionally (AQUATICS-004 and 022) supports the capacity of RHCAs in protecting those features."[6]

The BNF's use of project files to inform the analysis is certainly within its prerogative. Internal procedures for drafting an environmental assessment is not at question. However, the BNF does not include sufficient discussion, analysis or evidence from these project files in the EA. Rather, the above examples exemplify numerous instances where the BNF simply tiers to the project files themselves in place of providing the necessary scientific analysis NEPA requires in the EA, thereby precluding meaningful and informed public comment in violation of NEPA. We provide additional examples throughout our comments.

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[3] 36 C.F.R. § 220.7(a).

[4] FONSI Appendix C at 6.

[5] FONSI at 15.

[6] EA at 25.

Further, directing readers to the project files exceeds the meaning of what is reasonably available to the public. The BNF assumes that all interested members of the public have sufficient internet access and technical ability to view the project files. This is incorrect. Several Friends of the Bitterroot members have inconsistent and unreliable internet access, and the Forest Service cannot assume that all interested stakeholders utilize computers to obtain and respond to agency documents, especially those the BNF typically considers internal. Further, the BNF does not provide a reasonable method to obtain project files for those without reliable internet access.. Yet, the EA directs readers to these files for information that should be included as appendices rather than project files.[7] In a conversation with the BNF Environmental Coordinator, we learned that obtaining paper copies of the project files requires a Freedom of Information Act request that is subject to fees unless granted a waiver, which then requires filing a fee waiver form.[8] This is is hardly a format useful to facilitate planning, decision making, and public disclosure required under NEPA.

B. Failure to provide evidence supporting reliance on design criteria

Our previous EA comments raised concerns with the BNF's use and reliance on design criteria, which the agency uses as a rationale to forego conducting the requisite scientific analysis NEPA requires.[9] The updated EA lists numerous, specific design criteria explaining, "[d]esign features include best management practices (BMPs), which minimize effects on soil and water resources. For harvest and road management activities, BMPs are designed to assure compliance with the Clean Water Act and State of Montana water quality standards."[10] The BNF relies on design criteria specific to RHCA's to eliminate several indicators from the aquatics analysis.[11] The EA explains, "[a] substantial body of scientific literature (Project File AQUATICS-003) as well as project monitoring carried out locally (Project File AQUATICS-003 and 025; USDA Forest Service, 2017) and regionally (AQUATICS-004 and 022) supports the capacity of RHCAs in protecting those features."[12] While the discussion, evidence and analysis may support the BNF's assertion, the EA fails to incorporate any details to support its position and simply relies on the project files in violation of NEPA.

Further, the EA states, "[d]esign features (Table 3) would apply to all ground-disturbing activities that are described below [road/trail use]. Similar to standard BMPs applied during road location and construction, the design features do not totally eliminate sediment production, but they reduce its effects to the greatest extent possible."[13] The EA discusses potential sedimentation from road and trail use including log hauling on FR 321 along North Rye Creek and explains the following:

> BMP upgrades on FR 321 are proposed, and WEPP model output suggests that the application and maintenance of BMPs on this road would result in sediment delivery during log haul that is similar to what currently exists with passenger traffic (Table 8). In the long-term, after the log haul and final maintenance

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[7] See EA at 32. ("The reader should consult the BA/BE if they desire greater detail than what was provided above.).

[8] Phone conversation with BNF Environmental Coordinator Amy Fox on April 4, 2019.

[9] See our previous EA Comments at 13 and 23.

[10] EA at 11-20.

[11] EA at 25.

[12] Id.

[13] Id. at 27.

> is completed, sediment delivery to North Rye Creek from FR 321 is estimated to be 35-41% less than the present level (Project File AQUATICS-015).[14]

Here the BNF incorporates assumed benefits from the design criteria into the WEPP model to estimate potential sedimentation. The EA failed to provide analysis or evidence demonstrating how the BMPs reduce sedimentation that would support their inclusion in the WEPP model. Rather the BNF once again provides reference to a project file. This brings into question the WEPP model results and the BNF's claim that the, "...WEPP model predicts that hauling traffic is likely to deliver unmeasurably low amounts of sediment to Rye Creek (Project File AQUATICS-016)."[15]

The BNF continues its over-reliance on BMPs to address potential sedimentation regarding the construction of connector trails, stating, "[d]ue to these design features and BMPs (found in Table 3), sediment delivery would be reduced to the feasible minimum, but route-related sediment may still be observable in the bottoms of the draws immediately downstream of the crossings (estimated at up to 100 feet). For these reasons, further assessment of aquatic effects for the proposed connector trails is not warranted."[16] Here, even with the likelihood of sedimentation, the BNF relies on BMPs to forego assessing the potential environmental consequences in violation of NEPA.

Regarding sedimentation from road construction, the EA states, "[m]odeling of sediment delivery from the new roads indicates that the proposed design (outsloped) combined with BMPs and a vegetated stream buffer would limit sediment contributions from 0 to < 80 pounds/year in the Harlan Creek watershed until the disturbed soils revegetate, depending upon the exact slope of the buffer (Project File\ AQUATICS-015)." Once again the BNF relies on project files to support its conclusion and fails demonstrate how the BMPs will effectively limit sedimentation.

Due to the EA's over-reliance on BMP and design criteria,, it fails to properly analyze potential adverse environmental effects from the proposed action. For this reason, we urge the BNF to prepare an EIS to provide proper analysis and demonstrate compliance with all requisite laws and regulations, and adherence to Forest Service directives.

C. Failure to analyze vegetation impacts.

In our previous EA comments, we raised the issue that the analysis fails to provide an inventory of rare plants and fully disclose potential environmental consequences from the proposed action.[17] The EA project file for rare plants specifies that on the ground field studies were not completed for rare plants, only habitat surveys.[18] In the IDT meeting of August 1st 2017, botanist claims that it is too late to do a complete survey. The botanist report states, "Montana Natural Heritage Program database, aerial photographs, spatial information, and Bitterroot National Forest records were reviewed to identify known

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[14] EA. at 28.
[15] Id. at 29.
[16] Id. at 29-30.
[17] See our previous EA Comments at 14.
[18] EA project file BOTANY-001 at 2.

rare plant populations in or near the proposed project area. The project area was also surveyed for habitat that might be suitable for rare plant species. "[19] There is mention of a survey started in 2017 and completed in 2018 later in the document, but it is not specific and only a habitat survey is mentioned in the methodology for analysis. We requested the exact dates of any on the ground surveys in our previous comments.[20] The only mention of rare plants in the EA is in the design criteria.[21] The BNF warns that "all species listed are very susceptible to being outcompeted by invasive species and moderate to severe long term disturbance,"' yet these effects are not analyzed in the EA.[22]

The BNF fails to analyze the effects of commercial timber harvest on invasive weeds. Invasive weeds are a direct, negative effect of soil disturbance, which is "*an unavoidable consequence of forest management activities*."[23] Merriam et al. (2006) discuss the serious weed problem created by fuel treatments. Dodson and Fiedler (2006) studied weeds and forest management in a Montana Ponderosa forest, finding the biggest negative impacts for thinned and burned units, and the next biggest impacts on thinned-only units. Burned-only units had fewer weed problems, suggesting that the prescribed-burn-only treatment may have the lowest ecological cost-benefit ratio. The design criteria the BNF relies upon to mitigate the weed problem have been largely ineffective on other projects because the real problem is the soil disturbance. Results on the Hayes Creek project of a decade ago provide a good example of the ineffectiveness of these design features. Many areas there—10 years later--have a ground cover almost entirely comprised of knapweed, St Johns Wort, and cheatgrass. It probably did not help that the BNF failed to properly monitor or reclaim the area, but without funding guarantees for post-project reclamation on DDL2, the effects of timber harvest in the project area will probably be similar and significant.

D. Failure to utilize an accurate baseline and analyze the transportation system

Both our Scoping and previous EA comments explained the need to provide an accurate baseline of current conditions, including roads.[24] Here the BNF failed to address this issue, especially in regards to the transportation analysis. The EA displays Table 15 summarizing changes to the transportation system, and listing the miles of road open, closed or open with restrictions, all totaling 221.4 miles. However, the EA did not disclose the number of culverts and stream crossings, the miles of road in each maintenance level, the number of non-system roads or those with an undetermined status. It did not discuss the current condition of roads in the project area, their maintenance history and current backlog, the objective maintenance level of each road, or the BNF's projected maintenance capacity to achieve those objective maintenance levels.

The lack of detail is a systemic flaw in the EA and even the project files fail to provide the necessary information since the DLL Phase I and II Travel Analysis Report does not differentiate between the two

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[19] EA project file Botany 001 at 2.
[20] See Scoping Comments at 7.
[21] EA at 12.
[22] EA project file BOTANY-001 at 4.
[23] EA at 47.
[24] See our Scoping Comments at 6 and previous EA comments at 6.

phases.[25] In other words, it is impossible from looking at the travel analysis report to determine which roads are in the Phase II project area, or their associated risks and benefits. The failings preclude our ability to properly evaluate the potential environmental consequences of the proposed action and provide meaningful comment. For example, the BNF proposes to decommission approximate 39 miles of road and store an additional 16 miles.[26] Yet, the analysis does not explain which roads would receive specific road treatments. Rather, again the BNF relies on general design criteria where the EA explains:

> Activities will comply with Road Best Management Practices (BMPs) to minimize effects to soil resources. Rip, subsoil or decompact road surfaces where it appears ripping would help restore hydrologic function. If road surfaces are not eroding, have no culverts needing removal and have vegetation indicating appropriate recovery, they would not be ripped or recontoured.[27]

The EA omits the number of culverts on roads proposed for decommissioning or storage, their current condition, or what would trigger their need for removal. It is unclear how many culverts would remain on roads proposed for decommissioning or storage, and what potential environmental risk they may pose in the future if left in place. The EA also fails to list roads that need treatment in order to prevent adverse environmental consequences. Road abandonment is not a valid decommissioning treatment.

As we explained in our scoping comments, the baseline and no-action alternative can, and sometimes do differ.[28] Analysis of the road system should recognize and build on those distinctions. Current management direction does not compel the Forest Service to recognize non-system roads, but disclosure of the number and location of undetermined roads, decommissioned routes and unauthorized routes, as well as the impacts of those routes, is a necessary component of the no-action alternative that should be disclosed to inform meaningful public comment. An assessment of the no-action alternative should have been separate and distinct from the identification of the baseline (the official open road system). Yet, the EA failed to provide either.[29] The Forest Service should have disclosed the objective maintenance level, any decisions that have been subject to NEPA that may differ from those objective maintenance levels, and the proposed maintenance levels of each road under each alternative. It should have also disclosed the number of undetermined roads it proposed for decommissioning and those to be added to the system.

As we explained in our previous EA comments, the Forest Service must carefully consider and document the road management objectives, environmental impacts, and social and economic benefits associated with any proposed addition before adding roads to the system.[30] It also directs the agency to consider travel analysis and long-term road funding opportunities and obligations as part of any decision to add

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[25] Project file TRANS-001
[26] EA at 64.
[27] Id at 15.
[28] 3 See, e.g., FSH 1909.15, 14.2; Council on Environmental Quality's Forty Most Asked Questions (1981), #3 (explaining that "[t]here are two distinct interpretations of 'no action'"; one is "'no change' from current management direction or level of management intensity," and the other is if "the proposed activity would not take place").
[29] EA at 63-64.
[30] See previous EA Comments at 17. See also Forest Service Handbook 7703.26(1).

road miles to the system.[31] For roads that were previously identified for decommissioning in a NEPA decision, the Forest Service must assess the road management objectives, environmental impacts, and social and economic benefits associated with that road before identifying it for use as a temporary road and later adding it to the system as a closed road. Much of this necessary information remains missing from the analysis in the EA, without which the public is precluded from meaningful comment and the Forest Service's proposal runs contrary to its own policy for assessing and adding roads to the system.

This is especially problematic not just for the proposal to construct 4.3 miles of permanent specified road within the project area, but also for the additional 10.38 miles of undetermined roads the BNF proposes to add to the system.[32] The BNF must treat these as new road construction in order to fully analyze and disclose the potential environmental consequences from adding them to the national forest transportation system. Included in this information should be their road management objectives and discussion of how the BNF will ensure their proper maintenance. It is important to note, the BNF failed at any point to disclose the proposed action would add undetermined roads to the system, and it was only through a close evaluation of project file TRANS-001 that we saw undetermined roads were part of the travel analysis, with the exception of roads #13380 and #133881. The EA does not disclose how these two roads will be managed under the proposed action as they do not appear in the EA Appendix B.[33] It is unclear if the Darby Lumber Lands Phase II project address all undetermined roads in the project area, or indeed all roads in the project area. Other undetermined roads proposed to be added to the system are a particular concern:

- Road #62400 - In the DLL Phase I & II travel analysis report, the ID Team recommends this road be decommissioned noting another road provides access, yet the proposed action would add this to the system in order to provide loop opportunities.[34]
- Road #62781 poses a high risk to elk and only has moderate timber value, yet the BNF proposes to add this to the system as a stored road.[35]
- Road #73868 was recommended by the ID Team for decommissioning, but the proposed action is to add this to the system as open seasonally for a loop connector.[36]

The EA fails to address the new road construction as well as adding undetermined roads to the system. It also lacks any discussion of the undetermined roads proposed for decommissioning, specifically, if they have culverts that need removal or if any require other specific treatments to address hydrological concerns. In looking at the project's travel analysis report, we note the following roads have medium risks to soils and water: #62404, #62405, #62437, #62544 and possibly more. This is an example of how the BNF could have used the project's travel analysis report to inform better analysis and determine specific treatments for roads proposed for decommissioning. The EA references removal of 40 culverts at stream crossings, but it is not clear if these are the total number of culverts in the project area or just those that

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[31] Id. 7703.26. See also FSM 7715.03(7) (noting that "Ranger Districts should avoid adding routes to the Forest transportation system unless there is adequate provision for their maintenance")

[32] See Exhibit A - DLL Undetermined Roads Proposed Action provided by the BNF Environmental Coordinator Amy Fox in an email sent April 2, 2019.

[33] See Exhibit A and EA Appendix B

[34] See project file TRANS-001 and EA Appendix B at Table B-5.

[35] Id.

[36] Id.

will be removed.[37] It is also unclear how many culverts will remain on stored and decommissioned roads where there are medium or high risks to soils and water resources. The BNF needs to better disclose the potential environmental consequences from the proposed road construction, and from adding undetermined roads to the system. The BNF also should have specified the storage and decommissioning treatments for each road, if any, and disclosed the environmental consequences for any road not receiving treatment for storage or decommissioning.

Roads, Fire and Climate Change

Our scoping comments urged the BNF to analyze how climate change exacerbates the adverse environmental consequences from roads in the project area, and how roads affect instances of wildfire and behavior.[38] The BNF fails to appropriately respond to the issues omitting any discussion or analysis of how roads lead to increased instances of human caused wildfire as we explained.[39] Rather, the BNF focuses solely on fuels and the rate of fire spreading predicted by modeling and measured in chain lengths.[40] The EA failed to address how the proposed action, with its increased road and trail use, may contribute to increased occurrences of human caused wildfire.

Our scoping comments also urged the BNF to conduct a robust analysis under NEPA of the forest road system and its environmental and social impacts is especially critical in the context of climate change.[41] Climate change is a major challenge for natural resource managers because of the magnitude of potential effects and the related uncertainty of those effects. Climate change intensifies the impacts associated with roads. For example, as the warming climate alters species distribution and forces wildlife migration, landscape connectivity becomes even more critical to species survival and ecosystem resilience.[42] Climate change is also expected to lead to more extreme weather events, resulting in increased flood severity, more frequent landslides, altered hydrographs, and changes in erosion and sedimentation rates and delivery processes.[43] Many National Forest roads are poorly located and designed to be temporarily on the landscape, making them particularly vulnerable to these climate alterations.[44] Even those designed for storms and water flows typical of past decades may fail under future weather scenarios, further exacerbating adverse ecological impacts, public safety concerns, and maintenance needs. At bottom, climate change predictions affect all aspects of road management, including planning and prioritization, operations and maintenance, and design.[45]

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[37] EA at 30.

[38] See Scoping Comments at 11-13.

[39] Id. Attachment A at 9 (noting human-ignited wildfires account for more than 90% of fires on national lands and are almost five times more likely in areas with roads).

[40] EA at 56 and FONSI Appendix C at 7.

[41] See Scoping Comments at 11.

[42] See Scoping Comments, Attachment A at 9-14.

[43] See, e.g., Halofsky, J.E. et al. eds., USDA, Forest Service, Pacific Northwest Research Station, Adapting to Climate Change at Olympic National Forest and Olympic National Park, PNW-GTR-844 (2011), pages 21-27. (Scoping Comments, Attachment F).

[44] See, e.g., Halofsky, J.E. et al. eds., USDA, Forest Service, Pacific Northwest Research Station, Adapting to Climate Change at Olympic National Forest and Olympic National Park, PNW-GTR-844 (2011), pages 36-38. (Scoping Comments, Attachment F).

[45] See, e.g., id. at 21-27.

Yet the BNF failed to recognize this issue in the EA and in response to comments focused only on CO2 emissions.[46] The BNF ignored our call for the agency to conduct a vulnerability assessment, to determine the project area's exposure and sensitivity to climate change, as well as its adaptive capacity.[47] We explained the BNF should consider the risk of increased disturbance due to climate change when analyzing this proposed project, and include existing and reasonably foreseeable climate change impacts as part of the affected environment, assess them as part of the agency's hard look at impacts, and integrate them into each of the alternatives, including the no action alternative.[48] We urged the BNF to consider the cumulative impacts likely to result from the proposed project, proposed road activities, and climate change.[49] Finally, we commented that the BNF should consider: (1) protecting large, intact, natural landscapes and ecological processes; (2) identifying and protecting climate refugia that will provide for climate adaptation; and (3) maintaining and establishing ecological connectivity.[50] Again, the BNF failed to respond the our requests, ignored our supporting literature, and as such the EA does not meet the Forest Service direction in its own manual.[51] For these reasons, the BNF should prepare an EIS that carefully considers the role of climate change on the forest roads in the project area and adjacent lands.

E. Failure to analyze impacts to aquatic habitat and species

The BNF's failure to analyze the environmental consequences to aquatic habitat due to its over-reliance on design criteria we note in section B above, combined with its failure to properly analyze the road system we note in section D, undermines the EA's entire analysis on aquatic habitat for species such as bull trout, western pearlshell mussel, and cutthroat trout. Further, the EA failed to properly address road and trail use. The BNF notes the following:

> Road and trail use generates sediment by disturbing and loosening soil at road/stream crossings and other sites within sediment-contributing distance of streams. The loose soil is available for transport by surface flow. Surface flow occurs regularly on the compacted surfaces of trails and roads, making those trails and roads within sediment-contributing distance chronic sediment sources.[52]

We agree road and trail use are chronic sources of sediment and pose serious risks to water quality and aquatic habitat, as was described in detail in Attachment A of our scoping comments.[53] Yet, the EA fails to properly address this use. Rather it focuses solely on log hauling on the near-stream segments of FR

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[46] FONSI Appendix C at 15.
[47] See Scoping Comments at 12.
[48] Id.
[49] Id.
[50] Id at 13.
[51] See, e.g., FSM 2020.2(2) (directing forests to "[r]estore and maintain resilient ecosystems that will have greater capacity to withstand stressors and recover from disturbances, especially those under changing and uncertain environmental conditions and extreme weather events"); FSM 2020.3(4) ("[E]cological restoration should be integrated into resource management programs and projects . . . Primary elements of an integrated approach are identification and elimination or reduction of stressors that degrade or impair ecological integrity.").
[52] EA at 28.
[53] See The Wilderness Society, Transportation Infrastructure and Access on National Forests and Grasslands: A Literature Review (May 2014).

321 along North Rye Creek.[54] Absent is any discussion of increased traffic on roads and trails from future motorized recreation, and the resulting sedimentation or other environmental consequences from the area becoming a destination for the off-road community. This analysis is essential for complying with the minimization criteria under the Travel Management Rule, as we explained in our previous comments directing the BNF to demonstrate compliance with all applicable rules for designating roads and trails for off-road vehicle use.[55]

F. Failure to analyze impacts to wildlife

Threatened Species

Canada lynx

The BNF once again relies on design criteria to mitigate potential adverse environmental consequences from the proposed action, this time on Canada lynx. The EA explains the following:

> The construction of 225 feet of connector route through delineated lynx habitat is designed to allow, and would facilitate, ATV/UTV recreation and would accumulatively contribute to potential disturbance from these sources on this connector route and adjacent existing routes nearby. ATV/UTV use of this connector and adjoining routes is anticipated to be high between 16 June and 14 October. The rest of the year this connector would be seasonally closed.[56]

Our previous EA Comments raised the concern regarding the BNF's ability to enforce seasonal closures, noting "ATV's tend to not follow seasonal closures and tend to ride off route in many areas like Willow Creek and Como Lake to name just two."[57] Yet, the EA fails to discuss the Forest Service's ability to ensure compliance with seasonal closures, and notably absent is any mention of past unauthorized use or the BNF's enforcement history that could demonstrate the effectiveness of such closures. This is especially important given the BNF concludes, "[t]he proposed action ***May Affect but is Not Likely to Adversely Affect*** Canada lynx based on the potential for disturbance from recreation activity associated with construction of a connector route through 225 feet of delineated lynx habitat. However, this affect would be mitigated by a seasonal closure,..."[58] The BNF should prepare an EIS that includes a proper evaluation of the agency's ability to ensure compliance with travel management direction in the project area, especially in light of the increased use that is a likely outcome of the proposed action.

Grizzly Bear

In previous comments we raise the importance of the project area and the larger Sapphire Mountain Range as vital link and travel corridor for grizzly bears dispersing from recovery areas such as the Greater

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[54] EA at 28-29.
[55] See our Scoping Comments at 8, our previous EA Comments at 17, and 36 C.F.R. § 212.55(a).
[56] EA at 44, and Table 9 at 35 ("Design criteria would minimize potential adverse effects.").
[57] See previous EA Comments at 23.
[58] EA at 44.

Yellowstone Ecosystem.[59] Grizzly tracks have been documented by FWP near the Darby Lumber Land Phase II project area, and we provided a map showing documented grizzly bear tracks in close proximity to the project area.[60] The closest recovering population is from the Northern Continental Divide Ecosystem and a male grizzly bear was captured outside Stevensville on October 27, 2018.[61] The Montana Department of Fish and Wildlife notes, "[t]hrough the years, several grizzly bears have been confirmed in the Sapphire Mountains and in the northwest portion of the Bitterroot Valley, including the Lolo Creek drainage, and as far south as the Big Hole Valley. Grizzly bears in the Bitterroot remain relatively uncommon, compared to other parts of northwest Montana, but there have been increasing reports in recent years."[62] Yet, the EA fails to acknowledge the growing use and importance of the Sapphire Range and areas adjacent to the project area for grizzly bears. The EA does acknowledge that, "[t]he USFWS recently expanded the "Area Grizzly Bears May be Present Outside the GYA" to include all areas outside the GYA population and East of Highway 93 (USFWS 2017a). This expanded area includes the project and analysis areas."[63] However, even with this acknowledgement and the growing increasing instances of grizzly bears documented in the Sapphires, and in close proximity to the project area, the BNF asserts the proposed action is ***May Affect but not Likely to Adversely Affect*** grizzly bears.[64] This conclusion rests on the premise that there is no evidence grizzly bears use the project area and there are no recorded observations.[65] The EA does note what may occur should grizzly bears attempt to use the project area as a travel corridor:

> If grizzly bears move into the analysis area in the future...we would anticipate some level of incidental take of female grizzly bears in the form of harassment, and /or harm through significant habitat modification or degradation as a result of high road densities and associated disturbance...Project activities could cause disturbance to grizzly bears if they move into the analysis area in the future...The construction of ATV connector routes would likely increase the frequency and use of ATV activity in the project area increasing the potential for disturbance and mortality.[66]

The BNF dismisses these harmful effects by stating the area is unsuitable for grizzly bears and will remain so due to high road densities.[67] Yet, the analysis fails to address how the proposed action cumulatively affects the ability of grizzly bears to disperse throughout areas adjacent to the project boundaries. This lack of analysis, combined with the acknowledged harm grizzly bears may experience if they utilize the project area, suggests the proposed action would indeed adversely affect grizzly bears.

Finally the biological assessment for grizzly bears states, "[t]he EHE standard results in areas of secure habitat for a range of species including grizzly bears."[68] However, the BNF proposes amending the EHE standards in this project, which the agency fails to address in the context of secure grizzly bear habitat.

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[59] See our Scoping Comments at 26.
[60] Id. at 27.
[61] Montana Fish and Wildlife Press Release dated Oct. 29, 2018, see Exhibit B.
[62] Montana Fish and Wildlife Press Release dated Oct. 29, 2018, see Exhibit B.
[63] EA at 45.
[64] EA at 47.
[65] Id.
[66] Id. at 46-47.
[67] Id at 47 and 45.
[68] EA project file WILD-001 at 9.

Neighboring areas included in Darby Lumber Lands Phase I project also failed to protect EHE standards, and the BNF fails to address the cumulative reduction in grizzly bear habitat security.

Management Indicator Species

NEPA requires thorough analysis of impacts to Management Indicator Species MIS. BNF forest plan identifies Pileated Woodpecker, Elk and Pine Marten as MIS. EA concedes that all would be impacted by forest management yet no analysis has been provided in the EA as to the extent of that impact nor were on the ground surveys conducted to identify occupied areas. No similar projects are cited to prove that impact would be minimal. While the chart on Elk EA pg 42 claims "winter range is critical" it goes on to surmise that loss of Elk Habitat Effectiveness EHE will not affect Elk because many areas in the forest do not comply with EHE and elk numbers are increasing. There are too many variables involved to make such a simplistic assumption. According to the agency's own rules, an EA must provide sufficient evidence and analysis to determine whether to prepare either an EIS or a FONSI. 40 C.F.R. § 220.7(b)(3)(i). In our previous EA comments page 6-7 and scoping comments page 6, we asked the Forest Service to provide detailed, site-specific information and an accurate baseline to assess the impacts of the proposed action. We also asked for an inventory of old growth stands in the project area and the identification by map any 6th order drainage that is presently within elk habitat effectiveness (EHE) standards. Failing to provide sufficient information precludes meaningful and informed public comment in violation of NEPA.

In our previous EA comments on pg 5 we asked that a survey of Pileated Woodpeckers be provided. Though the chart claims no known nesting sites exist in the project area, it has been many years since an on the ground survey has been done. Too much reliance on Montana Natural Heritage Program Database is used in the EA for wildlife in lieu of on the ground specialist surveys. How can an analysis of impacts be provided without sufficient data? The EA finds that pine marten habitat will be affected by management activities. Again the benefits of mistletoe are not analyzed in conjunction with impacts to MIS. Little analysis is done concerning impacts to these indicator species and no other projects are cited to prove that a "minimal to none" conclusion is warranted.

E. Failure to analyze cumulative impacts

The Forest Service must disclose and consider all recent or currently proposed logging and prescribed fire projects that rely on site-specific Forest Plan amendments to the Bitterroot Forest Plan. Understanding the bigger picture regarding potentially numerous changes to the Bitterroot Forest Plan, when combined with the site-specific Forest Plan amendments proposed for this project, is essential to informing the public and decision makers. Disclosing the bigger picture of cumulative change to the Forest Plan is especially true where this project is tiered to the Bitterroot Forest Plan.

In our previous EA comments pg 13 as well as scoping comments pg 6, we asked for the following information to analyze cumulative impacts of multiple actions and proposals forest-wide: data for Equivalent Clearcut Area (ECA), old growth inventory, the effects of MA2 site specific amendment and forage capacity with an increase in invasive plants due to disturbance, on the ground surveys and data that demonstrate the effectiveness of design criteria in the reduction of invasives, quantification of all human-caused CO2 emissions and carbon sequestration for each alternative, the effects of climate change on ecological conditions in the project area, and an analysis of these conditions under climate change scenarios. The BNF failed to provide adequate evidence, discussion or analysis for any of our requested information.

EA fails to address the cumulative impacts under grazing allotments scoping pg 8, EA comments pg 14. No project mitigations were provided in the updated EA to minimize grazing competition which would reduce forage. The EA states that grazing competition might reduce forage pg 46, but later on pg 44 expects “winter range would be improved with increased stimulation of forage.”

In our EA comments pg 14 and scoping, we requested use of Forest Service on the ground surveys vs Montana Natural Heritage Program data for wildlife, invasive species, rare plants, and visual quality. There is no compliance with our request for an analysis of the loss of hunter opportunity EA comments pg 14 and scoping pg 10-11 and the cumulative effects of numerous site specific amendments across the BNF in the chart in section 10. EA comments. The cumulative effects of returning to the area for up to “seven more treatments” over time to bring the area to desired results has not been adequately analyzed. CWD and Snag Amendments are considered necessary in Soils 001 pg 14, but are not analyzed as to their cumulative effect. We requested this analysis in EA comments pg 14. We also asked specialists to analyze the benefits of mistletoe to wildlife and thinning for more resilient trees pg 14, but this analysis is lacking in the updated EA.

The haul route is an ever-changing beast. How can analysis of cumulative impacts even be properly conducted when the mark is constantly changing. Combine this with an overtaxed IDT team (meeting notes August of 2017) and a thorough analysis is certainly in question. There are still roads that butt up to private land. We previously commented on our concerns the temporary and specified roads in the Roan Gulch area. In units 10 and 1, there is no access but via private land, yet in a March 24 2019 Bitterroot Restoration Committee meeting Eric Winthers made it clear that there was no deal with the private landowner for hauling on private land. In the response to comments concerning the roads, FS said the northern units would be accessed via private land. In the interest of transparency, this deal with the land owner should be disclosed, and included as part of the cumulative effects analysis. There is also a mention in the EA that logging projects on neighboring private lands "can be reasonably expected". This suggests an agreement may have been reached between the timber company, the land owner and the FS. Yet such an agreement was not part of the analysis, even though the BNF’s response to comment references future forest management activities and the use of the road in conjunction with the road on adjacent land: "[t]he new Forest Service road will connect to this road and sawtimber removed from units on the north end of the timber sale will be hauled out this route.” Not only will this road be used during this project, but apparently in future projects as well. The questioned roads seem to provide private access both temporary (up to 10 years) and permanent to forest service land and to provide for the possibility of an alternative haul route. The specified road at the bottom of Roan Gulch leads to an alternative haul route that would change the value of the sale should this alternative route be implemented. The contract should be re-negotiated to reduce public expense and the new route should be fully analyzed.

NEPA requires thorough analysis which must be provided so the public can provide meaningful comment. We have asked for this information on cumulative effects in both scoping and EA comments pg 13-15.

F. Failure to use Best Available Science

NEPA requires the use of best available science, and requires you to obtain information if it is "relevant to reasonably foreseeable significant adverse impacts, and if it is essential to a reasoned choice among alternatives, if the overall cost of obtaining it is not exorbitant" (40 CFR 1502.22). Public comment by WEG/FOB and Jeff Lonn pointed out science opposing the proposed treatments, and included important references that were not included in the EA. Your only response to this opposing science was to review and comment on the new literature in Project File LIT-003. No explanation for rejecting this science was included in the EA. For example, a purpose and need of the project is to "improve forest health and stand resilience", including resilience to insect outbreaks (EA, p. 3-4). Yet, Six et al. (2014; 2016) found that there is little evidence that the commonly used timber harvest treatments are effective in reducing mortality from pine beetles, and that these may actually be harming forest health because the most resistant trees may be harvested. For more discussion of opposing science, refer to Jeff Lonn's discussion of Project File LIT-003 in Exhibit C of our Objection.

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II. Failure to articulate the statement of purpose and need to address the agency's duty to identify the minimum road system, and provide support for the claimed needs.

Failure to Identify the Minimum Road System

In our scoping and previous EA comments, we urged the Forest Service to provide support for its claimed needs for this project.[69] Here we urged the Forest Service to clearly articulate a statement of purpose and need that includes identification of the minimum road system, and to provide support for the claimed needs.[70] In response, the Forest Service improperly claimed that the BNF has already identified the minimum road system in the Appendix B of the EA and the associated travel analysis report found in project file TRANS-001.[71] There are two major problems with this response.

First, the response is incorrect. The Darby Lumber Lands Phase I and II travel analysis report did not identify the minimum road system for the forest. Rather, it provided the information necessary for the Forest Service to make that identification in subsequent projects with decisions subject to public scrutiny under NEPA. In fact, the referenced project file provides the following clarification:

> Travel Analysis will not change or modify any existing NEPA decisions, but should help to inform subsequent NEPA related to the road infrastructure...The TAP outcomes are a set of proposals for change to

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[69] Scoping Comment at 2-5, previous EA Comments at 5.

[70] Id.

[71] FONSI Appendix C at 3.

> the forest transportation system. These changes will be included in subsequent project proposals that will be documented with the NEPA process.[72]

In addition, we provided a Forest Service memorandum attached to our scoping comments that made it clear the travel analysis reports were to inform future NEPA projects that identify the minimum road system, including proposed actions:

> The next step in identification of the MRS [minimum road system] is to use the travel analysis report to ***develop proposed actions to identify the MRS***. These proposed actions generally should be developed at the scale of a 6th code subwatershed or larger. Proposed actions and alternatives are subject to environmental analysis under NEPA. Travel analysis should be used to inform the environmental analysis. [73]

The proposed actions for Darby Lumber Lands Phase II EA does not include identifying the minimum road system and does not clarify that changes to the transportation system will result in a minimum road system for the project area. In its response to our comment, the BNF asserts the EA Appendix B lists roads that will be minimum road system. Simply listing roads in an appendix and tiering to a project file is not sufficient analysis to support identifying the minimum road system. The EA Appendix B does not list or synthesize the risks and benefits associated with each road in the project area, and the EA fails to provide sufficient discussion, analysis or evidence regarding the environmental consequences of the road system in the project area that the BNF now asserts is the minimum road system.

The second major flaw is that the Forest Service's response fails to respond to the substance of the comment. We urged the Forest Service to revise the statement of purpose and need to address its duty to identify the minimum road system. The Forest Service failed to respond to this comment.

The BNF should develop an EIS that includes a purpose and need statement to identify the minimum road system. Such an effort must demonstrate consistency with subpart A of the Roads Rule. In doing so the Forest Service should consider the factors for identifying whether a road is likely needed or likely unneeded when making these types of decisions about whether to maintain the road on the system or not. [74] The Forest Service's analysis in the EA fails to consider these factors, or the risks and benefits of each road as analyzed in the project's travel analysis report, and whether the proposed road management measures listed in the EA Appendix B are consistent with the recommendations from the travel analysis report.

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[72] Project file TRANS-001 at 2.

[73] Emphasis added. See Scoping Comments Attachment C containing the memorandum from Leslie Weldon to Regional Foresters et al. on Travel Management, Implementation of 36 CFR, Part 212, Subpart A (March 29, 2012) (Attachment C). See also 66 Fed. Reg. at 3215 (explaining the 2001 "final rule requires that the agency use a roads analysis prior to making decisions about road construction, reconstruction, and decommissioning.").

[74] See 36 C.F.R. § 212.5(b)(1) (directing the Forest Service to consider whether each road segment is needed to: (1) Meet resource and other management objectives adopted in the relevant land and resource management plan; (2) Meet applicable statutory and regulatory requirements; (3) Reflect long-term funding expectations; and (4) Ensure that the identified system minimizes adverse environmental impacts associated with road construction, reconstruction, decommissioning, and maintenance).

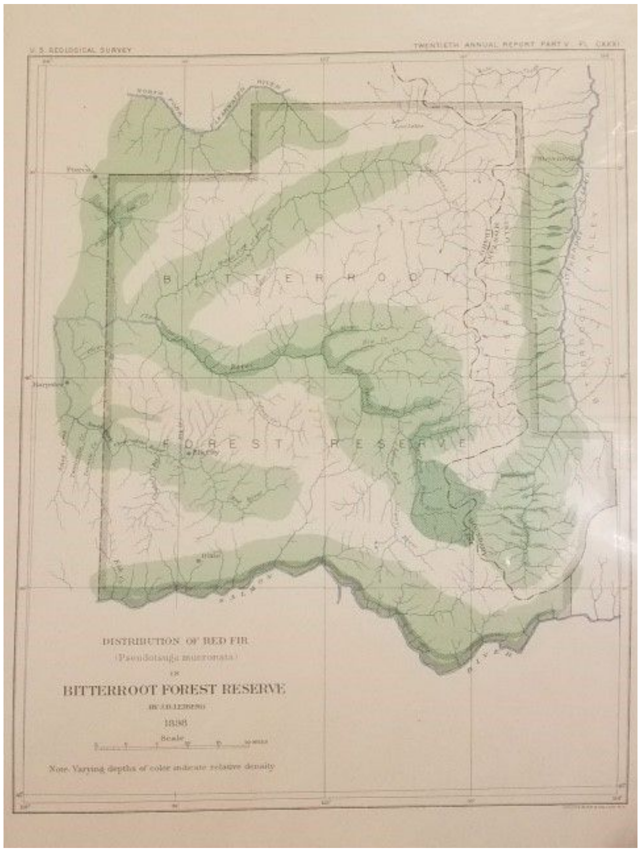
Failure to provide support for claimed needs

There is no stated Purpose and Need for this project that addresses, justifies, or directs commercial logging in MA8b with its distinct standards and objectives related to big-game and forage. On page 3, SILVI 001: "Stands proposed for harvest in MA8b do not meet the suitability of timber management as they have been withdrawn...unless timber harvest is permitted to help other resource management objectives related to wildlife according to the Bitterroot National Forest Plan." And while there is a cursory reference in the Draft Decision Notice: "Harvest units in this MA [8b] will help protect or enhance the other multiple use values identified in the Forest Plan (forage)", there is no explanation or justification in the project files under Silviculture or Wildlife where specialists connect how the proposed logging in MA8b units will optimize big-game forage production or winter range habitat. On page 19 of WILD 001 regarding timber harvest in MA8b: "Timber harvest and prescribed burning would improve winter range forage production." There is no effects analysis done or references cited to support how specifically timber harvest will improve winter range forage production. Nor is there any reference to other MA8b areas on the BNF that underwent similar treatment with measurement indicators utilized to demonstrate achieved goal of improving big-game forage production. In addition, p. 51 of the EA states "Timber treatments would potentially increase grazing pressure on the 1294 acres of units within grazing allotments. Increased grazing pressure may negatively influence the forage abundance and occupancy by elk and other big game." This suggests that timber harvest may actually **decrease** forage available for elk and other wildlife.

There is a Purpose and Need that directs treatment to restoring dry pine stands, but this VRU [1] makes up only 3.9% of the 3000 ac analysis area (Table 3: VRU by Unit)—page 7, SILVI 001. If this relatively small acreage has its own Purpose and Need then there should certainly be a separate Purpose and Need related to wildlife regarding MA8b timber harvest given the relatively large area involved.

Management actions do not fulfill stated purpose and need. On page 22 SILVI 001, Table 7, Purpose and Need "Improve Forest Health," it refers to BA measure of less than 80 in P-pine dominance types and that acres meeting this Purpose and Need is 1275. P-pine dominant acreage in the analysis area is only a small 3.9%, or 117 acres. Mixed conifer is the dominant stand type. The Purpose and Need does not refer to mixed conifers, only dry pine stands. By far mixed conifer is the dominant stand type in the project area.

Stated Purpose #2 to restore historic structure in dry pine stands (EA pg 2) is flawed. The map below of the BNF shows mixed conifer to be a large part of historical structure in low elevation dry areas.



Originally, one stated purpose and need for the timber production component of the project was to provide multiple use. This was removed from the list of purpose and needs after scoping comments were submitted. However, under the heading "Need for the project" the justification for timber production remains as the multiple use mandate. EA pg 3 "*Timber harvest activities were added to the project to provide timber to support the FS's multiple use mandate*." While it is within the Forest Service decision space to provide timber in support of multiple use, the BNF cannot violate the law to do so.

Finally, the proposed harvests may not even achieve the purpose and need without several additional treatments in the future raising the obvious question of why propose the action at all. Specifically, the EA states, "[m]ore than one treatment may be needed to reduce fuels and restore ecosystems. It may take up to seven treatments to return the area to acceptable conditions that mimic some historical range," (Reinhardt et al. 2008-EA page 23). If the BNF does not believe it can perform additional treatments, then it certainly does not need to build new system roads. However, if the BNF does anticipate seven more treatments in the future, then it is reasonably foreseeable and should be part of the cumulative effects analysis.

III. Failure to consider reasonable alternatives that meet the statement of purpose and need.

As we explained in our previous comments, the Forest Service's own regulations require an EA to "briefly describe the proposed action and alternative(s) that meet the need for action."[75] Here, the Forest Service considered the Proposed Action and a No Action Alternative. Based on the proposed actions, forest roads are an integral part of this project. Given the demonstrated harmful impacts of forest roads to aquatic habitat and watershed conditions, the Forest Service should have, but failed, to consider alternatives that decommissioned more forest roads and required fewer temporary roads. The Forest Service should consider an alternative that does not build any new roads, system or temporary.

The EA claims that current roads in the project area are deteriorating and without the proposed action, "[r]oad treatments designed to reduce sediment" would not occur.[76] As stated in our scoping comments, Darby Lumber Lands Phase I failed to complete promised road improvements.[77] An alternative should be considered that just repairs current roads and decommissions all roads not determined to be part of the minimum road system.

The BNF should have considered an alternative that did not propose logging within MA 8b. According to the supporting file (SILVI 001, page 18) the project's MA8b sections "could be prescribed burned without commercial harvest since most of the area is predominantly within desired basal area." Yet the EA fails to consider or analyze the alternative of using only prescribed burning in MA 8b without commercial timber harvest to meet the purpose and need.

The BNF failed to consider alternatives to clearcutting mistletoe-infested Douglas Firs, even in its own publications (Hadfield et al, 2000; Hoffman, 2004) state that mistletoe is not a concern unless timber harvest is the highest priority, which is not the case in MA 2 or MA 8b. Mistletoe is valuable in providing wildlife with habitat, forage, and a rich, insect-based food source as well as future snags and coarse woody debris (Bull et al., 1997; Hadfield et al, 2000; Watson and Herry, 2012; Worrel 2013). But "*dwarf mistletoe control projects have traditionally been pursued by the Forest Service in order to maximize timber production at the expense of ecosystem health*" (Pollock and Suckling, 1995). Geils et al. (2002) state that some Doug Firs are genetically resistant to mistletoe, but clearcutting eliminates these trees. A better approach would be to create a "donut" 30 feet wide around the infected area (Bull et al, 1997; Worrell 2013; Pollock and Suckling, 1995), allowing evolution to proceed and preserving ecosystem health.

IV. Failure to demonstrate compliance with the Travel Management Rule for all proposed changes to motorized access.

We previously commented on the need for the BNF to demonstrate compliance with Subpart B of the Travel Management Rule when designating motor vehicle use in the project area.[78] We noted that any decision to designate motorized use requires an assessment of whether those decisions satisfy the

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[75] See previous EA Comments at 18 citing 40 C.F.R. § 220.7(b)(2).
[76] EA at 26.
[77] See Scoping Comments at 15-16.
[78] See Scoping Comments at 22 and previous EA Comments at 17.

minimization criteria and other relevant legal requirements. When designating areas or trails available for ORV use, agencies must locate them to:

- minimize damage to soil, watershed, vegetation, or other resources of the public lands;
- minimize harassment of wildlife or significant disruption of wildlife habitats; and
- minimize conflicts between off-road vehicle use and other existing or proposed recreational uses of the same or neighboring public lands.[79]

Rather than complying with these requirements the BNF arbitrarily asserts, "[t]his project is compliant with this CFR as it has used resource specialists, important conservation measures, and multiple design features to minimize the effects of the project on natural resources."[80] The EA fails to demonstrate how design features will in fact result in the minimization to forest resources as required. Rather, the EA is silent, or relies on unsupported design criteria (we address in section I.B. of this Objection), or in fact discloses those potential adverse effects. In regards to damage to aquatic resources, the EA fails to mention increases in motorized use due to newly constructed and designated trails for OHV loop opportunities, rather it focuses solely on the actual construction, and then relies on design criteria to address potential impacts.[81] The BNF repeats this flaw in its discussion of aquatic species, once again failing to address long term sedimentation from increased motorized use.[82] Further, the EA explains in regards to soils, "[i]mpacts known to cause the greatest adverse effects on physical, chemical, and biological soil properties include soil compaction, displacement, puddling, burning, erosion, and mass wasting."[83] Yet, the soils section fails to mention adverse impacts to soils from motorized use. It is important to note that previous BNF projects also claimed use of design criteria to mitigate adverse environmental consequences, and then the agency failed to implement them or they were ineffective. Our scoping comments included evidence of previous instances where increased off-road vehicle use lead to significant resource damage after implementation of the Darby Lumber Lands Phase I project, and other commenters noted poorly constructed connector routes.[84] The BNF's assertion that the connector routes were built to Forest Service specification is contrary to the plain evidence provided to the agency.

In regard to wildlife, the EA notes in several places where the proposed action's motorized designations will adversely affect individuals, though not lead to jeopardizing populations. In the discussion on wolverine, fisher and pine marten, the EA states the benefits to the species from road decommissioning would be offset by the increased motorized recreation: "[t]his reduction would be somewhat offset by the opening of selected roads and construction of connector routes for OHV use, likely to locally increase the frequency and density of human presence and potential disturbance on these routes."[85] The result is that

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[79] Exec. Order No. 11,644, 37 Fed. Reg. 2877 (Feb. 8, 1972), as amended by Exec. Order No. 11,989, 42 Fed. Reg. 26,959 (May 24, 1977), § 3(a). The Forest Service codified these "minimization criteria" in subparts B and C of its travel management regulations. 36 C.F.R. §§ 212.55, 212.81(d). The Forest Service must show how it located the proposed motorized routes with the objective of minimizing resource damage and conflicts with other recreational uses.

[80] EA at 20.

[81] Id. at 29.

[82] Id. at 31.

[83] Id. at 52.

[84] See Scoping Comments at 14-17, and FONSI Appendix C at 4.

[85] EA at 47.

"[i]ndividuals and/or habitat may be impacted … but is not likely to cause a trend in Federal listing or loss of population viability."[86] In regards to big game species, the EA notes, "[d]isturbance potential from road use would be similar to that disclosed in the wolverine, fisher, and pine marten effects."[87] The construction and use of connector routes to create loop opportunities would affect Canada lynx and grizzly bear.[88] Here the BNF fails to recognize the bar for designating motorized vehicle use on roads and trails is not the same as it is when determining compliance with the ESA. The BNF must demonstrate, but failed to show, how new ORV designations and increased use will minimize harassment of wildlife and significant habitat disruption.

In sum, the BNF failed to demonstrate compliance with minimization criteria under the Travel Management Rule Subpart B, and therefore must do so, preferably through the development of an EIS.

V. Failure to comply with the National Forest Management Act.

A. Failure to provide a 60-day review period

As we stated in our previous environmental assessment comments, pursuant to Section 6(g)(3)(F)(iv) of the National Forest Management Act (NFMA), and Forest Service Manual 2400 Supplement No. R1 2400-2001-2, because this project proposes openings created by even-aged silviculture in the Northern Region larger than 40 acres the Forest Service should provide a 60-day public review period and Regional Forester approval. EA Comments at 1. In response the BNF erroneously asserts the following:

> "A 60-day "comment" period is not required. A 60-day review period is required. The Forest identified it had plans to use even-age harvesting, with openings larger than 40-acres, during public scoping in 2017. This more than satisfies the 60-day requirement."
> EA Appendix C at 15.

Looking closely at the Forest Service Manual, it states that a 60-day public notice and the approval by the Regional Forester shall be completed prior to signing the decision document to provide a basis for the NFMA finding related to consistency with Forest Plans.[89] It further states that forest supervisors are to submit to the Regional Forester that, among others, includes a statement of when the 60-day public notice began or when it will begin.[90]

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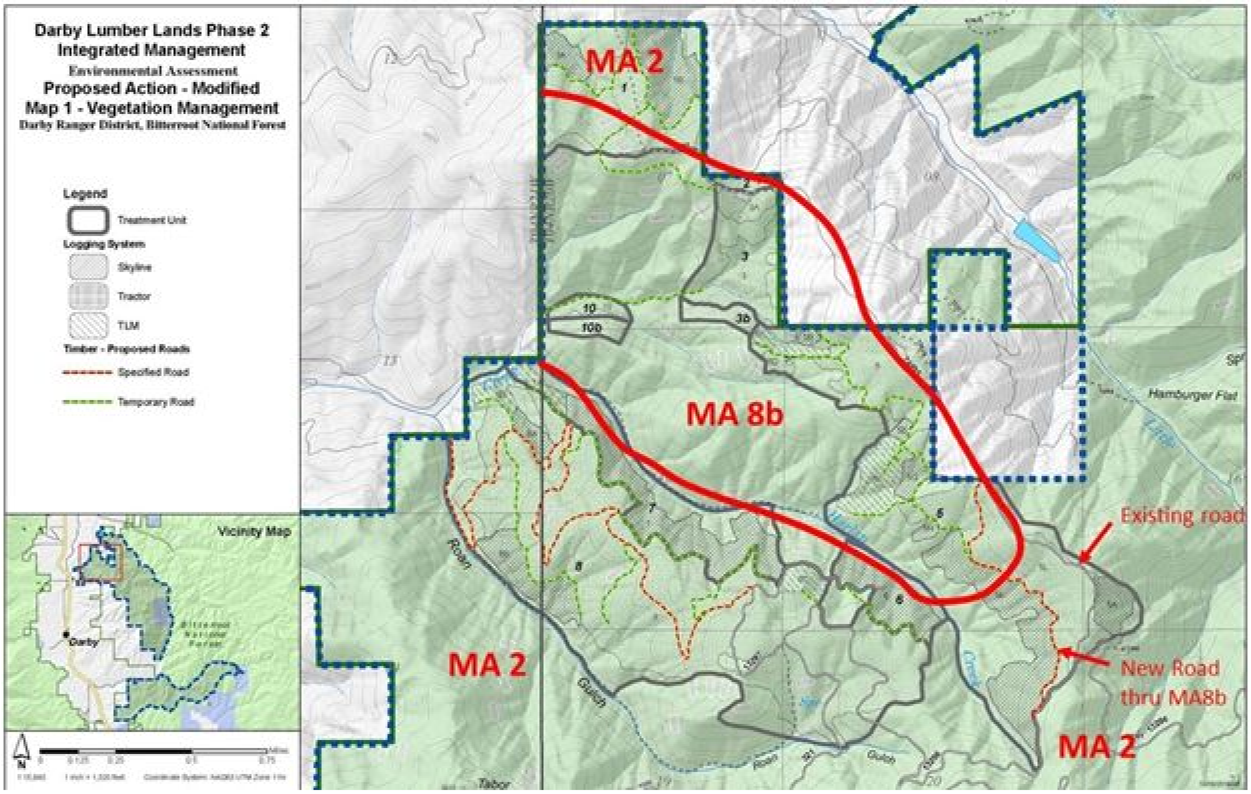
[86] EA at 48.
[87] EA at 50.
[88] EA at 47 (noting, "The construction of ATV connector routes would likely increase the frequency and use of ATV activity in the project area increasing the potential for [grizzly bear] disturbance and mortality;" and "The construction of 225 feet of connector route through delineated lynx habitat is designed to allow, and would facilitate, ATV/UTV recreation and would accumulatively contribute to potential disturbance from these sources on this connector route and adjacent existing routes nearby. ATV/UTV use of this connector and adjoining routes is anticipated to be high between 16 June and 14 October.").
[89] FSM 2400-2001-2 at 3.
[90] FSM 2400-2001-2 at 4.

Public review or notice is understood to be within the context of NEPA implementing regulations that provide the public an opportunity for meaningful participation in agency actions. Those regulations require at least a 30 day notice and comment period for an EA and FONSI. Given the requirements for a 60 day public notice for even-aged openings in excess of 40 acres, the opportunity for public review and COMMENT should have been 60 days for this project. The BNF asserts it has met this requirement simply by the amount of time that lapsed between scoping and the updated EA, seemingly forgeting that "comment" follows review in the regulations. The BNF needs to provide the specific dates it provided for the 60 day review and comment period.

B. Violation of MA 8b Forest Plan Standards

Road building in MA8b is in violation of the Forest Plan. Temporary roads proposed for construction into Units 10, 3, and parts of 5 do not access an adjacent MA and are therefore not allowed under the Forest Plan. Temp roads are in fact roads, just as TLM and Skid trails are according to DLL2–Appendix A—Table A-1. The permanent road in MA 8b also violates the Forest Plan because it is **not required** to access adjacent management areas.



The map above shows the existing permanent road in MA 2 that "does not meet specs" and the new permanent road that is proposed to replace it in MA 8b and MA 2. No justification is given for moving the road out of MA 2 and into MA 8b. The existing road could be brought up to specs with reconstruction or a modified alignment that would keep it in MA 2, and therefore the road through MA 8b is **not required** to access adjacent MAs.

C. Elk Habitat Effectiveness (EHE) amendment is unlawful and unnecessary

The Forest Service proposes site-specific Forest Plan amendments related to elk habitat effectiveness, thermal, and hiding cover as well as Management Area 2 standards of Elk Habitat Objectives. Site-specific amendments are meant to address unique characteristics of a particular forest area, not conditions that are common throughout an entire forest or region. For example, in League of Wilderness Defenders, et. al. v. Connaughton, et al., plaintiffs challenged that the Snow Basin project area did not have distinguishing characteristics, and therefore a site-specific amendment was not justified.[91] The court agreed with the plaintiffs, holding the agency's decision to make site-specific amendments was arbitrary and capricious because the Forest Service failed to explain what conditions within the project area supported selection of a site-specific amendment over a forest-wide amendment.[92] The court explained that a site-specific amendment "must be based on unusual or unique aspects of the site itself when compared to the forest generally."[93] Here, the Forest Service failed to explain the unusual or unique aspects of the project area itself that necessitate the proposed site-specific amendment over a forest-wide amendment. It failed to show how the site-specific amendment is based on unusual or unique aspects of the site itself when compared to the forest generally. The BNF has used EHE site specific amendments on 226,119 acres of BNF's total of 389,820 acres suitable timberland (FP, p. III-2) in the last 12 years. Adding to this already extensive list is egregious and in violation of NFMA.

In the updated appendix C, the BNF claims that EHE standards for thermal and hiding cover are unnecessary because they have not been followed for 7 previous projects (we calculated more in our findings) and "the Forest Plan objective of maintaining the current (1987) level of big-game hunting opportunities has been achieved C-1." The BNF also claims that because 3rd order drainages in the project area are small you are unable to meet the multiple use objective for recreation if standards are followed. To change a standard or consistently ignore a standard warrants due process and a forest wide amendment. The BNF further claims a new method of measure, an elk security analysis (Hillis et al. 1991) has been added to protocol (amended appendix C pg 5). It seems the Forest Service is using it in lieu of standards mandated in the forest plan, once again this warrants due process and is a violation of NFMA.

The BNF also revised the CWD standard so an amendment is no longer needed as originally recommended in the biologist report. "CWD requirements have been revised and will not require a Forest Plan amendment."[94]. Once again to revise a standard warrants a forest wide amendment and due process.

VI. Failure to comply with the Endangered Species Act.

As we noted in our previous comments, Section 7 of the Endangered Species Act (ESA) imposes a substantive obligation on federal agencies to "insure that any action authorized, funded, or carried out by

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[91] See No. 3:12-cv-02271-HZ (D. Or. Dec. 9 2014).

[92] Id. at 54-55.

[93] Id.

[94] FONSI Appendix C at 13.

such agency . . . is not likely to jeopardize the continued existence of any endangered or threatened species or result in the destruction or adverse modification of" habitat that has been designated as critical for the species.[95] We explained the Forest Service must consult with the U.S. Fish and Wildlife Service (FWS) under section 7 of the ESA as to the impacts of the project on species listed under the ESA and designated critical habitat, including bull trout and its designated critical habitat, grizzly bears, and Canada lynx. It must ensure its proposed logging and hauling activities that will require use of forest roads will not harm listed wildlife or degrade its critical habitat. We also explained the ESA is applicable to wolverine.[96] Section 7(a)(4) of the ESA requires a Federal action agency to conference with the Service if a proposed action is likely to jeopardize a proposed species, or destroy or adversely modify proposed critical habitat.[97] The agencies must record any results of a conference.[98]

Though the BNF appears to have consulted with the USFWS regarding its biological assessment for bull trout, similar consultation is absent for grizzly bears, and Canada lynx.[99] It also appears the BNF did not conference with the USFWS regarding wolverine.[100] These failures to consult are a direct violation of the ESA.

VII. Failure to comply with the Clean Water Act

We previously commented that the Forest Service must ensure that the project will comply with the Clean Water Act (CWA), including the prohibition against causing or contributing to a violation of Montana's water quality standards.[101] The Forest Service mistakenly relies on best management practices (BMPs) and project design criteria to minimize effects to water quality and aquatic resources. (See section I.B. of this Objection). This reliance is misplaced and runs contrary to best available science showing that forest roads are a primary source of sediment delivery and other water quality impairments. As just one example, the assertion that log hauling along Rye Creek Road below North Fork Rye junction "is likely to deliver unmeasurably low amounts of sediment to Rye Creek" despite 1.5 miles of that road being located within 100 feet of Rye Creek is arbitrary and capricious, and runs contrary to science.[102] Allowing use of these road alignments—including log hauling and transport of heavy equipment—will exacerbate the impacts of this road on the riparian area and water quality within Rye Creek itself. The Forest Service's analysis fails to support its conclusion that these actions will not cause or contribute to a violation of water quality standards in violation of the CWA. Another example is the 0.4 miles of road proposed for

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[95] See previous EA Comments at 22 citing 16 U.S.C. § 1536(a)(2); Nat'l Wildlife Fed'n v. Nat'l Marine Fisheries Serv., 524 F.3d 917, 924 (9th Cir. 2008).
[96] See our Scoping Comments at 28.
[97] Id. (citing 16 U.S.C. § 1536(a)(4); 50 C.F.R. § 402.10(a). See also 50 C.F.R. § 402.02 (defining "[c]onference" as "a process which involves informal discussions between a Federal agency and the Service under section 7(a)(4) of the [ESA] regarding the impact of an action on proposed species or proposed critical habitat and recommendations to minimize or avoid the adverse effects.").
[98] Id. (citing 50 C.F.R. § 401.10(e) ("The conclusions reached during a conference and any recommendations shall be documented by the Service and provided to the Federal agency").
[99] See Darby Lumber Lands Phase II Project File Index and Project File AQUATICS-002).
[100] Darby Lumber Lands Phase II Project File Index at 10-11.
[101] See Scoping Comment at 28-30, and previous EA Comments at
[102] EA at 29.

construction within the 100-foot Riparian Habitat Conservation Area (RHCA) surrounding Roan Gulch.[103] Again, the Forest Service relies on BMPs to limit any sediment contributions, ignoring the limitations of BMPs to address sediment delivery – especially within the RHCA buffer.

The project will impact two streams impaired for sediment. Contributions to violations of water quality standards for turbidity would also violate the Bitterroot Forest Plan. Failing to provide assurances such as monitoring to ensure maintenance of summer water temperatures to protect existing on and off-forest beneficial uses of water is inconsistent with the Forest Plan.

Given its design, the project will result in adverse impacts to water quality and the proposed monitoring is inadequate. Based on the scope of activities it is authorizing, the Forest Service may not reasonably ensure its action will not cause or contribute to a violation of water quality standards.

VIII. Failure to Prepare an Environmental Impact Statement

Our previous comments on both the scoping notice and environmental assessment urged the Forest Service to prepare an environmental impact statement (EIS) because the Darby Lumbers Land – Phase II Project may have a significant impact on the environment.[104] Further, our previous EA comments provided specific examples demonstrating this project will have significant impacts warranting the development of an environmental impact statement. Rather than acknowledge the project's significance, the Forest Service erred in its issuance of a Draft ROD and FONSI. Again, we reiterate and expand on our previous comments demonstrating this project may have a significant impact because, inter alia, it:

A. Will cause significant impacts, both beneficial and adverse.

The project will have significant environmental consequences both beneficial and adverse from commercial timber sale and road management activities.[105] The BNF acknowledges the project's significant benefits in the FONSI and several sections in the EA, including the following:[106]

- "With 40 (known) culvert crossings being removed, about 2,000 to 4,000 feet of stream bank riparian area would be restored to functioning condition."[107]
- "In the long-term, after the log haul and final maintenance is completed, sediment delivery to North Rye Creek from FR 321 is estimated to be 35-41% less than the present level (Project File

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[103] EA at 30.

[104] See our Scoping Comments at 1-2, Environmental Assessment Comments at 1-2. See W. Watersheds Project v. Abbey, 719 F.3d 1035, 1050 (9th Cir. 2010) (holding that if an EA shows that the proposed action may significantly affect the environment, then the agency must prepare a full EIS). An EA must describe the impacts in terms of context and intensity as described in the definition of "significantly." 40 C.F.R. § 220.7(b)(3).

[105] The Forest Service must prepare an EIS for any major federal action that may have significant environmental consequences, both beneficial and adverse. See 40 CFR § 1508.27(b)(1)

[106] FONSI at 14. (Beneficial effects of the proposed action include improved watershed health from road management activities due to the long-term reduction of sedimentation, improved resilience of vegetation to disturbances and overall improved ecosystem health.").

[107] EA at 28.

AQUATICS-015)."[108] However, the EA acknowledges, "[t]he sediment reductions gained by the Proposed Action Alternative would help meet TMDL water quality goals, and would improve water quality, stream habitat, and the quality of wetlands at the local site level. The ***magnitude of the benefits, however, would be difficult to quantify***, especially as the downstream distance from the project activities increases."[109]

  - The difficulty specifying this benefit in the long term supports the need for an EIS.
- The proposed action would decommission approximately 39 miles of road though a variety of treatments that "...may include soil decompaction, culvert removal, full and partial re-contouring and revegetation treatments. Unless natural recovery has made the roads inaccessible to motorized vehicles, the entrances of the roads would be physically blocked with a gate, earthen berm, rock barrier, or the first 50 to 100 feet would be recontoured." [110]
  - The corresponding Road and Access Management Appendix states decommissioning may not require any treatment.[111] The EA does not list which roads need specific decommissioning treatments, or if those roads receiving to treatment will pose no future environmental risk. An EIS is necessary to better specify and quantify the significant benefits from road decommissioning that the BNF claims this project will achieve. EA at 27.[112]

While there will be significant, though not clearly specified, benefits from the removal of approximately 39 miles of road, the proposed action will also result in significant environmental consequences as demonstrated by the following:

- The purported need to log 947 acres within Forest Plan Management Area 2 and 347 acres in Management Area 8b requiring a Forest Plan Amendment, and a 60 day public review with Regional Forester approval due to proposed regeneration harvests in excess of 40 acres.[113]
- Forest Plan direction for MA 8b precludes building roads except for specific purposes not applicable to this project, yet the BNF proposes to build both temporary and system roads in this area.[114]
- The EA analysis for potential aquatics impacts uses only sediment as an indicator and,. "… does not address effects to other water quality or stream habitat features, such as water chemistry, stream temperatures, stream flows, wood recruitment, habitat structure, passage barriers, etc. Project activities are expected to have no effect on those features because of the protection provided by RHCA buffers around all streams and wetlands."[115]

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[108] Id.

[109] Emphasis added, Id. at 30.

[110] Id. at 8-9.

[111] EA Appendix B at 1.

[112] "Road storage and decommissioning have similar conservation goals, treatments and effects. The road decommissioning and storage treatments in the Proposed Action would improve water infiltration and drainage, and reduce sediment delivery to streams, thus reducing the overall effect of the road system on hydrologic processes."

[113] EA at 8-10, 23-24. The Forest Service proposes site-specific Forest Plan amendments to allow logging activities that would otherwise be prohibited under the Bitterroot's Forest Plan components that are meant to protect elk habitat effectiveness, thermal, and hiding cover. EA at 10.

[114] Id. at 11.

[115] Id. at 25.

- The EA failed to demonstrate how focusing solely on sedimentation and not addressing other environmental factors will effectively mitigate potential environmental consequences. Rather, the EA simply references project files as proof without demonstrating how riparian buffers and other design criteria will result in “no effect” on water quality and stream habitat features.[116] We expand on this flaw further in section I.B. of this Objection. The BNF’s over-reliance on design criteria without adequate evidence or analysis necessitates an EIS.

In sum, the Forest Service relies on unsupported assumptions and fails to consider very real, harmful impacts from its decision. The EA ignores best available science showing that the forest system roads in the project area, and large equipment on those roads including log hauling, will have significant impacts on the landscape, wildlife and wildlife habitat, and water quality. In addition, impacts from all of the proposed activities will be significant to wildlife such as elk, westslope cutthroat trout, bull trout, and wildlife habitat (including designated critical habitat). Specifically, the proposed Forest Plan amendments will remove essential protections for elk. Further, “the fact that the Forest Service disclosed such effects does not necessarily render them insignificant.”[117]

B. Degree to which the proposed action affects public health or safety.

The project would cause unmitigated harm to human health by causing fugitive dust from haul roads that are not proposed for treatment. In EA comments pg 2 and scoping, we ask for analysis of the impacts of dust on residents. Design criteria mandates dust abatement for homes near log hauling activities in the project area. But as we pointed out, residents living along N Rye and Rye Creek would not be in the project area, so would not benefit from design criteria dust abatement. What are the cumulative health effects of dust created by 1200 truck rounds trips for the residents not protected by design criteria? No analysis was provided in the EA or updated EA.

C. An EIS is appropriate when the project involves effects on the human environment that are likely to be highly controversial.

The Forest Service limits the meaning of “highly controversial” listed in NEPA’s implementing rules to only include, “...cases where substantial scientific dispute exists as to the size, nature, or effects of a major Federal action on some human environmental factor, rather than to public opposition of a proposed action or alternative.”[118] Yet the Council on Environmental Quality, in its responses to frequently asked questions regarding NEPA, suggests otherwise when it answered under what criteria should a FONSI be made available for public review. Here, the CEQ responded, in part, “when there is either scientific or public controversy over the proposal;...”[119] It is unclear under what authority or interpretation of NEPA’s implementing rules the Forest Service determined controversy should only rest on disputes over science, but the CEQ suggests the Forest Service cannot dismiss public controversy, and without question the

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[116] Id.

[117] See Cascadia Wildlands v. U.S. Forest Service, No. 6:12-cv-00804 (D. Or. 2013).

[118] FONSI at 14.

[119] See Forty Most Asked Questions Concerning CEQ's National Environmental Policy Act Regulations at 37b.

Darby Lumber Lands Phase II project is highly controversial from a public perspective. It continues the BNF's continued use, rather abuse, of amending its forest plan's Elk Habitat Effectiveness standards so it can inappropriately log in areas that would otherwise be unsuitable , and it proposes building new roads in Management Area 8b in violation of the forest plan standards.

The project's proposed action is also highly controversial due to conflicts among facts and statements made within the EA and supporting project files. Specifically, in support for proposing even-aged silvicultural treatments in excess of 40 acres (i.e. regeneration harvests), the BNF cites dwarf mistletoe infestations.[120] Yet, when conducting travel analysis, agency officials noted that, "[d]ue in part to large fires in 2000, clearcutting practices on the Darby Lumber Co. lands and overall high levels of past harvest, there are currently no planned projects for controlling these elements [insects, disease, parasites] in the analysis area.[121] While the BNF found one specific area (Unit 7) to have a 90% dwarf-mistletoe infestation, the EA fails to demonstrate how its presence in this one discrete area justifies the need for a regeneration harvest when the travel analysis suggests there is no need for such a treatment in the context of the larger planning area. Another factual controversy is in regard to the miles of undetermined roads the proposed action would decommission.[122] Further, we explained in our previous comments that the project is premised on the agency's assumption that logging and silvicultural treatments will reduce insects, disease, and high intensity wildfires.[123] Yet, along with other commenters, we provided contradictory science that the Forest Service continues to ignores in its analysis.[124]

Finally, the documents included in section 3 of our EA comments under Detrimental Soil Damage contain contrasting disclosures regarding soil impacts. This suggests a 'controversy' regarding soil monitoring findings within the BNF, thereby necessitating an EIS. We asked for analysis of climate change and loss of carbon sequestration through large clearcuts and thinning in areas with desired basal area. Regeneration harvest is under question based on a new study at University of Montana. According to Davis et al 2018 (peer reviewed and published 2019), "We show that regeneration had a nonlinear response to annual climate conditions, with distinct thresholds for recruitment based on vapor pressure deficit, soil moisture, and maximum surface temperature. At dry sites across our study region, seasonal to annual climate conditions over the past 20 years have crossed these thresholds, such that conditions have become increasingly unsuitable for regeneration. (Davis et al 2019)" The study focussed on post fire regeneration. Thinning and clear cutting is meant to match fire conditions but also exacerbates these conditions by introducing roads, skid trails and soil compaction as well as reducing CWD which does not occur with fire. Again analysis is inadequate. A recent report from the UN's Intergovernmental Panel on Climate Change underscores that we have eleven short years to make "rapid transformation across all industrial

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[120] EA at 24.

[121] BNF Darby Lumber Lands – Travel Analysis for Phase I and II Project Areas at 18.

[122] See subsection F in our comments below regarding how the proposed action will establish future precedent and a decision in principle that defines the parameters of a further action.

[123] EA at 3 and 22. (concluding that "[w]ithout fire and silvicultural treatments designed to lower stand densities and help retain fire adapted shade intolerant species, such as ponderosa pine, stands will continue to see increases in insects and disease and will likely see wildfire at higher intensities.")

[124] See our previous EA Comments at 6, and our Scoping Comments Attachment D.

sectors."[125] The BNF needs to analyze current science on climate change, carbon sequestration and regeneration before considering regeneration harvests and thinning of large trees.

We contend the project meets the threshold of being highly controversial due to conflicting science, contradicting facts in the EA and project files, and due to public opposition.

D. Involves a geographic area with unique characteristics.

Our previous comments explained at length the area's ecological importance to fish and wildlife and proximity to important wetlands. Yet, the FONSI erroneously relies on, "riparian habitat conservation area standards," to dismiss adverse environmental consequences to these important wetlands, and it is silent on the area's ecological importance to elk and bull trout.[126] Further, the BNF mistakenly suggests NEPA's implementing rules measuring intensity requires, "measurable negative effects," where the rules articulate it is the unique characteristics of the geographic area that informs the determination if a project will significantly affect the environment.[127] Here the BNF ignores the fact that the project area is a "port in the storm" refuge for elk in the midst of habitat significantly damaged by excessive road building, wildfire and extensive commercial logging.

We have very little MA8b on the Forest. It has unique characteristics and is ecologically important for big-game. Of the 1,587,070 acres of the BNF, only 9499 acres are MA8b (.6 percent) and many of those are low elevation open grasslands. MA8b in the project area has unique characteristics that provide for critical elk winter range and is supposed to be managed for wildlife with very specific prohibitions on timber harvest and road building. Project area MA8b is unique as it is treed, roadless and provides refuge EHE for elk.

E. Involves effects that are highly uncertain or involve unique or unknown risks.

We explained in our previous EA comments that this project involves effects that are highly uncertain and involve unknown risks. The Forest Service continues to ignore highly controversial aspects of its proposal, including science questioning the benefits of logging to address insects, disease, and high intensity wildfires. It is uncertain whether the impacts of logging will in fact result in increased forest resiliency to wildfire or insect and disease outbreaks. Best available science contradicts, or at the very least, questions the Forest Service's assumptions. For example, a recent study found that during mountain pine beetle outbreaks, beetle choice may result in strong selection for trees with greater resistance to\ attack, and therefore retaining survivors after outbreaks (as opposed to logging them) to act as primary seed sources could act to promote adaptation.[128] Rather than properly address our referenced study, the BNF directs the public to review project file document PF-LIT-003 without providing any discussion, evidence or analysis within the actual EA.[129] The agency improperly ignores these highly uncertain and

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[125] See https://www.ipcc.ch/sr15/

[126] FONSI at 14.

[127] FONSI at 14, and see 40 C.F.R. 1508.27(b)(3).

[128] See previous EA Comments at 4.

[129] EA Appendix C at 7. See also Exhibit C of our Objection.

unknown risks based on contradicting science that should be addressed through additional research and data collection in an EIS. Moreover, the EA failed to address how climate change may affect silvicultural models and resulting assumptions that fail to recognize large openings would accentuate the problems of heat, drying, and wind. Additional impacts that are highly uncertain or involve unknown risks include logging, road building, and log hauling on roads adjacent to waters impaired for sediment; impacts to westslope cutthroat trout, bull trout, designated bull trout critical habitat, and elk.

F. The potential for establishing a precedent or representing a decision in principle that defines the parameters of a further action.

The BNF arbitrarily asserts the FONSI will not establish a precedent or represent a decision in principle that defines the parameters of further action. Through review of the project files and additional information obtained from the BNF, we learned the project area contains 25.4 miles of undetermined (UND) roads.[130] Our review also revealed an error within the EA Appendix B that showed the proposed action would decommission just one 0.4 mile segment of UND roads when the BNF's spreadsheet showed 15.02 miles.[131] The EA is unclear regarding the current status of UND roads in the project area or future management under the proposed action. The EA Appendix B suggests the BNF would not address the remaining 25 miles, but the spreadsheet shows the proposed action would add 10.38 miles to the national forest road system. If true, this scenario establishes a precedent of adding roads without proper analysis under NEPA and represents a decision defining parameters of further action for those roads since the BNF must establish road management objectives for each road that would inform future capital maintenance expenditures. As we explained in section I.D. of this Objection. The BNF cannot simply add undetermined roads to the national forest system without proper supporting analysis.

Further, allowing road building in MA8b that is not required to access adjacent MAs is prohibited under the Forest Plan. This is setting a precedent that may have significant future effects.

G. Is related to other actions with individually insignificant but cumulatively significant impacts.

Two roads, one specified and one temporary parallel each other above a stream. In the EA no analysis was performed on impacts of two roads in concert, only for each road individually. The two roads in combination would create cumulatively significant impacts to the stream below.

On page 8 of EA comments, we ask the BNF for an analysis of the cumulative impacts of activities authorized under the Medicine Tree allotment when combined with this project, and explain how it plans to mitigate those effects. This was not addressed in the EA. What are the cumulative impacts on elk forage caused by grazing competition increased by forest thinning that is justified to "improve elk forage."

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[130] EA AQUATICS-017 Project File at 1, project file TRANS-001, "DLL II Undetermined Roads Proposed Action" spreadsheet obtained via email message from BNF Environmental Coordinator on April 2, 2019.

[131] Comparing EA Appendix B at B-6, (listing Route #62690, 0.40 miles to be decommissioned) with the "DLL II Undetermined Roads Proposed Action" spreadsheet.

We also asked in EA comments pg 4 to consider the cumulative impacts of site specific amendments for elk habitat as referenced in our scoping 23-25. In 13 projects since 2001, BNF has used site specific amendments for EHE in 11, thermal cover in 8, CWD in 9, and snag retention in 3. See the chart in section 10 of our EA comments. The need for so many Forest Plan amendments over such a widespread area argues for need of an EIS level analysis of cumulative impacts. The BNF cannot continue amending EHE piecemeal without looking at cumulative impact across the forest.

We asked the BNF to analyze increases in adverse effects of Climate Change by depleting valuable carbon stores. The EA fails to address this issue as requested in scoping pg 11-13 or EA comments pg 5. The BNF failed to answer how does this project in concert with previous projects and the 2000 fire in the project area impact the forests ability for carbon sequestration, a vital resource?

H. May adversely affect species listed or critical habitat designated under the Endangered Species Act (ESA)

The EA notes the project area contains suitable habitat for threatened Canada lynx and grizzly bear, and a proposed species - wolverine, which may be present in the project area.[132] The EA contains conflicting information as to whether or not wolverine are present in the project area with Table 9 showing they are and Table 10 showing otherwise.[133] Table 9 also lists grizzly bears as not present in the project area, yet states, "USFWS (2017) delineates analysis area as grizzly bears may be present."[134] The EA also acknowledges the presence of threatened bull trout and corresponding critical habitat.[135] We previously commented on the need to prepare an EIS due to the fact that this project may adversely affect these protected species.[136] The BNF asserts otherwise, "...that implementation of the proposed Federal action May Affect – is not likely to adversely affect grizzly bears, Canady lynx, bull trout and bull trout critical habitat."[137] The conclusion rests erroneously on the project design criteria, the effectiveness of which the EA fails to demonstrate in its analysis. This is especially problematic for grizzly bears where the EA explains, "[i]ndividuals and/or habitat may be impacted (although the likelihood a grizzly bear is present is extremely remote) but is not likely to cause a trend in Federal listing or loss of viability."[138] As we stated in our previous EA comments, "[a] project need not jeopardize the continued existence of a threatened or endangered species to have a 'significant' effect on the environment."[139] Finally, as we explained in our objection under section I.E and I.F. the EA fails to properly analyze potential adverse impacts to water quality and thus bull trout and it critical designated habitat, Canada lynx and grizzly bear. This brings into question the validity of the BNF's assertion the proposed action will not adversely affect threatened species.

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[132] EA at 36 and 39.
[133] Id.
[134] Id. at 36.
[135] EA at 30.
[136] See previous EA Comments at 4-5.
[137] FONSI at 16.
[138] EA at 47.
[139] See Klamath-Siskiyou Wildlands Center v. U.S. Forest Service, 373 F. Supp. 2d 1069, 1080 (E.D. Ca. 2004).

Conclusion

The BNF failed to properly analyze the Darby Lumber Lands Phase II proposed action in violation of NEPA, and its determination the project will not result in significant environmental consequences is arbitrary and capricious, especially in light of the BNF's over reliance on design criteria and general lack of adequate analysis in the EA. The BNF failed to consider alternatives to the proposed action that does not include logging or road building. The BNF failed to identify the minimum road system, and it continues to violate forest plan requirements through the improper use of Elk Habitat Effectiveness amendments, as well as by proposing road construction in Management Area 8b. The BNF failed to properly consult and conference with the U.S. Fish and Wildlife Service in violation of the Endangered Species Act. Finally, the BNF's failed to demonstrate compliance with the Clean Water Act.

Suggested Resolution: To resolve these failures the BNF must prepare an environmental impact statement that provides the necessary analysis, properly considers a range of alternatives and complies with forest plan direction. We are prepared to discuss other avenues of resolution that results in the proposed action adhering to forest plan requirements, increases road decommissioning, limits road construction, and incorporates alternative vegetation treatments.

Submitted this 12th day of April, 2019.

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Exhibit A - DLL Undetermined Roads Proposed Action
Exhibit B - Montana Fish and Wildlife Press Release dated Oct. 29, 2018
Exhibit C - Response to EA Project File LIT-003
Exhibit D - Cited materials

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Friends of the Bitterroot| WildEarth Guardians DLL Phase II Objection Exhibit A

RTE_NO	RD_Name	Miles	System	Pro_Sys	Proposed Action	Notes
13229	(FDR) NORTH FORK RYE CREEK	2.12	UND	NFSR	Closed yearlong	Add to system, Closed by Travel Plan but database not changed
13380	(FDR) HARLAN CR-LIT SL CHILD	0.10	UND	NFSR	Store	Add to system and store for future use
13381	(FDR) HARLAN CR-LIT SL CHILD	0.07	UND	NFSR	Store	Add to system and store for future use
62400	(FDR) BURKE GULCH	1.03	UND	NFSR	Add to system	Add to system - open seasonally from 6/16 to 10/14 - provides loop opportunity
62401	(FDR) BURKE GULCH	0.87	UND	NOT	Decommission	
62402	(FDR) BURKE GULCH	1.03	UND	NFSR	Store	Add to system and store for future use
62404	(FDR) BURKE GULCH	0.64	UND	NOT	Decommission	
62405	(FDR) BURKE GULCH	0.37	UND	NOT	Decommission	
62407	(FDR) BURKE GULCH	0.38	UND	NOT	Decommission	
62431	(FDR) BURKE GULCH	0.93	UND	NOT	Decommission	
62432	(FDR) BURKE GULCH	1.49	UND	NFSR	Add to system	Closed yearlong
62433	(FDR) BURKE GULCH	2.45	UND	NFSR	Add to system	Closed yearlong
62434	(FDR) BURKE GULCH	1.04	UND	NOT	Decommission	
62436	(FDR) BURKE GULCH	0.40	UND	NOT	Decommission	
62437	(FDR) BURKE GULCH	0.20	UND	NOT	Decommission	
62520	HEAD OF MIKE CREEK	0.69	UND	NOT	Decommission	On CB Ranch - PVT, remove from system
62544	NORTH FORK RYE CREEK	1.99	UND	NOT	Decommission	
62544	NORTH FORK RYE CREEK	0.58	UND	NOT	Decommission	
62545	NORTH FORK RYE CREEK	0.23	UND	NOT	Decommission	
62575	NORTH FORK RYE CREEK	0.96	UND	NOT	Decommission	
62695	RYE CREEK	0.22	UND	NOT	Decommission	
62781	RYE CREEK	1.67	UND	NFSR	Store	Add to system and store for future use
62999	N.FORK RYE CREEK	0.18	UND	NOT	Decommission	Changed to match connecting road.
73858	NORTH FORK RYE	0.43	UND	NOT	Decommission	
73865	NORTH FORK RYE	0.26	UND	NOT	Decommission	
73866	NORTH FORK RYE	0.96	UND	NOT	Decommission	
73867	COLD SPRING HILL	0.45	UND	NOT	Decommission	
73868	COLD SPRING HILL	0.12	UND	NFSR	Add to system	Add to system - open seasonally from 6/16 to 10/14 - provides loop opportunity
73869	COLD SPRING HILL	0.30	UND	NFSR	Add to system	Closed yearlong - provides access to State Section 36
73870	NORTH FORK RYE	0.31	UND	NOT	Decommission	
		22.48				
	Roan Gulch - Non-System	1.75	UND	NOT	Decommission	Unauthorized ATV Path up Roan Gulch
	Harlan Gulch - Non-System	1.17	UND	NOT	Decommission	Unauthorized ATV Path up Harlan Gulch
		2.92				

Fish & Wildlife - Region 2

Mon Oct 29 13:08:41 MDT 2018

Montana Fish, Wildlife & Parks (FWP) captured a young male grizzly bear on Saturday, October 27 on the Whitetail golf course, north of Stevensville along the Bitterroot River.

Over the past few weeks, FWP received multiple reports of a bear extensively digging and causing damage to the golf course. Because the bear was staying in the area and damaging the property, wardens set a trap in response, expecting to capture a black bear. FWP trapped the bear early Saturday morning and later confirmed it was instead a young 249-pound male grizzly.

Through the years, several grizzly bears have been confirmed in the Sapphire Mountains and in the northwest portion of the Bitterroot Valley, including the Lolo Creek drainage, and as far south as the Big Hole Valley. Grizzly bears in the Bitterroot remain relatively uncommon, compared to other parts of northwest Montana, but there have been increasing reports in recent years.

Northwest Montana’s nearby Northern Continental Divide Ecosystem (NCDE) is the closest grizzly bear recovery zone with an established population of grizzlies. “The NCDE is not far away, and grizzly bears are expanding in several directions from there, slowly recolonizing historic ranges,” said FWP Region 2 Bear Management Specialist, James Jonkel.

The grizzly was relocated Sunday to the lower Blackfoot Valley, on the southern edge of the NCDE, in a spot previously identified as a good relocation area for bears.

This time of year, Jonkel added, it is common for bears to routinely follow drainages down into the rich valley bottoms, where food and water are more plentiful. “Where the bear was captured along the river, foods like rosehip, snowberry and various forbs are attracting bears right now. Therefore, it’s extra important to contain things that are under our control, like garbage and fruit trees, so that bears keep on moving to their natural foods and aren’t tempted to stay in our neighborhoods.”

Friends of the Bitterroot|WildEarth Guardians DLL Phase II Objection - Exhibit C

Project File LIT-003 is Consideration of Science and Literature Submitted by the Public that was not included in the DLL2 EA. Project File LIT-003 reviewed and responded to these papers. However, it appears that the Forest Service missed the point of many of them. Below are the papers, the FS response, followed by Jeff Lonn's comments on the FS responses.

Aquatics/Fisheries

Malison, R.L., and C.V. Baxter. 2010. The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. Canadian Journal of Fisheries and Aquatic Sciences 67: 570-579. *In ponderosa pine and Douglas-fir forests of Idaho at 5-10 years post-fire, levels of aquatic insects emerging from streams were two and a half times greater in high-intensity fire areas than in unburned mature/old forest, and bats were nearly 5 times more abundant in riparian areas with high-intensity fire than in unburned mature/old forest.*

Sestrich, C.M., T.E. McMahon, and M.K. Young. 2011. Influence of fire on native and nonnative salmonid populations and habitat in a western Montana basin. Transactions of the American Fisheries Society 140: 136-146. *Native Bull and Cutthroat trout tended to increase with higher fire intensity, particularly where debris flows occurred. Nonnative brook trout did not increase.*

Response: Both papers are similar as they address research that shows that high severity fire does have some positive effects on native trout species (bull trout and westslope cutthroat trout) and their aquatic insect food base.

The issue of high severity fire having positive effects on fish and aquatic insects, although valid, is generally not relevant to the Darby Lumber Lands Phase II Project. This is because the areas proposed for timber harvest in the Phase II project are located in non-fish bearing watersheds (Harlan Creek, Roan Gulch, McKinney Gulch). So, even if those areas are not harvested and do happen to burn at high severity, the fire and its after effects would convey no positive benefits to the nearest fish populations in the Bitterroot River, which are well downstream from the project area and mostly hydrologically disconnected from the project area.

The portions of the project area where only watershed improvement activities would occur (Rye Creek, North Rye Creek, Little Sleeping Child Creek, and Robbins Gulch watersheds) had large portions of their watersheds burned by high/moderate severity fire in 2000. As a result, the aquatic benefits mentioned in Malison and Baxter (2010) and Sestrich et al. (2011) already occurred in those watersheds back in 2001-2010. Because of the vast extent of the high/moderate severity fire that occurred across the Rye, North Rye, Little Sleeping Child, and Robbins watersheds in 2000, there is low risk of that type of fire revisiting the project area at the current time.

Lonn comments: These papers emphasize the point that your goal of reducing mixed and high severity fires is not an ecologically sound one.

Carbon Storage and Climate Change

Campbell, J.L., Harmon, M.E., Mitchell, S.R., 2011, Can fuel reduction treatments really increase forest carbon storage in the western US by reducing future fire emissions? Frontiers in Ecology and Environment, doi:10.1890/110057. *No evidence that thinning will decrease CO2 emissions in the long or short term; in fact it may be the opposite.*

Law, B.E., and Waring, R.H., 2015, Carbon implications of current and future effects of drought, fire, and management on Pacific Northwest forests: Forest Ecology and Management, v. 355, p. 4-14.

Law, B.E., Hudibug, T.W., Berner, L.T., Kent, J.J., Buotte, P.C., and Harmon, M.E., 2017, Land use strategies to mitigate climate change in carbon-dense temperate forests: PNAS, www.pnas.org/cgi/doi/10.1073/pnas.1720064115. *Logging is Oregon's biggestCO2 polluter, much more so than wildfire.*

Segerstrom, C., 2018, Timber is Oregon's biggest carbon polluter: High Country News, May 16, 2018.

Response: These papers all address the issue of climate change, either through carbon storage or CO2 emissions from logging. Campbell et al. examines the issue that wildfires may leave more carbon stored than mechanical fuel treatments. The paper concludes that fuel treatments do not have an additional benefit of increasing carbon storage. The Law et al papers conclude that longer rotations between harvests or selection harvests in Pacific NW forests would maximize carbon sequestration. Segerstrom discusses the research in the Law papers and that logging practices in Oregon are the largest contributor to CO2 emissions in the state, more so than wildfires. This paper is specific to logging practices in Oregon, where rotation between harvests is shorter and timber from private lands accounts for 63% of timber produced.

The DLL II project is not a primary contributor of global greenhouse gas emissions nor is it similar to the primary human activities exerting negative pressure on the carbon sink that currently exists in U.S. forests, namely land use conversion. The affected forests will remain forests, not converted to other land uses, and long-term forest services and benefits will be maintained. In lieu of the ability to dramatically alter climatic trends (at least in the short term), and with the inherent uncertainty regarding what specific long-term climatic changes may be, treatments proposed in this project may be one of the best options to maintain intact, healthy, functioning forests that can provide for a variety of future resource and social needs.

Lonn comments: These papers agree that logging is an overall carbon emitter, so even if it is not as significant as fossil fuel burning, for example, it is still deleterious. The best way to limit climate change is to limit ***all*** *carbon dioxide emissions. This needs to be discussed in your EIS.*

Fire and Fuels

Baker WL (2017) Restoring and managing low-severity fire in dry-forest landscapes of the western USA. PLoS ONE 12(2): e0172288. https://doi.org/10.1371/journal.pone.0172288. *Frequent low severity fire rates have been overestimated in dry forests, meaning that understory shrubs and small trees could* *fully recover between low severity fires. Therefore less restoration treatment (thinning) is needed before reintroduction of fire.*

Baker, W.L., T.T. Veblen, and Sherriff, R.L. 2007. Fire, fuels and restoration of ponderosa pine Douglas-fir forests in the Rocky Mountains, USA. Journal of Biogeography, 34: 251-269. *"Exclusion of fire has not clearly and uniformly increased fuels or shifted the fire type from low- to high-severity fires. However, logging and livestock grazing have increased tree densities and risk of high-severity fires in some areas. Restoration is likely to be most effective which seeks to (1) restore variability of fire, (2) reverse changes brought about by livestock grazing and logging, 3) ensure that degradation is not repeated."*

Response: These two papers examine fire return intervals in in dry ponderosa pine and Douglas-fir ecosystems and the effects of fire exclusion to these systems. The 2017 paper concludes that the fire return interval is likely greater than 25 years (the current commonly used time period) depending on the location of the ecosystem. The 2007 paper discusses that grazing and past forest management activities have shaped fuels greater than fire exclusion. Both papers acknowledge there is still a need for restoration in these ecosystems, and depending on the current condition of the areas prescribed for treatment, options could include a more passive, prescribed fire only option or active options, such as thinning and re-introduction of fire.

Lonn comments: The restoration that they advocate is to "restore the variability of fire, reverse changes brought about by livestock grazing and logging, and ensure that degradation is not repeated." DLL2 is designed to do none of these. A better approach would be to apply prescribed burns without commercial logging ahead of time.

Bradley, C. M., C. T. Hanson, and D. A. DellaSala, 2016, Does increased forest protection correspond to higher fire severity in frequent-fire forests of the western United States? Ecosphere 7(10):e01492. 10.1002/ecs2.1492. *Reviewed 1500 fires larger than 1000 acres in the western US and found that decreasing fire intensity corresponded to increased forest protection (prohibitions on logging). It questions your (and HFRA's—written by politicians, not scientists) whole premise.*

Response: This paper assesses whether active management of forests results in lower fire severity. It concludes that areas that are protected from logging burn the least severe. The authors maintain allowing more wildfires to burn under safe conditions can be an effective restoration tool. The researchers also acknowledge they could not rule out that low-intensity management could decrease the occurrence high-severity fires.

Lonn comments: By "low intensity management" the authors did not advocate commercial logging, but instead they argue for prescribed burning alone and brush management immediately surrounding structures.

Dellasala, D.A., Ingalsbee, T., and Hanson C.T, Everything you wanted to know about wildland fires in forests but were afraid to ask: Lessons learned, ways forward: https://forestlegacies.org/images/projects/wildfire-report-2018.pdf *Comprehensive summary of* *historical wildfire compared to modern conditions, ecological benefits of wildfire, best practices for home protection.*

Response: This paper addresses a number of issues and its key findings conclude that large wildfires lead to higher levels of biodiversity, today's wildfires are driven by climate change, human-caused ignitions, and forest type conversion, post-fire logging is damaging to forests and aquatic ecosystems, thinning small trees and prescribed burning can lower fire intensity (but is nuanced), and a number of new strategies are needed to address the WUI. DLL II was designed with several objectives, none of which include post-fire logging or forest type conversion. Treatments were planned to help with resilience to forest health related issues and climate change considerations.

Lonn comments: The paper gives evidence of the ecological benefits of mixed-severity fires, shows that those fires are not outside of historic norms, and suggests that the best way to protect homes is to address the home itself and lands within 100 feet of the structure. Logging the wildlands has net negative effects.

Nacify, C., Sala, A., Keeling, E.G., Graham, J., Deluca, T.H., 2010, Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies Ecological Applications, 20(7), 2010, pp. 1851–1864. *"Fire-excluded ponderosa pine forests of the northern Rocky Mountains logged prior to 1960 have much higher average stand density, greater homogeneity of stand structure, more standing dead trees and increased abundance of fire-intolerant trees than paired fire-excluded, unlogged counterparts. In other words, logging increases fuel loads and produces the densest, least diverse forest over the long term.*

Response: This paper discusses the effects of logging and fire exclusion in the northern Rocky Mountains. The conclusion of this paper shows that forests that were logged and had fire suppression are denser, less diverse, and less fire tolerant than similar unlogged and fire suppressed stands. The authors emphasize that forest health treatments should focus on stands that were previously logged and roaded and are located near communities. Stands that are previously unlogged and fire-excluded may not require as of intense management prescriptions.

Lonn comments: The DLL2 timber harvest is proposed for areas that have been undisturbed for a long time, and are mature forests. In addition, the area is mostly unroaded, but will require extensive new road building for timber harvest. This paper suggests that the timber harvest in DLL2 will have deleterious effects in the long run—higher stand density, more homogeneity, more roads, and higher fuel loads.

Odion D.C., Hanson C.T., Arsenault A., Baker W.L., DellaSala D.A., Hutto R.L., Klenner W., Moritz M.A., Sherriff R.L., Veblen T.T., Williams M.A. 2014. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. PLoS ONE 9: e87852. *"Our findings suggest that ecological management goals that incorporate successional diversity created by fire may support characteristic biodiversity, whereas current attempts to ''restore'' forests to open, low-severity fire conditions may not align with historical reference conditions in most ponderosa pine and mixed-conifer forests of western North America."*

Response: This paper recommends a variety of management practices to restore resilience to stands and landscapes including providing for open stands, age class diversity, and retention of fire-tolerant trees through a variety of mechanical and prescribed burning treatments. Project-wide conditions in the DLL II project area allow for a range of successional diversity. Treatments are not designed to convert every square inch of the project area to an open forest. The proposed vegetation management activities will treat approximately 5 percent of the area, helping create a landscape with a diversity of stand conditions in various successional stages.

Lonn comments: The 5% of the area being treated is misleading because the majority of the "project area" has been previously burned or clearcut or both. You are actually treating (logging) the majority of the undisturbed forest left in the area. This paper concludes that Ponderosa and mixed conifer forest in western North America, including the northern Rockies, were not historically dominated by low/moderate severity fire, but instead by mixed-severity fires that included much high severity fire even in Ponderosa forests. So, it challenges your perception that the low-elevation northern Rockies forests were dominated by frequent low severity fires. This paper recommends "incorporating historical mixed-severity fire into management goals. However, focusing fire risk reduction activities adjacent to homes is needed to protect communities [123], and this may expand opportunities for managed wildland fire–away from towns–for ecological benefits of fire-dependent biota. However, a major challenge lies with the transfer of information needed to move the public and decision-makers from the current perspective–that the effects of contemporary mixed-severity fire events are unnatural, harmful, inappropriate and more extensive due to fire exclusion–to embrace a different paradigm."

*Your previous treatments (Hayes Creek, Como, and Westside) resulted in open, evenly spaced P-Pine stands, in effect a pine plantation with **less** diversity. It is doubtful that DLL 2 will be any different.*

Rhodes, J.J.; Baker, W.L. 2008. Fire probability, fuel treatment effectiveness and ecological tradeoffs in western U.S. public forests. The Open Forest Science Journal 1: 1-7. *Fuel treatments have a 2.0-7.9% chance of being encountered by wildfire over their 20 year lifespan. This benefit does not counterbalance the adverse effects of fuel treatments.*

Response: This paper examines the probability that a treated area will encounter a wildfire within 20 years of treatment. The results are for the entire Western US and the authors caution that they should not be applied at a smaller analysis area scale. The results can be used to help with assessments of risk to watersheds and help with evaluating trade-offs. Fuel treatments allow fire managers a wider range of management efforts than would be viable if fuels treatments had not occurred, providing more options to address fire on a broader scale.

*Lonn comments: The paper did not state that results **should not** be applied at a smaller scale, but rather that it is "not applicable to **all** smaller analysis areas". The study did examine Ponderosa forests separately, finding "that in 92.1-98.0% of treated areas, fuel treatment impacts on watershed processes are not likely to be counterbalanced by a reduction in higher-severity fire".*

Rogers, G., Hann, W., Martin, C., Nicolet, T., Pence, M., 2008. Fuel treatment effects on fire behavior, suppression effectiveness, and structure ignition. Grass Valley Fire, San Bernardino Forest. USDA Forest Service, Pacific Southwest Region, R5-TP-026b. *Mixed brushland and pine forests. While fuel* *treatments concentrated in the CPZ slowed the fire, many homes burned anyway, ignited by firebrands. Homes burned, while surrounding vegetation did not, suggesting that the homes themselves provided the main fuel source, and not the vegetation.*

Response: This citation is specific to the southwestern U.S. where vegetation conditions (chaparral) are much different than the northern Rockies and those landscapes burn under much different conditions. The DLL II project does have fuels management objectives and all units are located within the WUI, however, treatments were not developed specifically to prevent structures from burning in the event of a wildfire.

Lonn comments: The neighborhoods burned in this fire were dominated by Jeffery Pine, similar to Ponderosa, not chaparral. The hot, dry, windy weather was similar to the conditions under which the northern Rockies "catastrophic" fires occur (like the Roaring Lion Fire). My point is that logging in the wildlands away from homes will do little or nothing to protect those homes, despite the fact the the WUI officially extends 1.5 miles from the forest boundary. WUI boundaries were established by politicians, not scientists. You can use the WUI to justify this logging, but it demonstrates a lack of scientific integrity.

Williams, M.A., W.L. Baker. 2012. Comparison of the higher-severity fire regime in historical (A.D. 1800s) and modern (A.D. 1984-2009) montane forests across 624,156 ha of the Colorado Front Range. Ecosystems 15: 832-847. *Recent high severity fires in Ponderosa-Doug Fir forests in Colorado are not outside historical (1800s) averages.*

Response: This paper is specific to the Front Range in Colorado. Steve Arno's extensive work in the Bitterroot, cited in FIRE-001, found an average fire-free interval of 11-16 years in ponderosa and Douglas-fir and 16-27 years in Douglas-fir, lodgepole pine dominated sites.

Lonn comments: The study examined Ponderosa-Doug Fir forests in Colorado that are akin to those in DLL 2. Similar conclusions were reached for the northern Rockies Ponderosa-Doug Fir forests by Odion et al. (2014) and Baker et al. (2007); both are discussed above.

Invasives

Dodson, EK., and Fiedler, C.E., 2006, Impacts of restoration treatments on alien plant invasion in Pinus ponderosa forests, Montana, USA: Journal of Applied Ecology, v. 43, p. 887-897. *Thin and burn had most weeds, then thin only, followed by burn only, and then control.*

Response: This paper discusses different restoration treatments in ponderosa pine and the resultant invasive species that come in post-treatment. Research showed that active restoration treatments (thinning, burning or both) led to increase in the abundance of invasive species. The control plots, areas that received no treatment, also had an increase in invasive species but at a lesser rate. The study also found that the percentage of total plant cover by invasive species was less than what might occur after a wildfire. The intent of this paper is to help land managers recognize there are trade-offs to restoration treatments. As stated on p. 894, "because of the multiple benefits that accrue with this treatment, which include killing fire-vulnerable Douglas-fir seedlings and saplings, reducing unnaturally high fuel build-ups, recycling nutrients bound in slash and down woody material and increasing the sprouting of important wildlife forage species. Land managers must weigh the benefits of restoration treatments against unwanted side-effects relative to their specific situations and management objectives."

Lonn comments: This paper did not actually find that total invasive species cover was less than after a wildfire; it cited another paper that stated that conclusion, without any specifics. This paper studied only the impacts of thinning, burning, or both as compared to untreated forest. It states that the costs of increasing invasive weeds should be considered along with the benefits of vegetation treatments, something the DLL2 EA has not done. The paper concludes does that (p, 892) "the active restoration treatments in our study (thinning, burning or both) increased the abundance of alien and transformer species. A response was evident even though these species were very minor constituents of the understory community initially. Our results are consistent with those from studies in ponderosa pine forests of other regions where invasion was facilitated by management treatments." Because burn-only treatments resulted in much less weed invasion than thin and burn treatments, DLL2 should consider using only the prescribed burn option. In not doing so, you have not considered all reasonable alternatives, and therefore violated NEPA.

Merriam, K.E., Keeley, J.E., Beyers, J.L., 2006, The role of fuel breaks in the invasion of non-native plants: U.S. Geological Survey Scientific Investigations Report 2006-5185. *A significant impact of all fuel treatments is the increase in invasive weeds, primarily due to soil disturbance.*

Response: This paper discusses the relationship between fuel reduction treatments, specifically fuel breaks, and the invasion of nonnative plants. The treatments evaluated in this paper are fuel breaks in California. They refer to fuel breaks with a number of different terms, such as shaded fuel breaks, defensible fuel reduction zones, defensible fuel profile zones, fuel reduction projects, fuel management zones, wildfire protection zones, and community protection zones. These types of treatments are not what is being prescribed in the DLL II project.

Lonn comments: In this paper (p. 1), all fuel reduction treatments are "collectively referred to as fuel breaks". It is disingenuous, therefore, to separate the fuel reduction treatments proposed in DLL2 from the results of this paper. The goal of fuel reduction is stated over and over in the DLL2 EA and the Fire and Fuels project files. While this paper examined projects In California, it included several sites of Ponderosa and mixed conifer forests. It concluded that "nonnatives were significantly more abundant on fuel breaks in all vegetation types". My own observations of BNF's Hayes Creek, Como, and Westside projects confirm these findings. BMPs will not solve the invasive weed problem in commercially logged areas.

Genetics

Bailey, J.K., Deckert, R., Scheitzer, J.A., Rehill, B.J., Lindroth, R.L., Gehring, C., and Whitham, T.G., 2005, Host plant genetics affect hidden ecological players: links among Populus, condensed tannins, and fungal endophyte infection: Canadian Journal of Botany, v. 83, p. 356–361 (2005) doi: 10.1139/B05-008. *Genetic differences in Cottonwoods that cannot be visually determined have profound effects on the forest ecosystem.*

Carswell, C., 2016, Genetic research lays foundation for bold conservation strategies: High Country News, June 8, 2016. *Pinyon pines susceptible to moths turn out to be the most drought resistant and survive over healthy appearing ones.*

McNulty, S.G., Boggs, J.L., and Sun, G., 2014, The rise of the mediocre forest: why chronically stressed trees may better survive extreme episodic climate variability: New Forests, v. 45, p. 403-415. *Finds that the healthy looking trees are not the ones that best survive climate change due to slower growth and higher root to foliage ratios. You cannot select for adaptive trees; only nature can do that.*

Six, D.L., Vergobbi, C. and Cutter, M., 2018, Are survivors different? Genetic-based selection of trees by mountain pine beetle during a climate-change-driven outbreak in a high-elevation pine forest: Plant Science, Plant Sci., 23 July 2018 | https://doi.org/10.3389/fpls.2018.00993 G*enetic differences that cannot be determined visually determine the variable susceptibility to bark beetles in lodgepole pine.*

Six, D.L., Biber, E., and Long, E., 2014, Management for Mountain Pine Beetle Outbreak Suppression: Does Relevant Science Support Current Policy? Forests, v. 5, p. 103-133, doi:10.3390/f5010103. *Thinning results in less live trees afterwards than just letting MPB go their course. You may actually be selecting the wrong (genetically less resistant) trees by thinning.*

Sthultz, C.M., Gehring, C.A., and Whitam, 2009, Deadly combination of genes and drought: increased mortality of herbivore-resistant trees in a foundation species: Global Change Biology, v. 15, 1949–1961, doi: 10.1111/j.1365-2486.2009.01901.x *The least vigorous pinyon pines, with their growth slowed by moth caterpillars, had much greater survival rates during drought than the healthy-appearing trees.*

Response: These papers all discuss genetic variations in different tree species. They discuss how the outward appearance of a tree is not always the best indicator of its ability to survive a disturbance. Some trees may appear unhealthy but have a genetic trait that makes them actually better adapted to survive a drought or insect outbreak. Several of the articles are specific to cottonwoods or piñon pine, which are not being treated or are not present in the DLL II project. Dr. Six's research is the most relevant to the treatments proposed in DLL II. Both of those papers recognize there is still a need for forest management and more research around this issue is needed moving forward in selecting how to manage for mountain pine beetle.

Lonn comments: These papers suggest that the outward appearance of a tree is not the best indicator of "resilience". Yet, outward appearance is exactly how you do select survivors. I realize that cottonwoods and pinon pine are not being treated (!), but the concepts presented in these papers do have application to all plants. Six et al.'s work (2014, 2018) certainly supports the application of these genetic concepts to the pine forests of western Montana. And while both papers recognize the need for more research, DLL 2 is a logging project, not a research project. Six et al. (2014) concluded that the policies of the USFS to reduce beetle epidemics were not at all justified.

Mistletoe

Geils, B.W., Tovar, J.C., and Moody, B., 2002, Mistletoes of North American Conifers: Gen. Tech. Rep. RMRS-GTR-98, USDA Forest Service, 123 p. https://www.fs.fed.us/rm/pubs/rmrs_gtr098.pdf *Points out that some individuals are genetically resistant to mistletoe infection, but they are impossible to identify.*

Hoffman, J.T., 2004, Management of Dwarf Mistletoe, 2004, USDA-FS https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5187427.pdf *Gives strategies for management when commercial timber production is the goal.*

Watson, D.M., and Herring, M., 2012, Mistletoe as a keystone resource: an experimental test: Proceedings of the Royal Society, v. 279, p. 3853-3860.. R. Soc. B (2012) 279, 3853-3860 doi:10.1098/rspb.2012.0856 *Mistletoe is an important part of the forest ecosystem, providing many benefits that are not entirely known yet.*

Worrall, J., 2013, Dwarf Mistletoes: Ecology and Management in the Rocky Mountain Region: Forest Health Management, Rocky Mountain Region, USDS Forest Service, 48 p. https://www.researchgate.net/publication/260968803_Dwarf_Mistletoes_Ecology_and_Management_in_the_Rocky_Mountain_Region

Response: These papers all discuss mistletoe and management of forests with mistletoe. The DLL II project does propose management activities to help manage mistletoe in the project area, however, the project was not designed to fully eradicate mistletoe from the project area. Treatments are intended to reduce mistletoe spread. The Silviculture report (SILV-001) states on p. 16, "We recognize that eradication of dwarf mistletoe is not possible or desirable."

Lonn comments: You left out several important references that I cited. Pollock and Suckling (1995) state: "dwarf mistletoe control projects have traditionally been pursued by the Forest Service in order to maximize timber production at the expense of ecosystem health". Hadfield et al. (2000), a USFS publication states that mistletoe "is a pest only where it interferes with management objectives, such as timber production". In other areas, it is important for wildlife habitat. It also states that spread rates are faster in open stands than dense stands. In neither MA 2 or MA 8b is timber production the priority; instead these Mas are to be managed for the benefit of wildlife as their first priority. If you want to slow mistletoe spread, then you should follow the guidelines supported by Bull et al. (1997), Worrell (2013), and Pollock and Suckling (1995), and create a "donut" 30 feet wide around the infected area, and thereby preserve ecosystem health. The science states that clearcuts are unnecessary and ecologically unsound. The science indicates there are alternatives to clearcutting, and you did not consider all reasonable alternatives in the EA as required by NEPA.

Wildlife

Bull EL, Parks CG, Torgerson TR. 1997. Trees and logs important to wildlife in the interior Columbia River basin. General Technical Report PNW-GTR-391. Portland, OR: US Dept. of Agriculture Forest Service, Pacific Northwest Research Station. 55 p.

Response: This document focuses on the importance of living trees with decayed parts, trees with hollow chambers, trees with brooms, dead trees, and logs and the value of these structures to wildlife. The DLL II project will retain snags and downed woody debris, where possible, within treatment units.

Lonn comments: "Where possible" is one point of disagreement. Your goals to reduce wildfire, reduce insects and disease, and harvest (remove) as much timber as possible conflict with the ecological value of leaving hollow trees, trees with brooms, dead trees, and logs. Their value to wildlife is completely disregarded.

Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.) conifer forests: Conservation Biology 9: 1041–1058.

Response: Hutto (1995) surveyed recently burned areas in western Montana and northern Wyoming and determined that 15 bird species are generally more abundant in early post-fire communities than in any other major cover type occurring in the northern Rockies. He also stated that one species, the black-backed woodpecker, seems nearly restricted in its habitat distribution to standing dead forests created by stand-replacement fires. Hutto recommends that public land managers "leave an adequate amount of standing, dead trees after a fire because of the species that depend on that forest element." DLL II project is not a post-fire salvage logging project.

Lonn comments: You missed my point: that severe burns have immense ecological benefits, and so to justify DLL2 on the basis of preventing severe wildfires is not ecologically sound. I realize that DLL2 is not a post-fire salvage project.

British Ecological Society

Impacts of Restoration Treatments on Alien Plant Invasion in Pinus ponderosa Forests, Montana, USA
Author(s): Erich K. Dodson and Carl E. Fiedler
Source: *Journal of Applied Ecology*, Vol. 43, No. 5 (Oct., 2006), pp. 887-897
Published by: British Ecological Society
Stable URL: https://www.jstor.org/stable/3838469
Accessed: 06-11-2018 03:38 UTC

Journal of Applied Ecology 2006
43, 887–897

Impacts of restoration treatments on alien plant invasion in *Pinus ponderosa* forests, Montana, USA

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Summary

1. Invasion by alien plant species represents a challenge to land managers throughout the world as they attempt to restore frequent fire-adapted ecosystems following decades of fire exclusion. In ponderosa pine *Pinus ponderosa* forests of western North America, the response of alien species to restoration treatments has not been well documented, particularly for alien species capable of altering environmental conditions (transformers). Understanding alien species dynamics is critical for developing treatments that accomplish restoration goals while minimizing alien invasion.

2. We used a replicated, randomized block experiment to compare the effects of an untreated control and thin-only, burn-only and thin-burn treatments on alien and transformer understorey species at multiple spatial scales (1 m^2, 100 m^2 and 1000 m^2). Data were collected pre-treatment and for multiple post-treatment years. We compared richness and cover of alien species and transformer species among treatments, and identified environmental variables correlated with transformer species cover. Indicator species analysis was used to identify transformer species associated with specific treatments.

3. Alien and transformer species richness and cover were significantly higher in the thin-burn than in all other treatments at all spatial scales. Thin-only and burn-only treatments showed greater alien and transformer species responses than the control at the larger 100-m^2 and 1000-m^2 scales.

4. Increased transformer cover was strongly correlated with increased tree crown scorch height and removal of overstorey trees.

5. The thin-burn treatment had four transformer species as indicators, the thin-only had one, while the burn-only and control had none.

6. *Synthesis and applications.* The results show that alien species, including transformers, respond to restoration treatments, especially the combined thin-burn treatment. Therefore monitoring for alien species invasion is an essential component of a restoration programme. Abundance of transformer species increased with increasing disturbance intensity, suggesting that less intense single-disturbance treatments (burn-only, thin-only) or incremental treatments may be preferred in some applications. Where more intense treatments are required to meet management objectives, specific strategies, such as seeding of native species, limiting grazing before and after treatment and harvesting over a protective winter snowpack, may be necessary to limit alien invasion.

Key-words: exotic species, forest management, fuel reduction, invasive plants, noxious weeds, prescribed burning, thinning

Journal of Applied Ecology (2006) **43**, 887–897
doi: 10.1111/j.1365-2664.2006.01206.x

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Introduction

Fire is a historically common disturbance process in many forested ecosystems (Rodriguez-Trejo & Fulé 2003) and prescribed burning is increasingly being used to reintroduce this process to ecosystems throughout the world. For example, prescribed burning is used to address declining conditions in eucalypt (*Eucalyptus* spp.) forests in Australia (Ellis, Mount & Mattay 1980), Scots pine *Pinus sylvestris* L. forests in northern Europe (Linder, Jonsson & Niklasson 1998) and longleaf pine *Pinus palustris* P. Mill. forests in the south-eastern USA (Brockway *et al.* 2005). Restoration treatments that employ thinning, burning or both are also being recommended to improve structure and function in historically fire-adapted ponderosa pine *Pinus ponderosa* P. & C. Lawson forests of western North America that have been fire excluded for decades (Moore, Covington & Fulé 1999; Fiedler *et al.* 2001; Allen *et al.* 2002).

The associated ecosystem effects of restoration treatments have been little studied over much of ponderosa pine's 11 million-ha range (which extends from Mexico northwards to southern British Columbia, Canada), particularly regarding effects on alien understorey species. However, alien plant invasions are increasingly being recognized as a threat to the success of restoration treatments (Sieg, Phillips & Moser 2003; Wolfson *et al.* 2005). A few recent studies have documented positive responses by alien species to treatments in pine forests of Arizona (Griffis *et al.* 2001; Fulé, Laughlin & Covington 2005) and South Dakota, USA (Wienk, Sieg & McPherson 2004). To our knowledge, the experiment presented here is the first designed to focus exclusively on alien species' responses to forest restoration treatments, and the first to differentiate treatment effects on alien and transformer species.

Alien invasion depends on the number of propagules of potential invaders, characteristics of the invading species, and susceptibility of the site to invasion (Lonsdale 1999). Treatments may enhance community invasibility by introducing propagules of exotic species (Harrod 2001) and imposing disturbance, which creates safe sites and reduces competition (Hobbs & Huenneke 1992; Petryna *et al.* 2002). Thinning (Kaye & Hart 1998) and burning (DeLuca & Zouhar 2000) treatments can also increase resource availability, which may facilitate invasion (Huenneke *et al.* 1990; Davis, Grime & Thompson 2000; Leishman & Thomson 2005) and provide alien species with a competitive advantage (Kolb *et al.* 2002; Brooks 2003). The combination of resource addition and decreased competition may have the greatest potential to facilitate invasion (Thompson *et al.* 2001; Minchinton & Bertness 2003), especially if propagule pressure also increases.

Invasion by alien plant species is only one post-disturbance recolonization scenario (Hobbs & Huenneke 1992). Indeed, there are instances where thinning and burning in pine forests have not led to alien invasion (Fulé *et al.* 2002; Fornwalt *et al.* 2003) and in some cases fire reduces alien abundance (Smith & Knapp 1999; Emery & Gross 2005). The outcome depends on community and environmental attributes, herbivory, stochastic factors and characteristics of the disturbance itself (Halpern 1988; Alpert, Bone & Holzapfel 2000), therefore different restoration treatments may have differential effects.

Alien species invasions pose threats to ecosystems throughout the world (Vitousek *et al.* 1996; Mack *et al.* 2000; Brooks *et al.* 2004); however, all alien species do not have equivalent impacts (Ortega & Pearson 2005; Williamson & Fitter 1996). A subset of alien species, which Richardson *et al.* (2000) terms 'transformers', has the potential to alter ecosystem properties. Because of their capacity to counteract restoration efforts, limiting the response of these species is pivotal to restoration success. However, sampling design influences alien and transformer detection, as invasion patterns can vary with spatial scale (Halpern & Spies 1995; Stohlgren, Bull & Otsuki 1998) and time since disturbance (Meiners, Pickett & Cadenasso 2002; Wienk, Sieg & McPherson 2004; Fulé, Laughlin & Covington 2005).

Our study evaluated four treatments in second-growth ponderosa pine forests: untreated (control), prescribed burning in the spring (burn-only), thinning (thin-only) and thinning followed by prescribed spring burning (thin-burn). It presented a unique opportunity to assess the effects of restoration treatments on alien invasions in a randomized and replicated field experiment. To thoroughly document alien response, we sampled over multiple years and spatial scales. We further evaluated a subset of alien species (transformers) because of their potentially profound ecosystem impacts. Our study addressed three key questions. (i) Do restoration treatments differ in their degree of invasion by alien and transformer species as measured by cover and richness? (ii) What environmental variables are correlated with increased transformer cover? (iii) Are individual transformer species associated with specific treatments?

Methods

The study was established on the 11 000-ha University of Montana Lubrecht Experimental Forest, which was located at 47°N, 113°W in western Montana, USA. The altitude of the study sites ranged from 1263 m to 1388 m a.s.l. Mean annual air temperature was 7 °C and mean annual precipitation was 50 cm, nearly half of which fell as snow (Nimlos 1986). We established three blocks of 36 ha each in second-growth stands comprised primarily of ponderosa pine and Douglas-fir *Pseudotsuga menziesii* (Mirbel) Franco, with lesser amounts of western larch *Larix occidentalis* Nutt. and lodgepole pine *Pinus contorta* Dougl. ex Loud. Most trees were 80–90 years old, with scattered clumps of regeneration and occasional trees up to 200 years old. Cattle grazing had been a traditional land use throughout the past century. Despite only modest grazing pressure in recent decades, study sites were fenced to isolate treatment effects on alien species invasion.

The three blocks were located about 3 km apart. Each block was subdivided into four square 9-ha treatment units. One replicate of each treatment was then randomly assigned within each block, with the exception of two burn treatment units that were strategically located to allow containment of prescribed burns. Ten 20×50-m (1000 m^2) modified Whittaker plots were established within each treatment unit, using a stratified random design to ensure dispersion. Each Whittaker plot was subdivided into 10 10×10-m (100 m^2) subplots. Each subplot had two 1×1-m (1 m^2) quadrats located in opposite corners (20 quadrats $plot^{-1}$), 12 of which were randomly selected to sample understorey vegetation.

TREATMENTS

Restoration treatments were developed to move forest density and structure towards historical conditions (Metlen & Fiedler 2006). The treatment referred to as thin-only consisted of silvicultural felling designed to reduce the density of small- and medium-sized trees, and leave an open fire-resistant stand composed primarily of seral species. Unfelled trees were marked to achieve a target reserve basal area (BA) of 11 m^2 ha^{-1}, which resulted in about half of the basal area being removed. Large-diameter ponderosa pine were favoured as unfelled trees, although some pine trees were retained in all size classes, if available. Logging slash (non-merchantable tree tops and limbs) was left on site and driven over by the harvesting equipment to condense fuel accumulations. Thinning was conducted during the winter of 2001 on a snowpack.

Prescribed broadcast burns were implemented during May and June of 2002, with a separate prescribed burn for each of the six burn treatment units (3 × burn-only and 3 × thin-burn). Burning was conducted using a strip-head fire technique (Kilgore & Curtis 1987). Relative humidity during burning ranged from 20% to 48%, temperatures from 9 °C to 29 °C, and winds from 2 km h^{-1} to 13 km h^{-1}. Flame lengths varied from 0·2 to 1·2 m in the burn-only and from 0·2 to 2·7 m in the thin-burn.

VEGETATION SAMPLING

All species present on each plot (1000 m^2) and associated quadrats (1 m^2) were identified prior to treatment in the summers of 2000 (thin-only and thin-burn) and 2001 (burn-only and control) and after treatment in 2002, 2003 and 2004. Over the course of the study, 178 native species and 25 alien species were recorded. Nomenclature followed the USDA PLANTS database (USDA-NRCS 2004), which was also used to determine if plants were alien or native. Alien species are listed in Appendix S1 in the supplementary material.

Cover was visually estimated for each species at the quadrat level (1 m^2). Pre-treatment cover was estimated using cover codes (0, 0%; 1, < 1%; 2, 1–10%; 3, 11–25%; 4, 26–50%; 5, 51–75%; and 6, 76–100%). For analysis, cover codes were converted to the median value for the code. Post-treatment cover was estimated to the nearest percentage, which is more sensitive than codes for temporal trend analysis, especially for rare species (Stohlgren, Bull & Otsuki 1998).

Noxious weed lists and the literature were used to identify a subset of alien species (transformers; *sensu* Richardson *et al.* 2000) that can alter environmental conditions and therefore are a priority for management. These species included *Bromus tectorum* L., *Carduus nutans* L., *Centaurea biebersteinii* DC., *Cirsium arvense* (L.) Scop., *Cirsium vulgare* (Savi) Ten., *Cynoglossum officinale* L., *Potentilla recta* L. and *Verbascum thapsus* L. In addition to the data collected at the 1000-m^2 and 1-m^2 scales, cover of transformer alien species was also visually estimated on each of the 10 subplots (100 m^2) per plot in 2003 and 2005 to provide further insights into transformer species invasion. A cover value of 0·2 was assigned to each species in a subplot with < 0·5% cover; species cover was estimated to the nearest percentage thereafter. The cover of exposed mineral soil at the subplot level was estimated in the same way.

BA was calculated pre-treatment and in 2003 for each overstorey tree > 10 cm diameter at breast height (d.b.h. = 1·37 m), and summed for each plot (1000 m^2). Saplings (trees > 1·37 m in height but < 10 cm in d.b.h.) were censused on five randomly selected 100-m^2 subplots per plot prior to treatment and in 2003. The proportional change in overstorey BA (m^2 ha^{-1}) and sapling density (stems ha^{-1}) was calculated by subtracting the post-treatment value from the pre-treatment value and dividing the difference by the pre-treatment value. In 2003, live canopy cover was sampled by densitometer at the 18 subplot corners in each plot.

Post-treatment cover was estimated to the nearest percentage at the quadrat level (1 m^2) for duff (i.e. partially decomposed and fully humified organic matter) and litter, rock, woody stems (live and dead stems > 1 m in height), natural wood (downed woody debris large enough to obstruct growth) and logging slash. In 2002, maximum crown scorch height was measured for every tree > 10 cm d.b.h. in a plot. Slope and aspect were measured for each plot, and effective aspect was calculated following Stage (1976).

STATISTICAL ANALYSIS

Prior to analysis, a significance level of $P = 0{\cdot}05$ was set for all tests. Treatment differences in alien and transformer species richness and cover were tested using blocked multi-response permutation procedures (BMRPP) in PC-ORD version 4 (McCune & Mefford 1999). Data were summarized at the treatment unit level ($n = 3$) prior to statistical analysis. Richness and cover were tested for treatment differences using a median alignment for block and a Euclidean distance measure, with each year (pre-treatment, 2002, 2003 and 2004) tested separately. Blocking with median alignment focuses the analysis on differences among treatments but does not provide a test statistic for a block effect (Mielke & Iyer 1982). Alien richness was tested at two spatial scales, 1000 m^2 and 1 m^2, while cover data were tested at the 1-m^2 scale only. Transformer species were evaluated similarly. The additional data on transformer species cover collected at the 100-m^2 scale in 2003 and 2005 were tested for treatment differences within each year.

Similar in purpose to ANOVA, MRPP is a technique that tests for differences among groups based on the measure of distance (or dissimilarity) between pairs of observations (Zimmerman, Goetz & Mielke 1985). However, assumptions of normality and equal variance among groups are not required with MRPP (Zimmerman, Goetz & Mielke 1985). An estimate of effect size is given by the chance-corrected within-group agreement (A), which ranges from zero to one. If all observations within a treatment are identical, A will equal one; however, if the observed mean equals the expected, A is zero.

Using MRPP, pair-wise comparisons with three replicates would not result in a meaningful P-value. Therefore, when the overall test for treatment differences was significant, data associated with each treatment were averaged at the plot level ($n = 30$) for between-treatment comparisons. Comparisons were performed using univariate MRPP tests without blocking. We are confident in the results because neither the thinning nor burning treatments were homogeneous across units, plot centres were separated by a minimum of 70·7 m, and tests for overall treatment effect had already shown significance. Pair-wise comparisons were Bonferroni-adjusted (significance level $P/6 = 0{\cdot}0083$).

Environmental and treatment-related variables correlated with transformer species cover were identified using univariate multiple regression in SPSS version 12·0 (SPSS Inc., Chicago, IL). Transformer species' cover data at the subplot level (100 m^2) were averaged to the plot level for all analyses ($n = 30$). All environmental variables were also averaged to the plot level prior to analysis. The plot level was used to account for variation within treatment units, because extremes may be more influential than averages (Underwood 1997). Cover of transformer species in 2003 and 2005 was used as a response variable, with a separate regression performed for each year. A rich model was fitted and stepwise backwards elimination was conducted until only significant ($P < 0{\cdot}05$) explanatory variables remained. Explanatory variables are listed in Appendix S2 in the supplementary material. A treatment variable was deliberately not included in these analyses to isolate environmental attributes that may facilitate transformer invasion. Levene's test for homogeneity of variance, scatterplots and normal probability-probability plots (P-P plots) were used to assess assumptions.

An indicator species analysis (Dufrêne & Legendre 1997) was conducted in PC-ORD version 4 (McCune & Mefford 1999) to compare how individual transformer species performed among treatments. This technique produces an indicator value (IV) for every species based on cover and frequency, where the IV ranges from 0 to 100, with 100 being a perfect indicator. Subplot-level (100 m^2) transformer cover data from 2003 and 2005 were averaged up to the plot level ($n = 30$), which provided a more accurate estimate of frequency for each species than averaging to the treatment unit level ($n = 3$). Separate analyses were performed for data collected in 2003 and 2005.

Results

TREATMENT EFFECTS

There were no among-treatment differences in richness or cover of either alien species or transformer species prior to treatment, but numerous differences after, indicating differential responses to alternative restoration treatments. Between-year comparisons within treatments were not performed because of pre- and post-treatment differences in cover estimation.

ALIEN RICHNESS AND COVER

Alien richness differed among treatments at the 1000 m^2 scale in all post-treatment years (Table 1). Pair-wise comparisons revealed that in 2002 the thin-only and thin-burn treatments both had significantly higher alien richness than the burn-only and control. In 2003, alien richness in the thin-only treatment remained higher than the control, while the thin-burn had higher alien richness than all other treatments. This same trend continued in 2004.

At the 1-m^2 scale, alien richness did not differ among treatments in 2002 (Table 1). In 2003 and 2004, there were marginally significant differences among treatments ($P = 0{\cdot}053$ and $P = 0{\cdot}052$, respectively). The thin-burn had significantly higher alien richness at the 1-m^2 scale than all of the other treatments in these years, based on pair-wise comparisons. Alien cover was significantly different among treatments in 2003 and marginally different among treatments in 2004 ($P = 0{\cdot}052$; Table 1). In both years, the thin-burn had higher alien cover than all other treatments.

TRANSFORMER SPECIES RICHNESS AND COVER

Following treatment, transformer species richness at the 1000-m^2 scale differed among treatments in each sampling year (Table 2). The thin-only and thin-burn had significantly higher richness in 2002 than the burn-only and control. In 2003, transformer richness in the thin-only remained higher than the burn-only and control, while the thin-burn had higher transformer

Table 1. Mean alien species richness and cover (SE; $n = 3$), by treatment, for each sample year. BMRPP was used to test for treatment differences for each variable in each year ($n = 3$). Where significant differences existed, MRPP tests of plot-level data were used for pair-wise comparisons ($n = 30$). Treatments that were significantly different within a year are denoted with different letters (Bonferroni corrected $P < 0{\cdot}0083$)

	Control	Burn-only	Thin-only	Thin-burn	A†	*P*
1000-m² richness						
Pre-treatment	2·17(0·66)	1·60(0·75)	2·33(0·68)	2·60(1·14)	0·01	0·440
2002	3·03(0·96)a	2·37(0·87)a	4·80(1·14)b	5·13(1·36)b	0·47	0·017*
2003	3·73(0·84)a	4·83(1·17)ab	6·23(1·19)b	9·37(1·89)c	0·55	0·005**
2004	4·40(0·89)a	5·93(2·03)ab	6·93(1·07)b	10·20(2·67)c	0·22	0·034*
1-m² richness						
Pre-treatment	0·17(0·07)	0·19(0·12)	0·23(0·08)	0·27(0·15)	–0·15	0·801
2002	0·18(0·08)	0·18(0·14)	0·26(0·10)	0·41(0·16)	0·10	0·207
2003	0·21(0·09)a	0·28(0·17)a	0·33(0·11)a	0·71(0·27)b	0·25	0·053‡
2004	0·30(0·13)a	0·47(0·21)a	0·41(0·15)a	1·28(0·55)b	0·24	0·052‡
Percentage cover						
Pre-treatment	0·14(0·07)	0·14(0·10)	0·58(0·30)	0·22(0·15)	0·27	0·068
2002	0·19(0·08)	0·20(0·17)	0·37(0·15)	0·55(0·25)	0·11	0·188
2003	0·24(0·09)a	0·34(0·23)a	0·44(0·16)a	1·95(1·10)b	0·22	0·024*
2004	0·33(0·14)a	0·59(0·27)a	0·58(0·25)a	2·44(1·29)b	0·18	0·052‡

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$.

†A in MRPP is the chance corrected within-group agreement (see text).

‡P < 0·055 was considered marginally significant; therefore post-hoc tests were performed.

Table 2. Mean transformer species richness and cover (SE; $n = 3$), by treatment, for each sample year. MRPP was used to test for treatment differences for each variable in each year ($n = 3$). Where significant differences existed, MRPP tests of plot-level data were used for pair-wise comparisons ($n = 30$). Treatments that were significantly different within a year are denoted with different letters (Bonferroni corrected $P < 0{\cdot}0083$)

	Control	Burn-only	Thin-only	Thin-burn	A†	*P*
1000-m² richness						
Pre-treatment	0·50(0·15)	0·60(0·38)	0·57(0·27)	0·83(0·43)	–0·03	0·543
2002	0·70(0·10)a	0·73(0·44)a	1·63(0·33)b	2·20(0·66)b	0·38	0·023*
2003	0·80(0·06)a	1·40(0·42)a	2·50(0·32)b	3·60(0·55)c	0·67	0·004**
2004	1·10(0·17)a	2·07(0·75)b	2·87(0·32)b	4·20(0·67)c	0·48	0·012*
1-m² richness						
Pre-treatment	0·03(0·01)	0·07(0·06)	0·08(0·05)	0·05(0·04)	–0·02	0·595
2002	0·04(0·02)a	0·07(0·07)ab	0·08(0·06)ab	0·13(0·06)b	0·29	0·027*
2003	0·03(0·02)a	0·09(0·08)ab	0·10(0·07)ab	0·23(0·09)b	0·46	0·014*
2004	0·05(0·03)a	0·14(0·07)a	0·12(0·07)a	0·60(0·27)b	0·36	0·029*
Percentage cover						
Pre-treatment	0·04(0·02)	0·08(0·07)	0·38(0·30)	0·07(0·06)	0·07	0·123
2002	0·05(0·02)a	0·09(0·09)ab	0·15(0·09)ab	0·20(0·12)b	0·21	0·045*
2003	0·06(0·03)a	0·16(0·15)a	0·18(0·11)a	1·21(0·74)b	0·26	0·016*
2004	0·08(0·04)a	0·25(0·14)a	0·21(0·11)a	1·43(0·79)b	0·27	0·031*

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$.

†A in MRPP is the chance corrected within-group agreement (see text).

species richness than all other treatments. By 2004, both the burn-only and thin-only had higher transformer richness than the control, while the thin-burn maintained higher transformer richness than all other treatments.

Treatments also differed in transformer species richness at the 1-m² scale in each post-treatment sampling year (Table 2). In 2002 and 2003, the thin-burn had significantly higher richness than the control. In 2004, the thin-burn had significantly higher transformer richness than all other treatments. Transformer species cover at the 1-m² scale was also significantly higher in the thin-burn than the control in 2002, and was significantly higher in the thin-burn than all other treatments in 2003 and 2004 (Table 2).

Transformer cover at the subplot level differed among treatments in 2003 ($P = 0{\cdot}025$) and 2005 ($P = 0{\cdot}032$; Fig. 1). In both years, the thin-only and burn-only had significantly higher transformer species cover than the control. The thin-burn had significantly higher transformer cover than all other treatments in 2003, and higher cover than the thin-only and control in 2005.

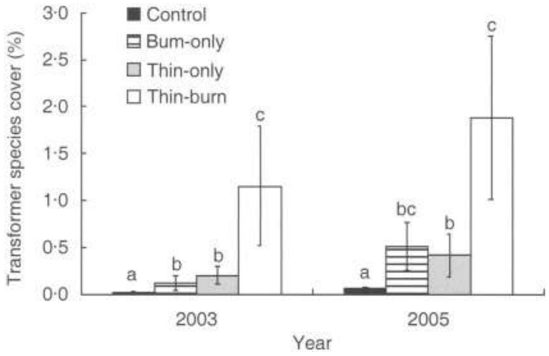

Fig. 1. Treatment means and standard errors ($n = 3$) for transformer species cover at the subplot level (100 m^2) in each treatment in 2003 and 2005. BMRPP was used to test for treatment differences within years ($n = 3$). Where differences occurred, pair-wise MRPP tests of plot-level data ($n = 30$) were used to test for between-treatment differences (represented by different letters). Pair-wise comparisons were adjusted by a Bonferroni procedure.

TRANSFORMER COVER AND ENVIRONMENTAL VARIABLES

Four environmental variables explained 43% of the variation in transformer species cover in 2003, and five variables accounted for 47% of the variation in 2005 (Table 3). In both years, transformer cover varied significantly among the three blocks, and was positively correlated with overstorey tree basal area removal and increasing crown scorch height. Parameter estimates revealed that, in both years, a 60% reduction in overstorey basal area would elicit nearly a 1% increase in transformer cover. With each 10 m of crown scorch height in 2003 and 7 m of scorch height in 2005, transformer cover would be expected to increase by 1%. In 2003, the relationship of transformer cover to saplings was opposite to that of overstorey trees, although sapling density was a much less significant explanatory variable. In 2005, transformer species cover was positively correlated with the cover of duff and litter, and of slash.

INDICATOR SPECIES

The indicator species analysis revealed the thin-burn had four significant transformer indicators (*Carduus nutans*, *Cirsium arvense*, *Cirsium vulgare* and *Verbascum thapsus*) in both 2003 and 2005 (Table 4). The only other significant indicator, *Cynoglossum officinale*, was an indicator of the thin-only in both 2003 and 2005. There were no transformer species indicators for either the control or burn-only treatments.

Discussion

The active restoration treatments in our study (thinning, burning or both) increased the abundance of alien and transformer species. A response was evident even though these species were very minor constituents of the understorey community initially. Our results are consistent with those from studies in ponderosa pine forests of other regions where invasion was facilitated by management treatments (Griffis *et al.* 2001; Wienk, Sieg & McPherson 2004; Fulé, Laughlin & Covington 2005). Similar relationships have been documented following harvest in coastal Pacific north-west forests, USA (Thysell & Carey 2001) and southern Canadian boreal forests (Haeussler *et al.* 2002), and following prescribed burning in Australia (Milberg & Lamont 1995) and South America (Petryna *et al.* 2002). The operational scale at which we implemented treatments, coupled with a replicated and randomized experimental design, which is rare in studies of forest stand manipulations (Bennett & Adams 2004), instil confidence in the differential responses of alien and transformer species in our study. However, follow-up analyses with $n = 30$ (including pair-wise comparisons) are limited in inference to our study site, and should be extrapolated with caution.

A clear pattern emerged in all the analyses, with invasion greatest in the combined thin-burn treatment,

Table 3. Final regression models for transformer species cover and environmental and treatment-related explanatory variables in 2003 and 2005. A parsimonious model was identified through stepwise backward elimination

Parameter	β	*t*	*P*
2003			
Intercept	0·10	0·67	0·506
Block†			0·001**
Proportional change in basal area	1·63	4·45	0·000**
Crown scorch height	0·10	5·43	0·000**
Proportional change in sapling density	–0·56	–2·03	0·045*
$R^2 = 0·429$			
2005			
Intercept	–4·22	–2·60	0·010*
Block†			0·016*
Proportional change in basal area	1·48	2·89	0·005**
Crown scorch height	0·14	5·64	0·000**
Percentage cover of duff and litter	0·06	2·65	0·009**
Percentage cover slash (tops and limbs)	0·11	3·28	0·001**
$R^2 = 0·472$			

$*P < 0·05$, $**P < 0·01$.
†Block was treated as a categorical variable, and an extra sums-of-squares F-test was used to ascertain significance.

Table 4. Indicator species analyses of supplemental subplot-level (100 m^2) cover of transformer species, collected in 2003 and 2005 only. Indicator values (IV) range from 0 to 100, with 100 being a perfect indicator of a treatment. *P*-values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1000 randomizations

	2003			2005		
Species	Treatment	IV	*P*	Treatment	IV	*P*
Bromus tectorum	Thin-burn	5·0	0·644	Control	7·6	0·566
Carduus nutans	Thin-burn	52·4	0·001**	Thin-burn	56·5	0·001**
Centaurea biebersteinii	Thin-only	25·3	0·243	Thin-only	31·1	0·238
Cirsium arvense	Thin-burn	26·5	0·005**	Thin-burn	31·5	0·002**
Cirsium vulgare	Thin-burn	71·3	0·001**	Thin-burn	62·4	0·001**
Cynoglossum officinale	Thin-only	24·4	0·003**	Thin-only	23·3	0·017*
Potentilla recta	Thin-burn	17·3	0·323	Thin-burn	19·1	0·406
Verbascum thapsus	Thin-burn	63·4	0·001**	Thin-burn	71·9	0·001**

*$P < 0·05$, **$P < 0·01$.

least in the control, and intermediate in the single active treatments (burn-only and thin-only). The much greater response of alien, and especially transformer, species to the thin-burn treatment was supported by multiple sources of evidence. For example, by 2004 alien cover in the thin-burn was more than four times the cover in any other treatment and more than seven times the cover in the control. Differences in cover of transformer species in 2004 were even more striking, as the thin-burn had more than five times the transformer cover of any other treatment, and more than 17 times the cover of the control. In addition, the thin-burn had numerous transformer species as indicators compared with the other treatments. Similarly, Wienk, Sieg & McPherson (2004) found that certain alien species had significantly higher biomass in treatments that involved partial harvesting and burning than in those that had neither treatment or only one treatment. Griffis *et al.* (2001) also reported significantly higher alien forb richness in treatments that were thinned and burned than in those that were untreated or thinned only.

The response in the thin-burn may have been the result of increased frequency of disturbance (Hobbs & Huenneke 1992; Ross *et al.* 2004), with two separate disturbance events in two consecutive years. However, the regressions of transformer cover on environmental variables suggest that the intensity of treatment also played a role. Overstorey tree reduction and increasing scorch height were strongly correlated with increased transformer cover in both 2003 and 2005. Many trees in the thin-burn were removed in the thinning and some additional trees died following burning, resulting in the largest reduction of overstorey trees of any treatment (data not shown). Also, the cut-to-length harvest system used to implement the thinning treatment left logging slash on site, which increased surface fuels and burn intensities in localized areas relative to the burn-only treatment. For example, the average crown scorch height in the thin-burn was more than 50% higher than in the burn-only (10·9 m vs. 7·0 m). Intense burning in slash piles can also create localized conditions that favour alien species (Haskins & Gehring 2004; Korb, Johnson & Covington 2004) and increase the germination and growth of certain aliens (Wolfson *et al.* 2005). Therefore, the increased intensity of the combined thin-burn treatment probably contributed to increased transformer species cover, a pattern consistent with other reports (Crawford *et al.* 2001; Griffis *et al.* 2001; Haeussler *et al.* 2002).

Increased alien invasion in the thin-burn may also be the result of increased availability of limiting resources (Davis, Grime & Thompson 2000). Thinning and burning treatments increase resource availability (Kaye & Hart 1998; DeLuca & Zouhar 2000), and removing overstorey competition in ponderosa pine forests can increase availability of limiting resources for the understorey (Riegel, Miller & Krueger 1992). For example, Gundale *et al.* (2005) studied soil nitrogen status at our site and found significantly higher total inorganic nitrogen (TIN) in the thin-burn than in any other treatment, and further found that certain alien species were correlated with high TIN (Gundale *et al.* 2006), providing evidence for the resource limitation model of alien invasion.

Noxious weed lists can be used to identify a subset of alien species that are likely to impact native communities (Skinner, Smith & Rice 2000; Ortega & Pearson 2005). Five of the eight species considered transformers in this study were recently classified as strong invaders in the inland north-west, USA (Ortega & Pearson 2005), and all eight were identified as possible noxious weed invaders following restoration treatments in south-western USA pine forests (Sieg, Phillips & Moser 2003). Strong invaders, such as the transformer species in this study, may drive changes in the community that have negative impacts on native species (Ortega & Pearson 2005). These species can trigger environmental changes that favour continued growth of the aliens themselves, including changes in fire regimes (Brooks *et al.* 2004) and below-ground processes (Ehrenfeld, Kourtev & Huang 2001). Alien species may also collectively set back natural regeneration of the dominant tree species (Keeley 2006). For example, *Cirsium vulgare* has been found to reduce growth of ponderosa pine seedlings (Randall & Rejmánek 1993). However, the identity of the dominant invaders may also change over time and with changing environmental conditions (Thompson *et al.* 2001; Ortega & Pearson 2005), requiring continued vigilance in identifying species likely to complicate restoration efforts. Other species in the northern Rocky Mountains that are not designated as noxious may also have the ability to invade both disturbed and undisturbed sites (Weaver, Gustafson & Lichthardt 2001). These potential role changes illustrate the need for monitoring and updating transformer species' classifications.

The ability to detect invasion differed with spatial scale (Tables 1 and 2 and Fig. 1). For example, richness and cover in the burn-only and thin-only differed from the control at the 100-m^2 and 1000-m^2 scales but not at the 1-m^2 scale. While only the thin-burn differed from the other treatments at the 1-m^2 scale, continuing invasion from 2003 to 2004 was evident in this treatment at the 1-m^2 scale but not the 1000-m^2 scale. Alien species richness in the thin-burn nearly doubled from 2·7 times the pre-treatment level in 2003 to 4·8 times that level in 2004 at the 1-m^2 scale, while barely changing from 2003 to 2004 at the 1000-m^2 scale. Our results support the recommendation by Stohlgren, Bull & Otsuki (1998) that a more complete understanding of invasion dynamics requires sampling at multiple spatial scales.

Our analyses showed that alien and transformer species were increasing from year to year in the control as well as the treated areas, although at a lesser rate. The only exception was cover in the thin-only, which probably decreased because of physical obstructions from slash, although interannual climatic variability and a change from using cover codes pre-treatment to percentage cover post-treatment may also have contributed. Increased richness and cover in the other treatments may have been because of an underlying rate of invasion across the landscape that was further expedited by active treatments. The proximate location of control units to active treatment units (in which significant invasion was documented) may have subsequently increased propagule pressure on the control as well. Because this was a large interdisciplinary study, the heavy human traffic on these sites from researchers may also have increased propagule pressure.

Regression analysis indicated that transformer species cover was different among blocks, even after other environmental variables were accounted for in the models. Despite these differences, the relative ranking of transformer cover among treatments was similar in all blocks. Blocks in this study were within 3 km of each other, had similar fire, grazing and *c.* 1900 logging histories, and were on gentle to moderate slopes at similar altitudes. Therefore, alien invasion may have been influenced by differences among treatment applications (such as intensity) and stochastic processes, as well as subtle environmental differences not measured in this study, suggesting caution in the extrapolation of the results to other locations where conditions differ. Further study is needed across the full range of ponderosa pine and other fire-adapted ecosystems (e.g. longleaf pine and eucalypt) where thinning and prescribed burning treatments are employed to understand the implications of restoration treatments over a range of environments and stand histories. Variations in treatment, such as harvest system and season of burning (Emery & Gross 2005), also have differential effects that warrant further investigation.

While decreasing alien abundance with time has been documented in other studies (Meiners, Pickett & Cadenasso 2002; Petryna *et al.* 2002), this trend was not yet evident at our study site, where transformer abundance increased in all treatments from 2003 to 2005. Similarly, Fulé, Laughlin & Covington (2005) found significantly higher alien cover in restoration treatments than in untreated areas 5 years after treatment application in south-western USA ponderosa pine forests. The ability of aliens to persist at least several years following treatment and to contribute heavily to the seed bank (Halpern, Evans & Nielson 1999) may complicate future restoration efforts, especially given that restoration treatments are not a one-time event but a series of re-entries (disturbances) over time (Arno *et al.* 1995; Allen *et al.* 2002). Conversely, the initial disturbances resulting from restoration treatments are probably the most intense, given that treatments must address many decades of vegetation development since the last disturbance (Arno *et al.* 1995). Further study and monitoring are needed to better understand the longer-term consequences of alien invasion.

SYNTHESIS AND APPLICATIONS

Alien and transformer species increased in all restoration treatments, underscoring the importance of post-treatment monitoring for early detection of invasion so that problematic treatments can be modified (Harrod 2001). The significant response of alien species in the thin-burn treatment presents a management dilemma because of the multiple benefits that accrue with this treatment, which include killing fire-vulnerable Douglas-fir seedlings and saplings, reducing unnaturally high fuel build-ups, recycling nutrients bound in slash and down woody material and increasing the sprouting of important wildlife forage species. Land managers must weigh the benefits of restoration treatments against unwanted side-effects relative to their specific situations and management objectives. Although the response of alien species in this study was significant, it was modest in real terms (about a 2% increase in cover in the thin-burn) and similar to the 2–3% increase reported by Fulé, Laughlin & Covington (2005) 5 years after implementing a full thin-and-burn restoration treatment in Arizona, USA. Three years post-treatment, aliens comprised 8% of the total plant cover in the thin-burn, the most intense treatment in our study. In contrast, Crawford *et al.* (2001) reported that alien species comprised 26% of the total plant cover following wildfire in an Arizona ponderosa pine forest. Paradoxically, doing nothing or applying treatments that are not effective in reducing fire hazard may lead to even more invasion after stand-replacing wildfire (Griffis *et al.* 2001).

Transformer abundance was positively correlated with variables that indicate greater treatment intensity. If higher intensity treatments are necessary to accomplish restoration goals, then specific management strategies to reduce alien invasion may be required. For example, Korb, Johnson & Covington (2004) found that soil amendments and seeding with native plant species reduced alien plant dominance after intense burning of slash piles in south-western USA pine forests. Conducting thinning treatments over a winter snowpack can also reduce or eliminate soil disturbance (Gundale *et al.* 2005) and is a viable option over most of ponderosa pine's range. Limiting grazing by domestic animals several years before and after treatments is an additional strategy to limit invasion (Keeley 2006). On sites where intense treatments are not required, application of single treatments (burn-only or thin-only) or incremental treatments designed to move gradually toward more historical conditions (Allen *et al.* 2002) may be used to limit alien invasion.

Acknowledgements

We thank field crewmembers Kerry Metlen, Seth Kahn, Matt Judd, Tucker Bishop, Robert Nelson, Holly Miller, Doug Bushey, Amber Harrison, and Shelly Saras. This manuscript benefited from comments by Kerry Metlen and three anonymous referees. This research is contribution 109 of the National Fire Surrogates Project (FFS), funded by the US Joint Fire Science Program.

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Received 31 October 2005; final copy received 25 May 2006
Editor: Phil Hulme

Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Alien species.

Appendix S2. Environmental variables.

The Role of Fuel Breaks in the Invasion of Nonnative Plants

Scientific Investigations Report 2006–5185

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The Role of Fuel Breaks in the Invasion of Nonnative Plants

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Suggested citation:
Merriam, K.E., Keeley, J.E., and Beyers, J.L., 2007, The role of fuel breaks in the invasion of nonnative plants: U.S. Geological Survey Scientific Investigations Report 2006-5185, 69 p.

Executive Summary

Fuel reduction projects have become an increasingly important component of state and federal fuels management programs. However, an unintended result of some pre-fire fuel manipulation projects may be the introduction of nonnative invasive plants. The establishment of nonnative plants within fuel breaks is a serious concern because the presence of invasive species in areas treated to reduce fuels could make adjacent wildland areas more susceptible to invasion, particularly following widespread disturbances such as fires.

This report presents the results of a research project investigating the relationship between fuel reduction treatments and the invasion of nonnative plants. Throughout the rest of this document, we will collectively refer to these treatments as *fuel breaks,* although we sampled a range of fuel breaks described variously as fuel breaks, shaded fuel breaks, defensible fuel reduction zones, defensible fuel profile zones, fuel reduction projects, fuel management zones, wildfire protection zones, and community protection zones.

Antelope Border Defensible Fuel Profile Zone (DFPZ),
Plumas National Forest

In **Chapter One** we discuss overall results compiled from 24 separate fuel breaks located across California. These fuel breaks represent a variety of different construction and maintenance methods, and different fire histories. Our primary findings were:

- Fuel breaks may promote nonnative plants.
- Fuel breaks with more canopy and ground cover may be less likely to be invaded.
- Nonnative plants were more abundant adjacent to older fuel breaks and in areas that had experienced more numerous fires.
- Native species may also be promoted by fuel breaks, particularly native annual forbs and grasses.

Our data suggest that fuel breaks provide establishment sites for nonnative plants, and that surrounding areas may be susceptible to invasion, particularly after disturbances such as fire. Fuel break construction and maintenance methods that leave some overstory canopy cover and minimize exposure of bare ground may be less likely to promote nonnative plant invasion.

Etz Meloy fuel break, Santa Monica Mountains National Recreation Area

In **Chapter Two** we evaluate the association between nonnative plants and fuel breaks within vegetation types, including mixed coniferous forest, oak woodland, chaparral, and coastal scrub plant communities. We found that:

- Nonnative abundance and species richness was significantly different among vegetation types: conifer forests had the lowest nonnative cover and richness while coastal sage scrub had the highest.
- Differences in elevation, fire history, grazing, canopy cover, and disturbance history may explain some vegetation type differences.
- Nonnatives were significantly more abundant on fuel breaks in all vegetation types.
- Fuel break construction method was associated with nonnative abundance in all vegetation types.
- Fire and grazing was positively associated with nonnative abundance in all vegetation types with adequate sample sizes to evaluate these factors.

This analysis suggests that although different vegetation types experience varying degrees of invasion by nonnatives, our general recommendations described in Chapter One also may be applied within individual vegetation types. Fuel break construction and maintenance methods that retain some overstory canopy and minimize the exposure of bare ground will likely minimize the probability of nonnative invasion across vegetation types.

In **Chapter Three** we provide a brief summary of each individual fuel break sampled in this study. Each site had a unique history, including various dates of construction and construction methods, different maintenance regimes, varying fire histories, and different land use histories. Our general findings were:

- Individual sites differed greatly in nonnative cover, fire history, and environmental variables.
- Nonnative cover was higher within fuel breaks than in adjacent wildlands at 19 of our 24 study sites.
- Fuel breaks that were not invaded by nonnatives had very deep duff layers, were constructed by methods other than bulldozing, were very young, or had very infrequent maintenance regimes.
- Cheatgrass (*Bromus tectorum*) was the most common nonnative plant species at 8 of our study sites.
- A number of different nonnative species dominated the other 16 sites, suggesting that many nonnative species may be well adapted to take advantage of the disturbed conditions associated with fuel breaks.

Our site level review suggests that fuel breaks may create conditions favorable to a number of different nonnative plant species. The colonization of a fuel break by a particular species may reflect which species has a nearby seed source or is able to disperse into the treated area. Regardless of which nonnative species is of greatest concern in the region, retaining overstory canopy and ground cover will likely be the best way to prevent nonnative invasion on fuel breaks.

When reviewing this report, please remember that our study was observational and additional research using controlled, replicated experiments will be necessary to fully understand the mechanisms that influence nonnative plant invasion within fuel reduction treatments.

Aguanga fuel break, Cleveland National Forest

Acknowledgments

We would like to thank the Joint Fire Science Program for funding this study (project #01B-3-2-08). Sequoia and Kings Canyon National Parks were instrumental in supporting our research. This project would not have been possible without the generous cooperation of the Angeles, Cleveland, Lassen, Los Padres, Mendocino, Plumas, San Bernardino, Sequoia, Shasta-Trinity, Sierra, Six Rivers, and Lake Tahoe Basin Management Area USDA National Forests; the Whiskeytown and Santa Monica National Recreation Areas; the San Luis Obispo District of the California Department of Forestry and Fire Protection; the Bakersfield District of the Bureau of Land Management; the Los Angeles County Fire Department Division of Forestry; and the Orange County Department of Parks, Casper's Wilderness Park. We also want to thank Katie VinZant, Lea Condon, Clara Arndt, Trent Draper, and Elizabeth Martin for their expert field assistance.

Canterbury bells *(Phacelia minor)* in the Cleveland National Forest

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Chapter One: Overall Results

Reduction of hazardous fuels has become a priority for federal, state, local, and private land managers across the United States. High fuel loads resulting from fire suppression, population growth at the wildland-urban interface, and large catastrophic fires have focused unprecedented national attention on pre-fire fuel manipulation projects. As a result, a growing number of federal, state, and local fuel reduction programs have dramatically increased the number of hectares (acres) treated to reduce fuels nationwide, and extended the scope of these projects to include a wider range of vegetation types and treatment prescriptions.

Fuel reduction treatments are generally implemented to change fire behavior, to provide firefighter access, as an anchor point for indirect attack on wildland fires, or to contain prescribed fires (Agee and others, 2000). They range in configuration from narrow linear features along individual ridge lines, to large landscape-scale treatments spanning thousands of acres. The amount of surface and ladder fuels removed within these treatments can vary widely, with reduction of overstory canopy cover ranging from complete to less than 40%.

Here, we will collectively refer to these treatments as *fuel breaks,* although they have been variously termed shaded fuel breaks, defensible fuel reduction zones, defensible fuel profile zones, fuel reduction projects, fuel management zones, wildfire protection zones, and community protection zones. Fuel break construction and maintenance methods have changed over time, and differ according to terrain, vegetation type, and implementing agency (Los Angeles County Fire Department 1962; Omi 1979). For example, fuel break maintenance by aerial application of herbicides and seeding with nonnative grasses was common until the 1970s (Bentley 1967; Clark 1973; Edmunson & Cornelius 1961; San Diego County 1974; US Department of Agriculture 1959, 1960). More recent fuel break construction and maintenance measures include selective thinning, mastication, and increased use of prescribed burning (Farsworth & Summerfelt 2002).

An unintended consequence of large-scale fuel break construction of new fuel breaks, and increased maintenance of existing fuel breaks, may be the establishment of nonnative plant species. A number of studies have documented an association of nonnative plant species with disturbed areas similar to fuel breaks, such as logging sites, roads, trails, and pipeline corridors (e.g., D'Antonio and others, 1999).

These disturbance corridors can promote the invasion of surrounding areas by providing a nearby seed source (Gelbard & Belnap 2003; Parendes & Jones 2000; Tyser & Worley 1992; Zink and others, 1995). Wildland areas adjacent to fuel breaks might be particularly susceptible to invasion following landscape-scale disturbances such as fire, because fire has been shown to promote the invasion of nonnative plants in a number of habitats (D'Antonio 2000). In many cases invading species are well adapted to fire and can invade fire prone ecosystems, particularly when natural fire regimes have been altered through fire suppression, increased anthropogenic ignitions, or by feedback effects with changes in plant species composition (D'Antonio and Vitousek 1992; Keeley 2001).

In this study we evaluated the potential for fuel breaks to function as establishment sites for nonnative plants, and for nonnative species to invade surrounding wildland areas (see Text Box 1-1). The goals of this research were to provide fire and resource managers with information to develop fuels management strategies that both accomplish fuel hazard reduction goals and minimize the potential for nonnative plant invasion.

Text Box 1-1: Our primary research questions were:

- ***Do plant communities differ within fuel breaks compared with adjacent wildland areas?***
- ***What environmental and anthropogenic factors are correlated with the abundance of nonnatives?***
- ***Are nonnative species more abundant in areas adjacent to fuel breaks after disturbances such as fire?***

METHODS

We investigated 24 fuel breaks across the State of California (Figure 1-1). Study sites were located primarily in the Sierra Nevada and coastal mountain ranges, including coastal scrub, chaparral, oak woodland, and mixed coniferous forest vegetation types ranging in elevation from 200 to 2000 m.

The fuel breaks varied in age from those constructed by the Civilian Conservation Corps during the 1930s to fuel reduction projects implemented as recently as 2003. We attempted to include fuel breaks constructed by a variety of different methods such as bulldozers, mechanical equipment, and hand crews. Mechanical equipment included rubber tired and tracked vehicles used for thinning and mastication of forest and chaparral vegetation; hand crews relied primarily on hand tools such as shovels, Pulaskis, McCleods, and other hand line construction tools.

The land use history of each study site was complex, and we could not control for many of the disturbance related factors that may have affected nonnative abundance on the fuel breaks we studied. Additional information about each fuel break is provided in Chapter Three.

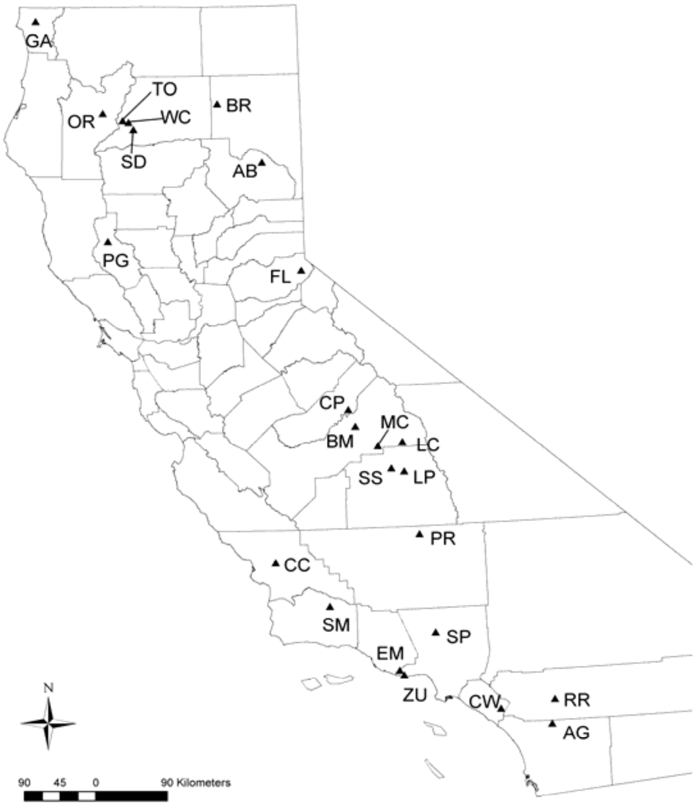

Figure 1-1. Map of 24 fuel breaks study sites across the State of California. Site codes are explained in Table 3-1.

Sampling Protocol

Data were collected during the spring and summer of 2002 and 2003. At each site we established between 8 and 10 transects perpendicular to the fuel break, beginning at the origin nearest a road or urban interface, and continuing at discrete intervals of between 200 and 1500 m, depending on the total size of the treated area. Transects were 50 m in length, extending 10 m towards the center of the fuel break and 40 m into the surrounding vegetation. Two 1 m^2 plots were placed inside the fuel break, and four 1 m^2 plots were placed in the adjacent wildland area at discrete distances of 5, 10, 20, and 40 m from the edge of the fuel break (Figure 1-2).

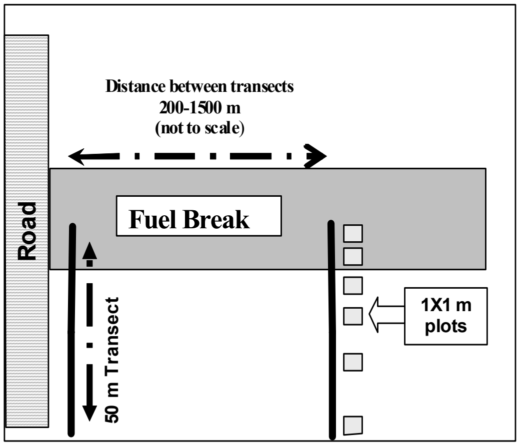

Figure 1-2. Diagram of transect orientation along fuel break and quadrat locations along transects.

We collected a range of data at each fuel break (see Text Box 1-2). We estimated species cover by cover class according to Daubenmire (1959), and estimated the density of each species, including overstory trees and shrubs. All plants were identified according to Hickman (1993). Plant communities were identified according to categories developed by Sawyer and Keeler-Wolf (1995).

Data on fire history was obtained from a state-wide fire perimeter GIS data layer containing fires recorded since 1953 (California Department of Forestry and Fire Protection 2003), and from individual cooperators when available. Information about the distance and density of roads and urban interfaces to our plots was generated from GIS data layers using the ArcView Spatial Analyst extension (ESRI 2000). Information about fuel break age, construction and maintenance methods, and grazing history were obtained from GIS data, environmental and biological assessments, resource management plans, fire incident reports, and agency technical reports. Additional information was collected through personal communications with fuels and fire managers, botanists, range managers, and other staff familiar with each site.

Text Box 1-2. Data Collected:

At each plot:
- Species composition, cover and density
- Ground cover (bare ground, litter, etc.)
- Overstory canopy cover
- Litter and duff depth

At the end points of each transect:
- Soil nitrogen, carbon, moisture
- Slope, aspect, elevation
- Fire and grazing history
- Distance to roads and Wildland Urban Interface (WUI)
- Fuel break age, construction, and maintenance
- Vegetation type

Data Analysis

We used a number of different statistical methods to analyze the data we collected, including paired t-tests, Analysis of Variance (ANOVA), and multiple regressions. Data analysis was performed using SYSTAT version 10 (SPSS 2000). Residuals from each analysis were plotted to identify outliers and evaluate homogeneity of variance (Wilkinson and others, 1996). Percentage values were arcsine square root transformed to improve normality and homogeneity of variance. Sites were not equally distributed across all vegetation types, or with past land use such as grazing and fire history, and some data was missing, so N-values reported for different analyses below may vary.

RESULTS

We identified 736 plant species in our 1 m^2 plots both in and adjacent to 24 separate fuel breaks. Approximately 85% were native, 11% were nonnative, and 4% could not be identified due to dessication, phenology, or lack of plant material. Fifty-one percent of our quadrats contained no nonnative plants. The most frequently occurring nonnative plant was cheatgrass. Our primary findings are summarized in Text Box 1-3, and more detailed results are provided in the sections that follow.

Text Box 1-3. Our primary findings were:

- Nonnative plants had higher relative cover, density, species richness, and diversity within fuel breaks than in adjacent wildlands.
- Some fuel breaks are less likely to support nonnative species, particularly those with more overstory canopy and ground cover.
- Nonnative plants are more abundant adjacent to older fuel breaks and in areas that have experienced more numerous fires.
- Native species diversity was also higher in fuel breaks.
- Both nonnative and native annual forbs and grasses were more abundant in fuel breaks than in adjacent wildlands.
- Nonnative plants were generally more common on fuel breaks, but some species showed no response.
- Native species were generally more common outside fuel breaks, but some species were more abundant in fuel breaks.

1. Nonnative cover, density, and species richness

Absolute and relative nonnative cover, density, and species richness were significantly higher on fuel breaks than in adjacent areas outside of fuel breaks (Figure 1-3).

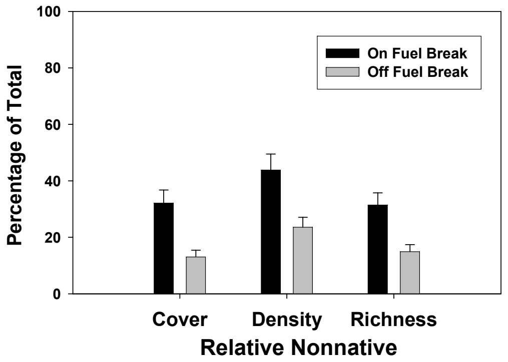

Figure 1-3. MANOVA found that relative nonnative cover, density, and species richness (expressed as the percentage of total plant cover, density, and richness) was significantly higher on fuel breaks compared with sites outside fuel breaks (N= 48, df=3, 44, F= 5.645, *P*<0.001). Error bars indicate + 1 SE.

Nonnatives occurred more frequently on fuel breaks, where they were found in 65% of quadrats, compared with outside of fuel breaks, where only 43% of quadrats contained nonnative plants.

2. Differences among fuel breaks

Elevation, slope, duff depth, overstory canopy, bare ground, litter cover, and rock cover were significantly associated with the presence and abundance of nonnative plant species (Table 1-1).

Table 1-1. Multiple linear stepwise regression analysis of the relationship between environmental variables and relative nonnative plant cover across all quadrats where nonnatives were found.

Effect	Standard Coefficient	Tolerance	T	P
Constant	0.000		29.25	<0.001
Canopy cover (%)	-0.354	0.763	-10.00	<0.001
Elevation	-0.229	0.895	- 7.02	<0.001
Bare ground (%)	-0.129	0.739	- 3.58	<0.001
Slope (%)	-0.097	0.722	- 2.66	0.008
Litter cover (%)	-0.094	0.651	- 2.46	0.014
Transect	0.076	0.741	2.13	0.034
Site	0.067	0.975	2.14	0.032

Notes: Variables with *P (probability)*>0.15 were removed from the model, including rock cover, litter depth, and duff depth (N=754, adjusted multiple r^2=0.281, standard error of estimate=0.225). The T-value is the estimate divided by its standard error.

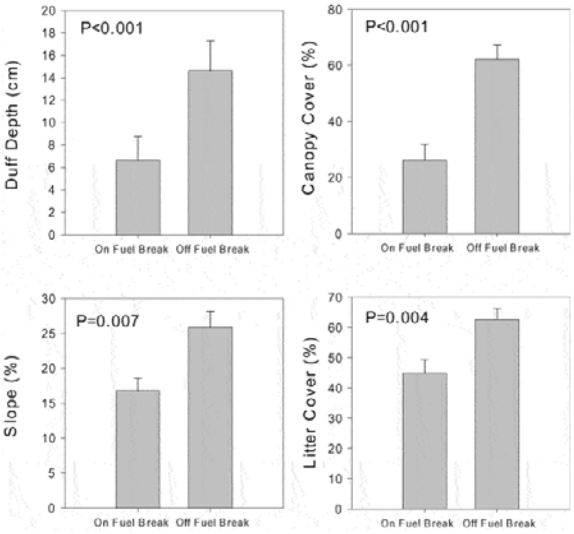

Figure 1-4. MANOVA found that environmental variables associated with nonnative plant presence and abundance were significantly different on and off fuel breaks (N=48, df=4, 43, F=4.165, P=0.002). Error bars indicate + 1 SE. Univariate *P*-values shown on graphs.

Several of these variables were significantly lower in quadrats on fuel breaks (Figure 1-4).

The anthropogenic variables of fuel break construction method, maintenance method, maintenance frequency, fuel break age, and distance to roads were significantly associated with relative nonnative cover on fuel breaks (Table 1-2).

Table 1-2. Multiple linear stepwise regression analysis of the association between anthropogenic variables and relative nonnative plant cover on fuel breaks.

[Data represent plots on the fuel break only, pooled to provide one value per transect]

Effect	Standard Coefficient	Tolerance	T	P
Constant	0.000		14.44	<0.001
Construction Method	-0.631	0.698	13.49	<0.001
Maintenance Frequency	0.221	0.733	4.84	<0.001
Site	0.121	0.821	2.82	0.005
Fuel Break Age	0.084	0.711	1.82	0.071
Maintenance Method	0.068	0.892	1.64	0.103
Distance to Roads	-0.062	0.925	1.53	0.127

Notes: Variables dropped from the multiple stepwise linear regression as not being significant at $P>0.15$ included distance of the fuel break to urban interfaces, prescribed burning, and use of precautions against nonnative invasion such as washing equipment ($N=220$, adjusted multiple $r^2=0.666$, standard error of estimate= 0.207).

Fuel breaks constructed by bulldozers had significantly higher relative nonnative cover than fuel breaks constructed by hand crews, and fuel breaks thinned mechanically had significantly lower relative nonnative cover than fuel breaks constructed by other means, even with elevation and slope included as covariates (Figure 1-5).

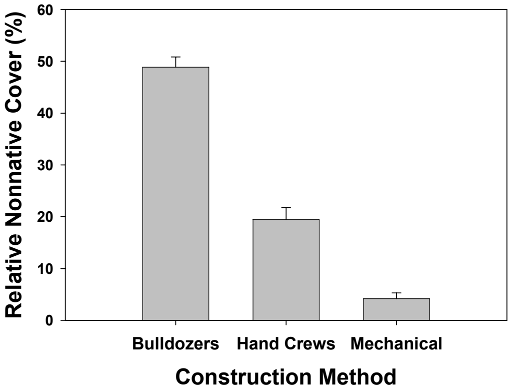

Figure 1-5. Differences in relative nonnative cover with fuel break construction method. Error bars indicate + 1 SE. The effect of construction method was significant based on Analysis of Covariance (ANCOVA) with slope and elevation as covariates (N=220, effect of construction method: df=2, 217, F=118.655, *P*<0.001).

Fuel break constructed by bulldozer, Santa Monica Mountains National Recreation

Environmental variables significantly associated with nonnative cover, including overstory canopy cover, litter cover, duff depth, and bare ground, also varied significantly among fuel breaks constructed by different methods (Figure 1-6). Fuel breaks constructed by bulldozers had the least duff depth, litter cover, and canopy cover of any fuel break construction method.

The presence of nonnatives also was associated with fuel break construction method; 49% of quadrats contained nonnatives on fuel breaks constructed by bulldozers, compared with 20% of quadrats on fuel breaks constructed by hand crews, and only 4% of quadrats on mechanically thinned fuel breaks contained nonnative species.

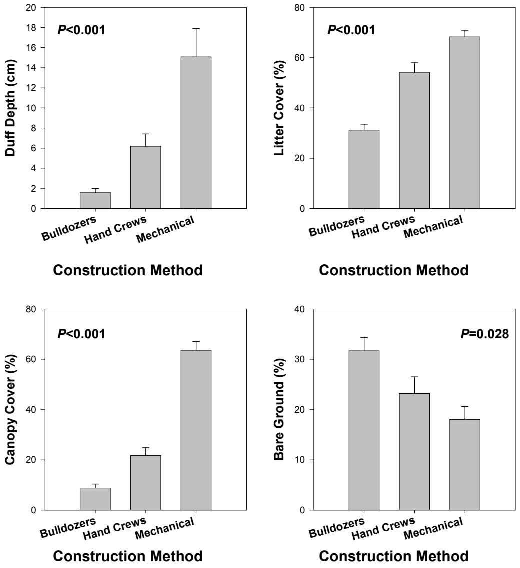

Figure 1-6. Relationship between fuel break construction method and environmental variables significantly associated with nonnatives, including duff depth, litter cover, canopy cover, and bare ground were determined using MANOVA (N=220, df=4, 214, F=11.608, *P*<0.001). Univariate *P*-values are indicated on graphs. Error bars represent + 1 SE.

This mechanically cleared fuel break in Whiskeytown National Recreation Area maintained some overstory canopy cover and ground cover.

3. Patterns adjacent to fuel breaks

Relative nonnative cover significantly declined with distance from the fuel break, and this effect was more significant with fuel break age category (Figure 1-7).

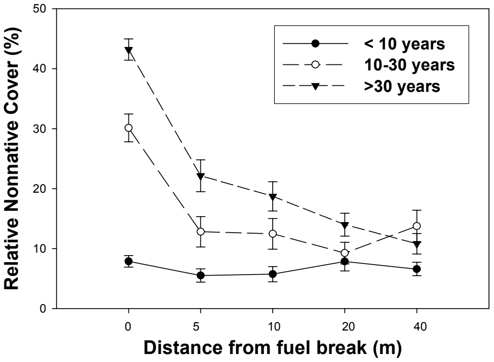

Figure 1-7. Two-way ANOVA found significant differences in relative nonnative abundance with distance from the fuel break and with fuel break age (interaction effect with plot distance nested within transects, N=1543, df=12, 1523, F = 15.377, *P*<0.001). Error bars represent + 1 SE.

The relationship between relative nonnative cover and distance from the fuel break was also influenced by number of fires (Figure 1-8). In the absence of fire, relative nonnative abundance in wildland areas adjacent to fuel breaks did not change with increasing distance from the fuel break. However, in areas that had experienced one or more fires, relative nonnative abundance in wildland areas adjacent to fuel breaks significantly declined with increasing distance from the fuel break.

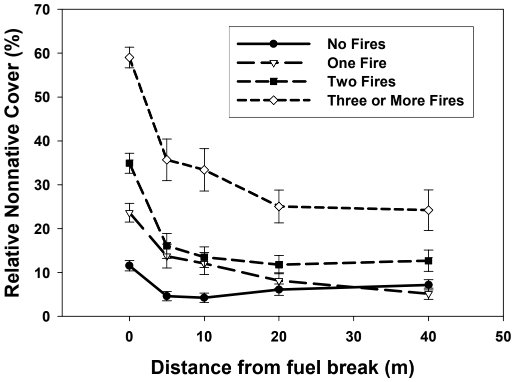

Figure 1-8. Two-way ANOVA found significant differences in relative nonnative cover with distance from fuel break and with the number of fires (interaction effect with plot distance nested within transects, N=793, df=12, 773, F=2.366, *P*<0.001). Error bars represent + 1 SE.

4. Species Diversity

Both native and nonnative species diversity was higher within fuel breaks than in adjacent wildland areas (Figure 1-9), and native and nonnative diversity were significantly positively correlated (Pearson correlation=0.326, *P*=0.024).

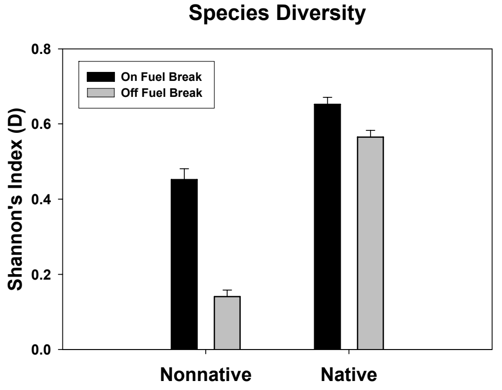

Figure 1-9. Both native and nonnative species diversity was significantly higher on fuel breaks according to paired t-tests. (native species diversity: t=2.983, df=216, *P*=0.003, nonnative species diversity: t=10.284, df=217, *P*<0.001)

Nonnative species diversity at the site level was most strongly correlated with duff depth and elevation, and together these variables explained over half of the variation in nonnative diversity (adjusted multiple R^2=0.521). Duff depth and bare ground were most strongly correlated with native diversity at the site level, although the explanatory power of these variables was lower (adjusted multiple ^{2} = 0.211).

5. Life history types

Fuel breaks were characterized by higher numbers of annual plant species than adjacent wildland areas, including native and nonnative grasses and forbs, which were significantly more common in treated areas than in adjacent wildlands (Figure 1-10). Native perennial forbs and nonnative perennial grasses also were significantly more common on fuel breaks. Native trees, shrubs, and subshrubs were more common outside of fuel breaks. We did not encounter any species of nonnative trees, and only two species of nonnative shrubs and five species of nonnative perennial forbs were sampled in this study.

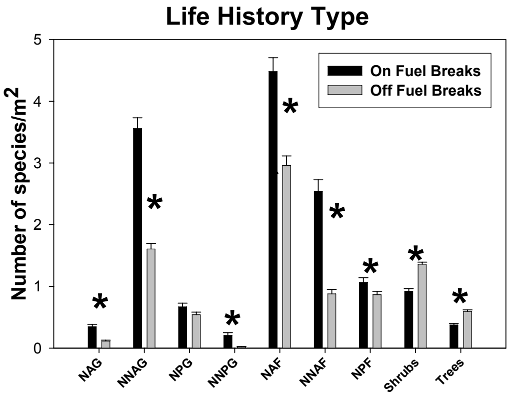

Figure 1-10. Differences between fuel breaks and adjacent wildland areas in the number of species from each life history type were evaluated using paired t-tests (**NAG**=Native annual grass, **NNAG**=nonnative annual grass, **NPG**=native perennial grass, **NNPG**= nonnative perennial grass, **NAF**=native annual forb, **NNAF**= nonnative annual forb, **NPF**= native perennial forb). Error bars indicate + 1 SE. Significantly different means indicated with an asterisk and determined by Bonferroni adjusted method with significance level at *P*=0.006 for nine comparisons.

6. Variation among nonnative species

Of the 79 nonnative species we identified, 21 (26.6%) only occurred on fuel breaks, and 9 (11.4%) were restricted to plots in wildland areas. Of the 32 nonnative species found in 10 or more plots, 17 were statistically equivalent in cover both on fuel breaks and in adjacent wildland areas, and 15 were more common on fuel breaks. Six of the ten most common nonnatives were equally common on fuel breaks and in adjacent wildlands (Table 1-3). The nonnative species we observed were primarily annual grasses and forbs.

Table 1-3. Differences in mean cover on and off fuel breaks of the ten most frequently occurring nonnative plant species.

[Differences between mean cover in wildland areas (OFF), and inside areas treated to reduce fuels (ON) were evaluated using paired t-tests, and significance was determined using Bonferroni adjusted *P* value of 0.005. Species with *no significant difference* in abundance are shown in **bold]**

Scientific Name	# of plots	Mean OFF	Mean ON	P
Bromus tectorum	**244**	**1.4169**	**1.8157**	**0.041**
Bromus madritensis	**223**	**1.9604**	**2.3**	**0.237**
Vulpia myuros	**217**	**1.2763**	**2.2591**	<0.001
Bromus hordeaceus	**184**	**1.1588**	**2.5721**	<0.001
Bromus diandrus	**177**	**1.9572**	**2.136**	**0.570**
Erodium cicutarium	**150**	**0.6409**	**3.1544**	<0.001
Torilis arvensis	**122**	**1.6898**	**1.4028**	**0.313**
Centaurea melitensis	**99**	**1.613**	**2.375**	**0.051**
Aira caryphyllea	**82**	**1.303**	**1.876**	**0.229**
Avena barbata	**79**	**0.816**	**2.645**	<0.001

7. Variation among native species

Of the 551 native species observed in this study, 142 (25.8%) only were found outside of fuel breaks, while 108 (19.4%) only occurred inside fuel breaks. Of the 178 native species that were found in ten or more plots, 46 were statistically more common outside of fuel breaks, 12 species were more common inside fuel breaks and 111 native species did not differ in abundance in fuel breaks compared with adjacent wildland areas. Native species that were more common on fuel breaks were found in all vegetation types and represented a range of life history types, including annual grasses, annual forbs, perennial forbs, subshrubs, and shrubs (Table 1-4).

Both native and nonnative species may be found on fuel breaks, such as this one in the Sierra National Forest.

Table 1-4. Native species that were significantly more common on fuel breaks, based on paired t-tests.

[Life history abbreviations are **AG**=annual grass, **AF**=annual forb, **PF**= perennial forb, **SS**=subshrub, and **S**=shrub. Vegetation type abbreviations are **CF**=coniferous forest, **OW**=oak woodland, **CH**=chaparral, and **CS**=coastal sage scrub. Significance assessed with Bonferonni adjusted *P* value of 0.002 for 10 comparisons]

Scientific Name	Life History	Vegetation Type	P
Vulpia microstachys	**AG**	**CF, OW, CH**	**<0.001**
Lupinus bicolor	**AF**	**OW, CH, CS**	**<0.001**
Lotus strigosus	**AF**	**CH, CS**	**0.002**
Lotus argophyllus	**PF**	**CF, CH**	**0.001**
Epilobium brachycarpum	**AF**	**CF, OW, CH**	**<0.001**
Trifolium albopurpureum	**AF**	**OW, CH, CS**	**0.001**
Lotus purshianus	**AF**	**CF, OW, CH**	**0.001**
Lotus wrangelianus	**AF**	**CH, CS**	**0.002**
Eriophyllum lanatum	**SS**	**CF, OW,**	**0.002**
Micropus californicus	**AF**	**OW, CH,**	**0.002**
Arctostaphylos glandulosa	**S**	**CH**	**0.001**
Madia glomerata	**AF**	**OW, CH**	**0.001**

DISCUSSION

Pre-fire fuel manipulations, such as fuel breaks, are an important component of fire management programs, particularly in areas where prescribed fire or wildland fire use is impractical. Our study demonstrates that fuel breaks have the potential to promote the establishment and spread of nonnative plants. The management implications of our findings are summarized in Text Box 1-4.

Text Box 1- 4. Some management implications of our findings are:

- Fuel breaks may promote nonnative plants.
- Fuel breaks with more canopy and ground cover may be less likely to be invaded.
- Nonnative plants are more abundant adjacent to older fuel breaks and in areas that have experienced more numerous fires.
- Native species may also be promoted by fuel breaks, particularly native annual forbs and grasses.
- Managers will have to balance maintaining natural disturbance regimes against the potential risk of nonnative invasion.

Blacks Ridge DFPZ, Lassen National Forest

1. Canopy and ground cover

We found that fuel breaks had significantly less overstory canopy, litter cover, and duff depth than adjacent wildland areas. These environmental variables were significantly associated with nonnative species presence and abundance. Removing overstory canopy within fuel breaks may benefit nonnative plants by reducing competition with natives and changing light, nutrient, and water levels (Berlow and others, 2003; McKenzie and others, 2000; Parendes & Jones 2000). Removing litter and duff and disturbing soils on fuel breaks could provide sites for nonnative plant establishment, stimulate seed germination, eliminate native seed banks, and disrupt soil profiles (Burke & Grime 1996; D'Antonio 1993; Hobbs & Atkins 1988). Removing litter and duff also may change the physical characteristics of the soil, such as temperature, moisture, and nutrient availability, in ways that benefit nonnative plants (Parker and others, 1993; Reynolds and others, 2001; Shaw & Diersing 1990). These findings suggest that fuel break construction and maintenance strategies that retain some overstory canopy and ground cover may reduce the establishment and widespread invasion of nonnative plants.

Fuel breaks might be constructed and maintained to retain overstory canopy and ground cover. We found that fuel breaks constructed by selective thinning had significantly lower nonnative cover and higher canopy and ground cover than those constructed by bulldozers. Fuel breaks with on-site chipping or mastication of fuels had deeper layers of litter cover and less exposed bare ground, which may have reduced nonnative germination and establishment at these sites. Increasing the time between fuel break maintenance might allow ground and canopy cover to increase and also lower the probability of nonnative invasion.

Altering the type of machinery used to construct and maintain fuel breaks might also influence patterns of invasion by nonnative plants. We found that even in relatively uninvaded vegetation types such as coniferous forests, use of bulldozers significantly increased the abundance of nonnative plants. Bulldozers have large blades specifically designed to remove surface soil layers, and may be more likely to introduce nonnative seeds into fuel breaks by disrupting soil seed banks and transporting seeds between sites.

The presence of overstory canopy cover and ground cover in a fuel break may be more important to preventing nonnative species invasion than employing specific methods of fuel break construction. For example, we might have expected that fuel breaks built by hand crews would be the least disturbed, but instead we found that these fuel breaks had significantly lower overstory canopy cover, litter cover, and duff depth than fuel breaks constructed by mechanical equipment. This result is consistent with the emphasis of hand crews on exposing bare mineral soil to construct effective fire lines. These fuel breaks had significantly higher cover of nonnatives than fuel breaks constructed by mechanical thinning.

2. Fuel break age and fire history

We found that nonnative cover decreased with distance from the fuel break, suggesting that fuel breaks act as sources of nonnative plant propagules in the invasion of adjacent areas. Fuel breaks may act as nonnative seed reservoirs because they support higher numbers of nonnative plants, and they also receive external inputs of seeds through vehicles, equipment, or humans traveling on them (Lonsdale & Lane 1994; Schmidt 1989; Tyser & Worley 1992).

Wildland areas adjacent to fuel breaks were more likely to be invaded by nonnative species when the wildlands had been subject to recurrent fires. Numerous studies have found that fire can promote nonnative plant invasion, even in fire adapted vegetation types (Brooks and others, 2004; Keeley 2001). Increased fire frequencies can kill native plants in fire prone ecosystems because native species develop life histories in response to specific fire frequencies; these native species may be extirpated when fires occur more frequently (Keeley & Fotheringham 2003; Moreno & Oechel 1991). The establishment of nonnative annual grass species, the most common nonnatives in our study, has been found to alter fuel characteristics such that fires become less intense and more frequent in many areas (Brooks and others, 2004; D'Antonio & Vitousek 1992; Keeley 2001). Reduced fire intensity on fuel breaks may increase the survivorship of nonnative seeds (Keeley & Fotheringham 2003). The establishment of nonnatives in fuel breaks could lead to feedback effects with fire that increase the abundance of nonnatives in fuel breaks and promote the invasion of surrounding areas.

We found nonnative plant abundance on fuel breaks and in adjacent wildlands continued to increase with fuel break age. Although some authors have suggested that dispersal does not limit alien plant abundance in later stages of invasion (e.g., Wiser and others, 1998), we found that fuel breaks may continue to provide inputs of alien propagules even after periods of 30 years. Giessow (1997) found a similar pattern in fuel breaks 80 years of age and older in coastal scrub habitats in southern California.

Post-fire regeneration along the
Rouse Ridge fuel break,
San Bernardino National Forest

3. Native species

Fuel management treatments may also promote native plants, particularly native annual forbs. Other studies have found that the native annual forbs respond positively to disturbances such as grazing (Hayes & Holl 2003) and fire (Safford & Harrison 2004). Annual plants may be better able to colonize disturbed areas because of their short life cycles and dormant seed banks. Six of the twelve native species that were more abundant on fuel breaks than in adjacent wildlands were in the Fabaceae family, which is known to have long-lived seed banks (Auld 1996; Holmes & Newton 2004).

We found that native and nonnative diversity were significantly correlated. Although it has been suggested that native diversity should be negatively related to nonnative diversity because diverse native plant communities may be more resistant to invasion by nonnative plant species, our results support the idea that natives and nonnatives respond similarly to habitat conditions such as heterogeneity, resource availability, and disturbance history (Levine & D'Antonio 1999; Stohlgren and others, 2003).

Disturbance related variables, including fire number, overstory canopy cover, and duff depth significantly influenced both native and nonnative plant species at our study sites, and both native and nonnative diversity was most strongly negatively related to the depth of the duff layer. The depth of duff and litter layers have been found to be important indicators of plant species richness, probably by controlling plant establishment and germination (Battles and others, 2001; Facelli 1991; Hayes & Holl 2003; Xiong & Nilsson 1999). Our data suggest that deep duff layers suppress both native and nonnative plant species.

Although many native trees and shrubs were more common outside of fuel breaks, there were native trees and shrubs that were either more common in fuel breaks, or equally common within fuel breaks and outside of fuel breaks. This may reflect selective application of treatments to avoid specific tree and shrub species of interest, such as Ponderosa pines (*Pinus ponderosa)*. Some shrub species may have adaptations such as stump sprouting that would allow them to persist in treated areas. Pine and other tree seedlings may be able to utilize germination sites and high light availability created in fuel breaks.

Many native species, particularly annual forbs, require periodic disturbance to persist in natural ecosystems. The best management regime for maintaining native plant diversity is likely one that restores natural disturbance processes of the frequency, intensity, and duration with which native species evolved.

It is important to emphasize that the relative abundance of nonnative species was significantly higher on fuel breaks, indicating that native plants represented a smaller proportion of the total plant community on fuel breaks. Land managers may have to weigh the benefits of maintaining natural disturbance regimes to restore some ecosystem processes against the potential risks of promoting nonnative invasives.

This study was observational, and there were many environmental and anthropogenic factors that we could not control for. Research using controlled, replicated experiments will be necessary to fully understand the mechanisms that influence nonnative plant establishment within pre-fire fuel manipulation projects and invasion into adjacent wildland areas. Here we have identified potentially important variables influencing patterns of nonnative abundance with respect to fuel breaks and suggested ways that the probability of nonnative invasion might be minimized. If these methods are strategically implemented as part of a long-term fuel reduction program, it may be possible to both achieve fuel management goals and reduce the probability of nonnative plant invasion on fuel breaks and in surrounding wildland areas.

Rouse Ridge fuel break, San Bernardino National Forest

Chapter Two: Vegetation Type Differences

INTRODUCTION

We examined fuel breaks in a number of different plant communities throughout the California floristic province. Each study site was dominated by different plant species, which we classified into four major vegetation types; mixed coniferous forest, mixed oak woodland, chaparral, and coastal scrub communities.

We found that a number of variables differed significantly among these four vegetation types. For example, the relative cover of nonnative plants was lowest in coniferous forests, greater in oak woodlands, even higher in chaparral vegetation types, and the highest in coastal scrub vegetation types (Figure 2-1).

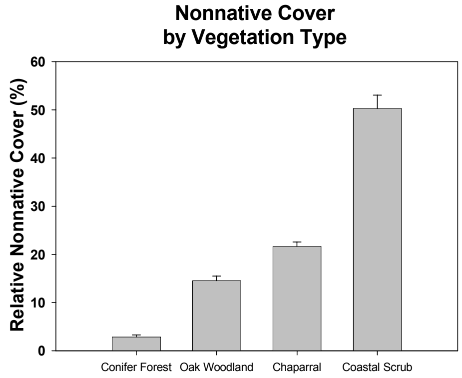

Figure 2-1. ANOVA indicated relative nonnative cover differed significantly among vegetation types (N=1543, df=3, 1539, F=150.7, *P*<0.001). Error bars represent + 1 SE.

Nonnative species richness was also significantly different among vegetation types. Coniferous forests had the lowest numbers of nonnative species of any vegetation type, followed by oak woodlands and chaparral. Coastal scrub vegetation types had the highest nonnative species richness of any vegetation type we studied (Figure 2-2).

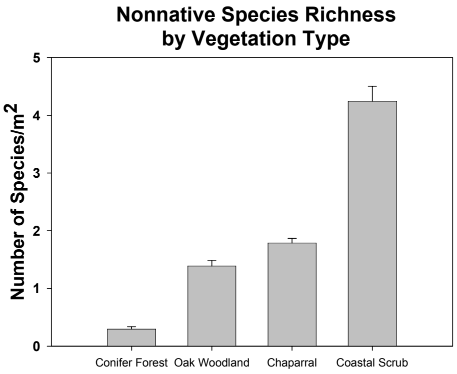

Figure 2-2. ANOVA found significant differences in nonnative species richness among vegetation types (N=1543,df=3, 1539, F = 124.726, *P*<0.001). Error bars represent + 1 SE.

Many environmental variables also varied among vegetation types. For example, the depth of the duff layer was highest in coniferous forests, lower in oak woodlands and chaparral vegetation types, and duff depth was lowest in coastal scrub vegetation types (Figure 2-3).

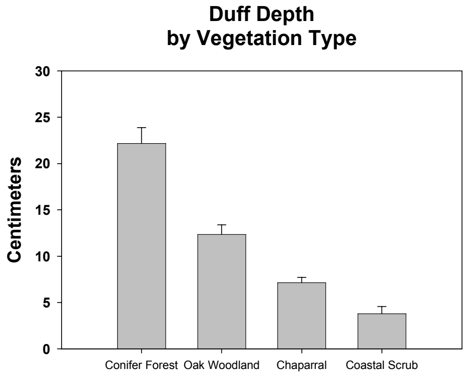

Figure 2-3. ANOVA found significant differences in duff depth among vegetation types (N=1498, df=3, 1493, F=31.955, $P<0.001$). Error bars represent + 1 SE.

Other environmental variables such as overstory canopy cover were significantly different in some vegetation types but not in others (Figure 2-4). Canopy cover was similarly high in coniferous forest and oak woodland plant communities, but lower in chaparral and coastal scrub vegetation types.

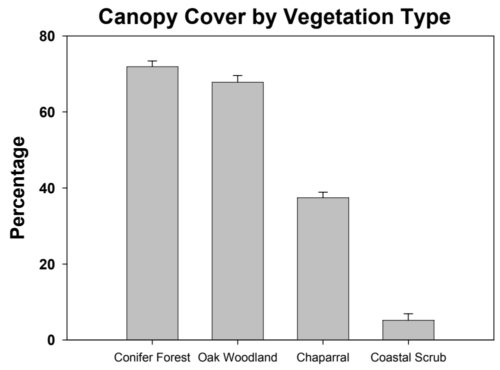

Figure 2-4. ANOVA on canopy cover found significant differences among vegetation types (N=1502, df=3, 1498, F=60.203, $P<0.001$).
Error bars represent + 1 SE.

Relative nonnative cover was much higher on fuel breaks in all vegetation types (Figure 2-5).

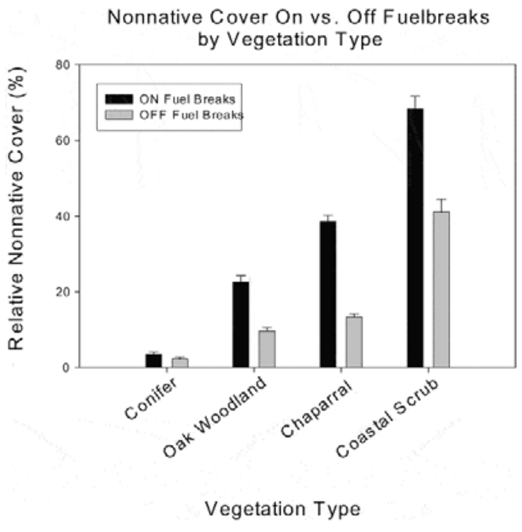

Figure 2-5. ANOVA determined that relative nonnative cover was significantly higher ON fuel breaks compared with OFF fuel breaks in all vegetation types (interaction effect: N=1543, df=3, 1535, F = 27.699, $P<0.001$).
Error bars represent + 1 SE.

Environmental variables that were significantly related to nonnative cover were associated with fuel breaks in each vegetation type. For example, duff depths were significantly higher outside of fuel breaks in each vegetation type (Figure 2-6). Plots on fuel breaks had significantly lower canopy cover in each vegetation type as well (Figure 2-7).

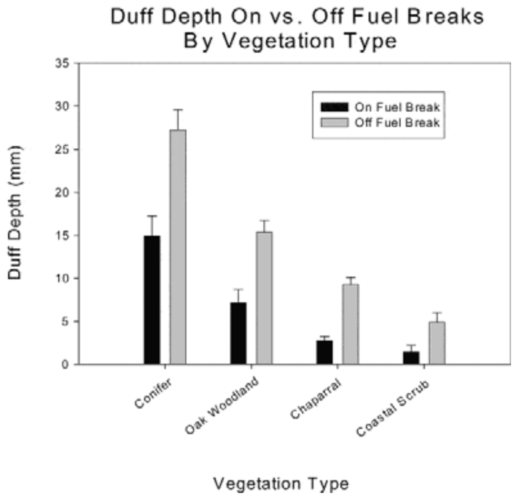

Figure 2-6. ANOVA found that duff depth was lower on fuel breaks within each vegetation type (interaction effect of vegetation type and position on or off fuel break: N=1498, df=3, 1490, F=29.72, P<0.001). Error bars represent + 1 SE.

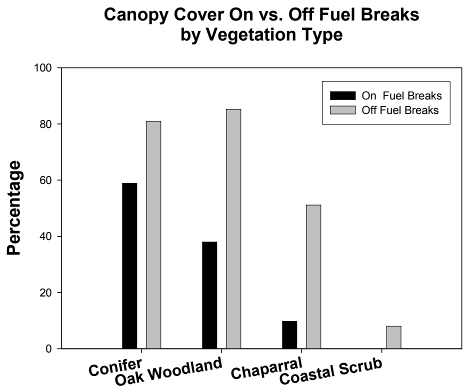

Figure 2-7. ANOVA found canopy cover was significantly lower on fuel breaks in each vegetation type (interaction effect of vegetation type and position on or off fuel break N=1502, df=3, 1494, F=19.116, P<0.001). Error bars represent + 1 SE.

These general results suggest that different vegetation types vary in abundance of nonnative plants, as well as environmental variables such as canopy and ground cover. However, despite these differences, the general pattern we found of increased nonnative abundance on fuel breaks, and associated patterns of decreased canopy cover and duff depth were evident within each vegetation type.

These results suggest that nonnative species may respond to fuel breaks in similar ways across vegetation types. Patterns of nonnative abundance within individual vegetation types are discussed in more detail below.

CONIFEROUS FOREST

There were six fuel breaks which contained mixed coniferous forest vegetation types, typically dominated by Ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense cedar (*Calocedrus decurrens*) and white fir (*Abies concolor*).

Coniferous forest vegetation type in the Plumas National Forest

Coniferous forest sites included the McKenzie Ridge fuel break in the Sequoia National Forest, the Pilot Grove fuel break in the Mendocino National Forest, the Fallen Leaf Lake fuel break in the Lake Tahoe Basin Management Area, portions of the Palos Ranches fuel break in the Sequoia National Forest, the Antelope Border defensible fuel profile zone in the Plumas National Forest, and the Blacks Ridge defensible fuel profile zone in the Lassen National Forest.

Our study sites within mixed coniferous forest vegetation types ranged in elevation from 1194 to 2017 m, and were constructed by mechanical thinning, hand crews, and bulldozers. These sites ranged in age from 1 to 42 years, and had experienced between 0 and 2 fires. At the time of our study, most of these sites were being grazed, and had been subject to logging in the past 50 years.

Coniferous forests had the lowest relative nonnative cover of the four vegetation types we identified (mean = 4.0% of total plant cover). This vegetation type was also characterized by significantly greater duff depths than other vegetation types, while canopy cover and litter depth were equivalent to oak woodlands, but higher than chaparral and coastal scrub habitats. We identified a total of 185 plant species in our 1m^2 plots in coniferous forest sites.

We found that fuel break construction method was significantly associated with relative nonnative cover in coniferous forests. Fuel breaks that had been constructed by bulldozers had significantly higher relative nonnative cover than sites constructed by other means. However, in coniferous forests, mechanically constructed fuel breaks and those constructed by hand crews had statistically similar cover of nonnative species (Figure 2-8).

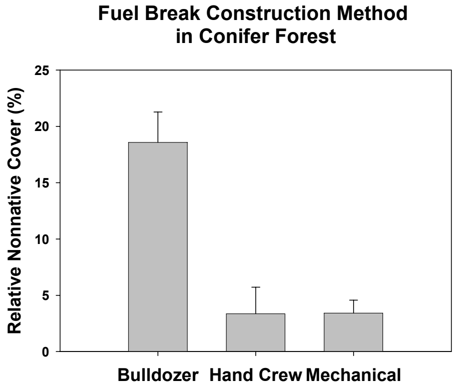

Figure 2-8. ANOVA found significant differences in relative nonnative cover among different construction methods in coniferous forests (N=39, df=2, 35, F=5.30, P=0.01). Error bars represent + 1 SE.

Coniferous forest vegetation types were the only plant communities where there was not a significant decline in relative nonnative cover outside of the fuel break when only unburned sites were considered. However, this pattern was significantly altered at sites that had experienced one or two fires (Figure 2-9). Conversely, areas that had experienced one or two fires had a significant increase of relative nonnative abundance, particularly in plots located closer to fuel breaks.

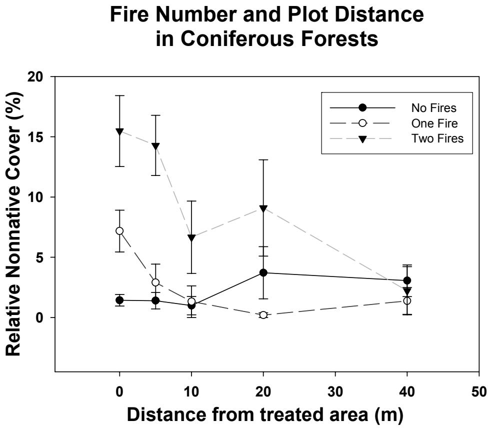

Figure 2-9. ANOVA found a significant interaction effect between fire number and distance from the fuel break on relative nonnative cover in coniferous forests (N=339, df=12, 325, F=3.789, *P* <0.001). Error bars represent 1 SE.

MIXED OAK WOODLANDS

We sampled nine fuel breaks that included mixed oak woodland vegetation types. These sites were typically dominated by black oak (*Quercus kelloggii*), canyon live oak (*Quercus chrysolepis*), and tan oak (*Lithocarpus densiflorus*) species.

Oak woodland vegetation type
in the Shasta Trinity National Forest

Fuel breaks within oak woodland plant communities included the Shepard Saddle and Lookout Point fire lines in Sequoia and Kings Canyon National Parks, the Oregon fire line in the Shasta Trinity National Forest, the Gasquet fuel break in the Six Rivers National Forest, the Cascadel Point and Burrough Mountain fuel breaks in the Sierra National Forest, the Shasta Divide fuel break in Whiskeytown National Recreation Area, the Pilot Grove fuel break in the Mendocino National Forest, and the Sierra Pelona fuel break in the Angeles National Forest.

Fuel breaks in oak woodland vegetation types spanned a wide range of elevations, including sites from 200 to 1400 m. They included fuel breaks constructed by mechanical thinning, hand crews, and bulldozers, and ranged in age from 1 to 82 years. Oak woodland sites had experienced between 0 and 3 fires. At the time of our study, about half (6 of 13 transects) of these sites were being grazed.

Oak woodlands had the second lowest relative nonnative cover of the four vegetation types we identified (mean = 25.0% of total plant cover), as well as the second lowest nonnative species richness. We identified a total of 313 plant species in our oak woodland sites. Oak woodlands had significantly higher species richness (at the 1m2 scale) than other vegetation types. Oak woodlands were comparable to coniferous forests in canopy cover, litter cover, and bare ground, but had significantly lower duff depth and litter depth than coniferous forest vegetation types. Oak woodlands had higher duff depth, litter depth, canopy cover, and litter cover than either chaparral or coastal scrub vegetation types.

We found that fuel break construction method was significantly associated with relative nonnative cover in oak woodland vegetation types (Figure 2-10). Fuel breaks that had been constructed by selective thinning and mastication in oak woodlands had significantly lower relative nonnative cover than fuel breaks constructed by other means.

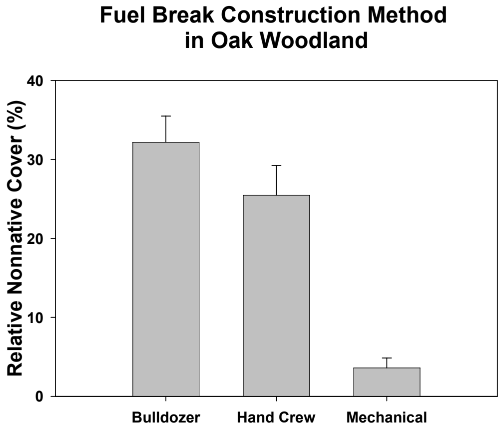

Figure 2-10. ANOVA found significant effect of construction method on relative nonnative cover in oak woodlands (N=57, df=2, 54, F=20.432, *P*<0.001). Error bars represent + 1 SE.

Relative nonnative cover in oak woodland vegetation types was significantly higher in areas that had experienced more numerous fires, and in plots that were closer to fuel breaks (Figure 2-11).

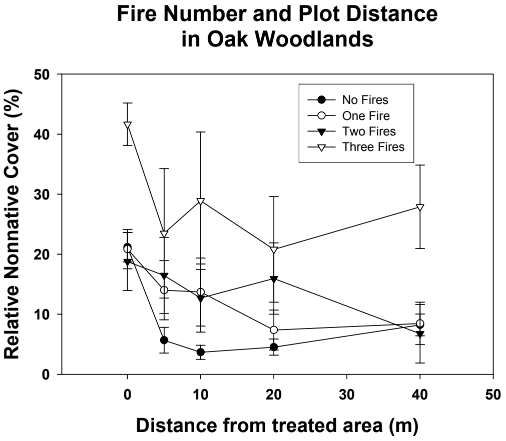

Figure 2-11. ANOVA found significant effects of fire number and distance from the fuel treatment on relative nonnative cover in oak woodlands (N=385, number of fires, df=3, 365, F=11.827, *P*<0.001; distance, df=4, 365, F=6.588, *P*<0.001). Error bars represent + 1 SE.

Relative nonnative cover also was significantly greater in oak woodland vegetation types that had been grazed, and this effect was significant at distances up to 40 m from the fuel break (Figure 2-12).

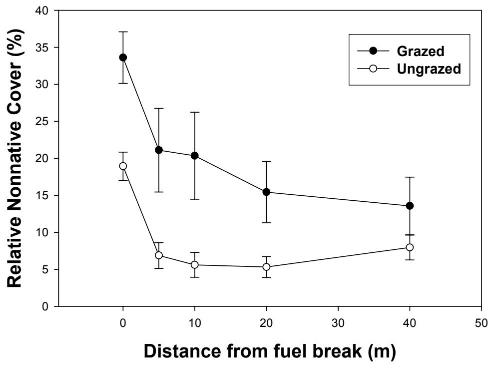

Figure 2-12. ANOVA found significant effect of grazing and distance from the fuel treatment on relative nonnative cover in oak woodlands (N=385, grazing effect: df=1, 375, F=29.991, *P*<0.001, plot distance effect: df=4, 375, F=13.018, *P*<0.001). Error bars represent + 1 SE.

CHAPARRAL

We studied 15 fuel breaks that contained chaparral vegetation types, typically dominated by chamise (*Adenostoma fasciculatum*), manzanita species (*Arctostaphylos spp.*), and scrub oak species (*Quercus spp.*).


Chaparral vegetation type in the Mendocino National Forest

Fuel breaks located in chaparral type plant communities included the Shepard Saddle, Lewis Creek, and Lookout Point fire lines in Sequoia and Kings Canyon National Park, the Oregon fire line in the Shasta Trinity National Forest, the Tower fire line and Whiskey Creek fuel breaks in the Whiskeytown National Recreation Area, the Pilot Grove fuel break in the Mendocino National Forest, the Sierra Pelona fuel break in the Angeles National Forest, the Calf Canyon Fuel Break administered by the Bakersfield District of the Bureau of Land Management, the Palos Ranches fuel break in the Sequoia National Forest, the Etz Meloy and Zuma Ridge fuel breaks in the Santa Monica National Recreation Area, the Sierra Madre Ridge in the Los Padres National Forest, the Rouse Ridge fuel break in the San Bernardino National Forest, and the Aguanga fuel break in the Cleveland National Forest.

Chaparral study sites ranged in elevation from 300 to 1600 m, and included fuel breaks constructed by mechanical thinning, hand crews, and bulldozers. These sites ranged in age from 1 to 51 years, and included areas that had experienced between 0 and 4 fires. About half (17 of 32 transects) of these sites are currently being grazed.

Chaparral had the second highest relative nonnative cover of the four general vegetation types we identified (mean=39.0% of total plant cover). Chaparral sites had significantly more exposed bare ground than any other vegetation type, and less ground cover than oak woodland or coniferous forest vegetation types. However, ground and canopy cover were significantly higher in chaparral than in coastal scrub vegetation types. We identified a total of 438 plant species in our $1m^2$ plots in chaparral vegetation types. Species richness at the $1m^2$ scale was statistically similar to coniferous forest and coastal scrub vegetation types.

We found that fuel break construction method was significantly associated with differences in relative nonnative cover in chaparral vegetation types (Figure 2-13). Fuel breaks constructed by bulldozers had significantly higher relative nonnative cover than fuel breaks constructed by other means.

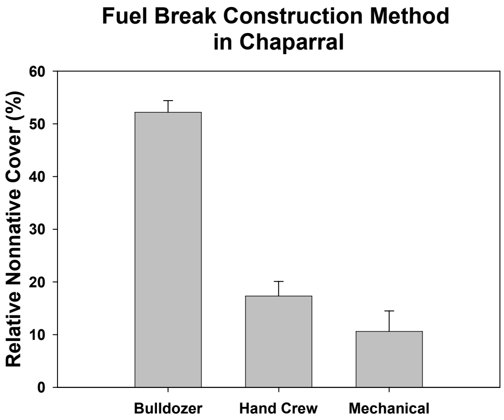

Figure 2-13. The effect of construction method on relative nonnative cover in chaparral vegetation types. ANOVA found significant differences (N=108, df=2, 105, F=58.294, *P*<0.001). Error bars represent + 1 SE.

Wildland areas adjacent to fuel breaks in chaparral vegetation types were more likely to have higher relative nonnative cover when they had experienced grazing or recurrent fires (Figures 2-14 and 2-15). There was a significant interaction effect between fire number and distance from the fuel break, while there was no interaction between grazing and distance from the fuel break. Distance to the fuel break was an important factor at all chaparral sites, and plots closer to fuel breaks had higher relative nonnative cover, even when those sites had experienced multiple fires or had been grazed.

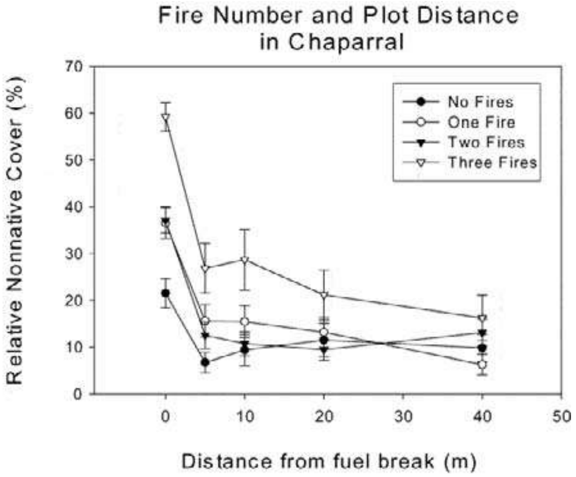

Figure 2-14. The effect of fire number and distance from the fuel treatment on relative nonnative cover in chaparral. ANOVA found significant interaction effect (N=720, df =12, 700, F=13.030, *P* <0.00), main effect of fire number (N=720, df=2, 700, F=15.365, *P*<0.001) and main effect of plot distance from fuel break (N=720, df=4, 700, F=48.314, *P*<0.001).
Error bars represent + 1 SE.

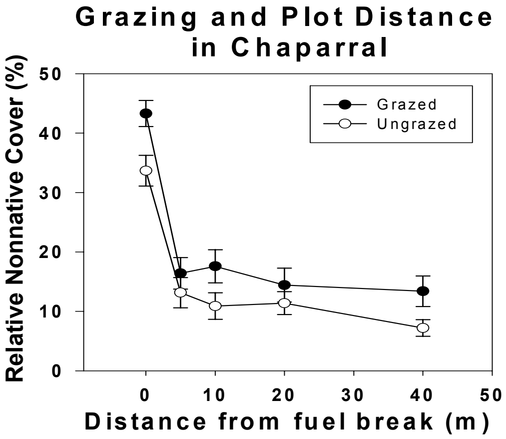

Figure 2-15. The effect of grazing and distance from the fuel treatment on relative nonnative cover in chaparral. ANOVA found significant main effects (grazing: N=719, df=1, 710, F=11.723, *P*<0.001, plot distance: N=719, df=4, 710, F=52.187, *P*<0.001). Error bars represent + 1 SE.

COASTAL SCRUB

There were only three fuel breaks that contained coastal scrub vegetation types, typically dominated by California sage (*Artemisia californica*), black sage (*Salvia mellifera*) and California buckwheat (*Eriogonum fasciculatum*).

Coastal scrub vegetation type in Casper's Wilderness Park

Coastal scrub plant communities were found at the Oso Ridge fuel break in Casper's Wilderness Park, Zuma Ridge fuel break in the Santa Monica National Recreation Area, and on a small portion of the Rouse Ridge fuel break in the San Bernardino National Forest.

Coastal scrub study sites were limited in elevation to below 700 m. All of these fuel breaks were constructed by bulldozers, and ranged in age from 19 to 55 years. We did not sample any unburned areas in coastal scrub vegetation types; all fuel breaks sampled had experienced between 1 and 5 fires.

Coastal scrub vegetation types had the highest relative nonnative cover of the four vegetation types we identified (mean=68.3% of total plant cover). Coastal scrub sites had significantly less duff depth, litter depth, canopy cover, and litter cover than other vegetation types.

We identified a total of 108 plant species in our 1m^2 plots at the three coastal scrub study sites we sampled in this study. Native species richness at the 1m^2 scale was statistically similar to coniferous forest and chaparral vegetation types. While many of the coastal scrub sites we sampled had experienced one or more fires during the past 50 years, very few of these sites were grazed. Therefore, we were not able to evaluate the effect of grazing within coastal scrub vegetation types; we found that fire number had no effect on relative nonnative cover. However, relative nonnative cover declined significantly with distance from the fuel breaks in coastal scrub vegetation types (Figure 2-16).

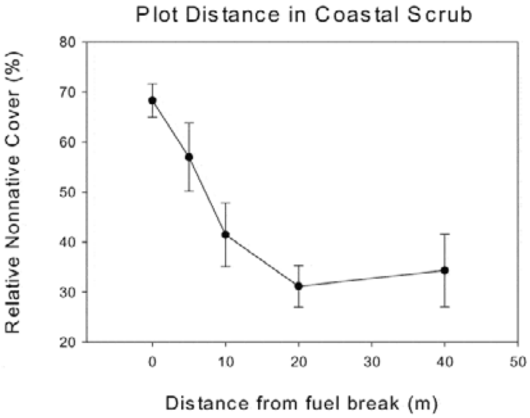

Figure 2-16. ANOVA found significant effect of distance from the fuel treatment on relative nonnative cover in coastal scrub vegetation types (N=95, df=4, 90, F=5.695, *P*<0.001). Error bars represent + 1 SE.

DISCUSSION

We found significant differences in relative nonnative cover and nonnative species richness among vegetation types. Vegetation type has been found to be among the most important factors influencing nonnative plant abundance, either because of the life history characteristics of the dominant plant community, or because of the association of different vegetation types with specific resources, such as soil nutrients or water availability (Aragon & Morales 2003; D'Antonio 1993; Larson and others, 2001; Mack 1989; Stohlgren and others, 2001).

The effect of vegetation type on nonnative abundance may be related to elevation. Our study sites in coniferous forests occurred at relatively high elevations (above 1000 m) and had the lowest relative cover of nonnatives. Conversely, the coastal scrub plant communities we sampled were located at relatively low elevations (generally below 300 m), and had the highest relative nonnative cover. Elevation has been found to be strongly negatively correlated with nonnative plant invasion in California, and most nonnative plants are not adapted to the climate at high elevations (Keeley and others, 2003; Schwartz and others, 1996).

The chaparral and oak woodland vegetation types we sampled in this study spanned a wide range of elevations (400–1600 m). We found that chaparral plant communities had higher nonnative plant cover and species richness than oak woodland sites. The difference in nonnative abundance between oak woodland and chaparral vegetation types may reflect differences in land use and disturbance history (Keeley 2000). For example, the chaparral sites we sampled had experienced more frequent fires than oak woodland sites. Chaparral sites also had significantly less duff depth and canopy cover, and more exposed bare ground than oak woodland sites.

Despite the strong influence of vegetation type on nonnative abundance and species richness, we found that a number of variables, including fuel break construction method, distance to the fuel break, fire number, and grazing still had significant effects on nonnative abundance when evaluated within individual vegetation types separately. This suggests that although important, vegetation type alone does not determine the abundance of nonnatives. We found that fuel breaks appear to promote nonnative abundance in all vegetation types, and this pattern may be compounded by more numerous fires or by grazing.

Text Box 2-1: Summary of Findings
Vegetation Type Differences

- Nonnative abundance and species richness differed among vegetation types.
- Elevation, fire, grazing, and disturbance history may have explained some differences among vegetation types.
- Nonnatives were significantly more common on fuel breaks in all vegetation types;
- Environmental variables such as canopy cover and duff depth were significantly lower outside of fuel treatments in all vegetation types.
- Fuel break construction method altered nonnative abundance in all vegetation types where it could be examined.
- Fire and grazing were associated with higher abundance of nonnatives in most vegetation types.

Chapter Three: Site Specific Results

INTRODUCTION

We sampled 24 different fuel breaks in this study, representing a wide range of vegetation types, construction and maintenance regimes, and grazing and fire histories. Table 3-1 provides a brief overview of the different fuel breaks sampled in this study.

Table 3-1. Selected characteristics of fuel breaks included in this study ordered from lowest to highest elevation.

[A range is shown for some variables because there were multiple transects on each fuel break, and individual transects often varied in year of construction, fire history, construction method, and vegetation type. Abbreviations are: NF = National Forest; SMNRA = Santa Monica National Recreation Area; WNRA = Whiskeytown National Recreation Area; CDF = California Department of Forestry and Fire Protection; BLM = Bureau of Land Management; SEKI = Sequoia and Kings Canyon National Parks, LTBMU= Lake Tahoe Basin Management Unit; MT= mechanical thinning, BD= bulldozer, HC= hand crews, CF=Coniferous Forest, OW=Oak woodland, CP=Chaparral, CS=Coastal Scrub]

Site Code	Site Name	Managing Agency	Elev. (m)	Year Constructed	Number of Fires	Construction Method	Vegetation Type	Grazing or Logging	UTM X, Y
GA	Gasquet	Six Rivers NF	202	1995	0-1	MT	OW	None	420382E 4631797N
ZU	Zuma Ridge	SMNRA	244	1952	3-5	BD	CS/CP	None	885589E 3774442N
CW	Oso Ridge	Casper’s Park	273	1963	2-3	BD	CS	None	1007681E 3730835N
WC	Whiskey Creek	WNRA	390	2001-2003	0	MT	CP	None	537636E 4499983N
TO	Tower	WNRA	447	1980	1-4	BD	CP	Grazed	530298E 4502212N
CC	Calf Canyon	CDF and BLM	474	1965-2002	1-3	BD	CP	None	723242E 3921383N
SD	Shasta Divide	WNRA	492	1985	0	BD	OW	None	543785E 4490521N
EM	Etz Meloy	SMNRA	652	1957	2-3	BD	CP	None	879828E 3780738N
OR	Oregon	Shasta-Trinity NF	922	2001	0	BD	OW	None	505186E 4511552N
SS	Shepard Saddle	SEKI	983	1960	2-3	BD	CP/OW	Grazed	869150E 4045923N

Site Code	Site Name	Managing Agency	Elev. (m)	Year Constructed	Number of Fires	Construction Method	Vegetation Type	Grazing or Logging	UTM X, Y
BM	Burrough Mtn	Sierra NF	1109	1935	1	HC	OW	Grazed	823660E 4100650N
AG	Aguanga	Cleveland NF	1189	1974	0-2	HC	CP	Grazed	1072233E 3711374N
PG	Pilot Grove	Mendocino NF	1194	1960	1-2	BD	CP/OW/CF	Grazed	511751E 4343359N
CP	Cascadel Point	Sierra NF	1294	1920	2-3	HC	OW	Logged	814871E 4122622N
RR	Rouse Ridge	San Bernardino NF	1298	1984	1-2	BD	CS/CP	Grazed	1075390E 3743619N
SP	Sierra Pelona	Angeles NF	1302	1960	1-2	BD	OW/CP	Grazed	925013E 3831072N
LC	Lewis Creek	SEKI	1461	1981	0-2	HC	CP	None	882984E 4080437N
BR	Blacks Ridge	Lassen NF	1533	2002-2003	0-1	MT	CF	Grazed Logged	649479E 4524209N
SM	Sierra Madre	Los Padres NF	1535	1962-1966	0-2	BD	CP	Grazed	791673E 3864508N
PR	Palos Ranches	BLM	1544	1977-2001	0	HC/BD	CF/CP	Logged	904704E 3959471N
LP	Lookout Point	SEKI	1579	1997	0	HC	OW/CP	None	885263E 4042110N
AB	Antelope-Border	Plumas NF	1590	2001	0	MT	CF	Grazed Logged	705805E 4447632N
MC	McKenzie Ridge	Sequoia NF	1646	1960	0-2	MT	CF	Grazed Logged	852223E 4075163N
FL	Fallen Leaf	LTBMU	1899	1995	0	MT	CF	Grazed	755427E 4305872N

Many of the variables we measured differed greatly among fuel breaks. For example, mean relative nonnative cover ranged from 0 to over 50% (Figure 3-1). Native species richness also varied among sites ranging from between almost 2 to over 6 species per m^2 (Figure 3-2).

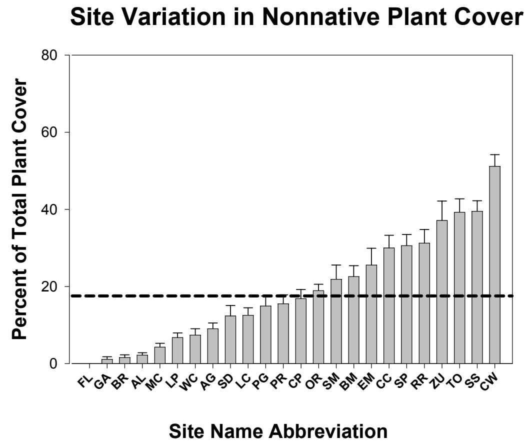

Figure 3-1. Variation in relative nonnative plant abundance between fuel breaks. N=1543. The mean value of 18% is shown as a dashed line. Error bars indicate + 1 SE.

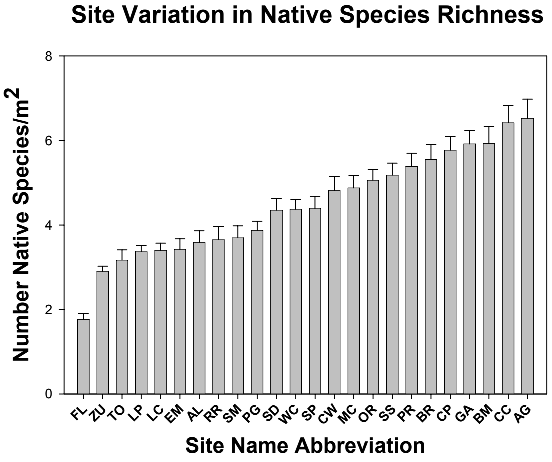

Figure 3-2. Variation in mean native species richness among fuel breaks. N=1543. Error bars indicate + 1 SE.

We found that duff depth and canopy cover together explained over 70% of the variation in relative nonnative cover (R^2=0.721, P<0.001). These environmental variables also varied considerably among sites. Duff depth ranged from less than 2 cm to over 50 cm (Figure 3-3). Overstory canopy cover ranged from 5 to 88% as shown in Figure 3-4.

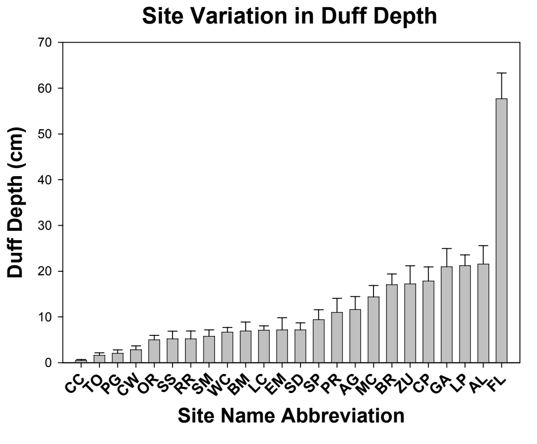

Figure 3-3. Variation in duff depth among fuel breaks. N=1543. Error bars indicate + 1 SE.

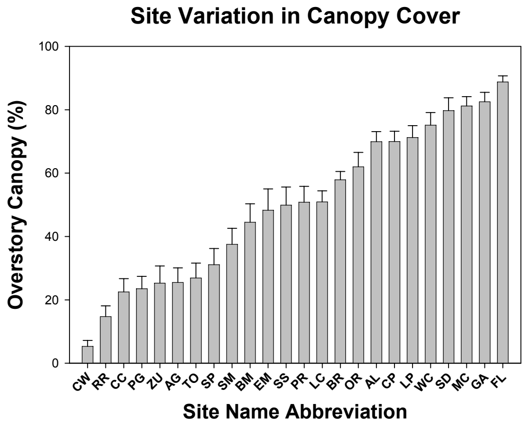

Figure 3-4. Variation in canopy cover among fuel breaks. N=1543. Error bars indicate + 1 SE.

We have described some of the factors that may explain differences in relative nonnative cover among fuel breaks, including construction methods and environmental factors (Chapter One), and the potential role of vegetation type (Chapter Two). In this chapter we focus on patterns observed at individual sites. A description of each fuel break is given separately below, arranged from lowest to highest elevation. Only a general description of the location of each study site is provided here. See Figure 1-1 for general location of each site. More specific information, including GIS shapefiles of plot locations, is available upon request.

This fuel break near Lake Tahoe had the highest duff depth and overstory canopy of any of our sites.

Gasquet Shaded Fuel Break, Six Rivers National Forest

The Gasquet shaded fuel break is located in the Six Rivers National Forest near the town of Gasquet in the Smith River National Recreation Area of Del Norte County. This shaded fuel break was constructed in 1995 by mechanical thinning and prescribed burning. Only two transects at the Gasquet fuel break contained nonnative plants, and these were located within the perimeter of the 1996 Panther Fire.

Gasquet shaded fuel break, Six Rivers National Forest

The Gasquet shaded fuel break is located in a tan oak and Douglas fir (*Pseudotsuga menziesii*) forest. Other dominant species include incense cedar (*Calocedrus decurrens*) and black huckleberry (*Vaccinium ovatum*). Our plots on the Gasquet shaded fuel break were located predominately on the Jayel soil series. These are moderately deep, well drained soils formed in material weathered from serpentinized peridotite.

We identified 60 plant species in our $1m^2$ plots at the Gasquet shaded fuel break. Only 3 of these species were nonnative. The most common nonnative plant in our plots was Scotch broom (*Cytisus scoparius*).

Nonnative plants occupied 12% of the total plant cover at the Gasquet shaded fuel break in plots where they occurred, which represented only 10% of all plots. The mean relative nonnative cover (1%) on the Gasquet shaded fuel break was much lower than the mean (18%) of the 24 sites in our study. Relative nonnative plant cover was not significantly higher on the Gasquet fuel break than in the adjacent wildland off of the fuel break (Figure 3-5).

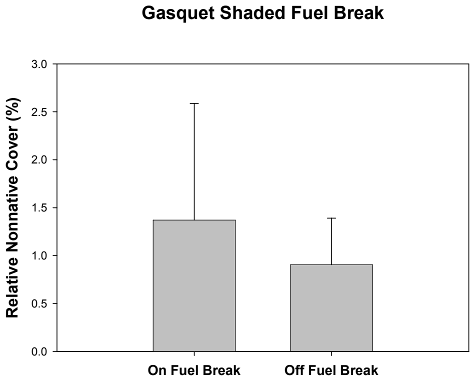

Figure 3-5. ANOVA did not find significant differences in relative nonnative abundance on the Gasquet fuel break compared to outside of the fuel break. (N=62, df=1, 60, F=0.022, *P*=0.883). Error bars indicate + 1 SE.

Santa Monica Mountains National Recreation Area

We sampled two fuel breaks in the Santa Monica Mountains National Recreation Area, near the city of Thousand Oaks in Los Angeles County. These were the Zuma Ridge and Etz Meloy fuel breaks.

The Etz Meloy fuel break was constructed in 1957 by bulldozers, and was maintained by bulldozers on an annual or biennual rotation by the Los Angeles County Fire Department until 1985. Portions of this fuel break were also maintained by goat grazing on an experimental basis. The Etz Meloy fuel break is not currently maintained. The area around the fuel break burned in the 1993 Green Meadows fire.

Etz Meloy fuel break, Santa Monica Mountains National Recreation Area

The Etz Meloy fuel break is located in a chaparral habitat, dominated by black sage (*Salvia mellifera*), bigpod ceanothus (*Ceanothus megacarpus*), and redshank (*Adenostema sparsifolium*). Our plots were located primarily on soils from the Hambright series. These are shallow, well drained soils formed in material weathered from basic igneous rocks.

We found 49 species in our 1m^2 plots at the Etz Meloy fuel break, including 13 nonnatives. The most common nonnative species in our plots on the Etz Meloy fuel break was red brome (*Bromus madritensis*).

The Zuma Ridge fuel break was constructed in 1952 by bulldozers. The fuel break was maintained by bulldozers on an annual or biennial rotation by the Los Angeles County Fire Department until 1985. Our plots along the Zuma Ridge fuel break were located in areas that have burned up to five times between 1935 and 1995.

Zuma Ridge fuel break, Santa Monica Mountains National Recreation Area

The Zuma Ridge fuel break is located in a coastal scrub type plant community, dominated by bigpod ceanothus, California encelia (*Encelia californica*), and purple sage (*Salvia leucophylla).* Our plots were located primarily on sandy soils classified as beaches. We identified 51 plant species in our 1m^2 quadrats at the Zuma Ridge fuel break, including 17 nonnative species. The most common nonnative species on the Zuma Ridge fuel break was wild oats (*Avena fatua).*

Nonnative plants were found in 100% of our 1 m^2 plots on both the Etz Meloy and Zuma Ridge fuel breaks, while nonnatives were only present in 22% and 45% of plots outside of these fuel breaks, respectively. Nonnative plant cover was significantly higher on both the Etz Meloy and Zuma Ridge fuel breaks than in the adjacent wildland. Zuma Ridge had higher nonnative plant cover than Etz Meloy both on and off the fuel break (Figure 3-6).

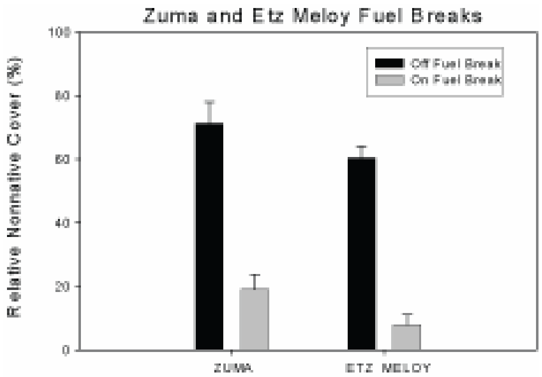

Figure 3-6. ANOVA found significant differences between nonnative abundance on the Zuma Ridge and Etz Meloy fuel breaks compared with adjacent wildlands. (Difference between fuel breaks, N=106, df=1, 102, F=6.528, *P*=0.012; and position on or off fuel breaks, N=106, df=1, 102, F=103.8, *P*<0.001). Error bars represent + 1 SE.

Oso Ridge Fuel Break, Casper's Wilderness Park

The Oso Ridge fuel break is located within Casper's Wilderness Park, near the town of San Juan Capistrano, in Orange County. Casper's Wilderness Park is administered by the Orange County Parks and Recreation Department. The Oso Ridge fuel break was constructed in the 1960s by bulldozers, and has been maintained annually. A number of fires have occurred in the vicinity of this fuel break, including the 1993 Ortega fire.

Oso Ridge fuel break,
Casper's Wilderness Park

The Oso Ridge fuel break is located in a coastal scrub plant community, dominated by California sage, black sage, and California buckwheat. Our plots on Oso Ridge were located primarily in the Alo soils series. The Alo series consist of moderately deep, well drained soils formed in material weathered from shale or sandstone on mountains.

We identified 80 species in our 1m^2 quadrats along Oso Ridge, including 18 nonnative species. The Oso Ridge fuel break had the highest relative cover (51%) of nonnative plant species of the 24 sites in our study. The most common nonnative was black mustard (*Brassica nigra*). Nonnative species were found in 100% of our plots both on and off the Oso Ridge fuel break. Nonnative plant cover was significantly higher on the Oso Ridge fuel break than in the adjacent wildland off of the fuel break (Figure 3-7).

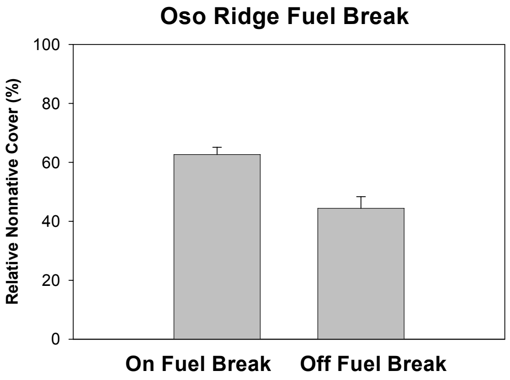

Figure 3-7. ANOVA found significant differences in relative nonnative abundance on the Oso Ridge fuel break compared with adjacent wildlands (N=60, df=1, 58, F=4.812, *P*=0.032). Error bars represent + 1 SE.

Whiskeytown National Recreation Area

We studied three separate fuel breaks within the Whiskeytown National Recreation Area, located west of the town of Redding in Shasta County. These included the Tower fire line, the Shasta Divide fuel break, and the Whiskey Creek fuel break.

The Tower fire line was constructed in 1980 by bulldozers to contain the Tower wildfire. The fire line has not been maintained and was seeded with native plants after 1980. At the time we conducted our sampling in 2002, the area surrounding the Tower fire line had experienced four separate fires since 1959, the most recent in 1999. This area was burned again during the 2004 French fire.

Tower fire line, Whiskeytown National Recreation Area

The Tower fire line is located in a chaparral type plant community dominated by chamise (*Adenostoma fasciculatum*), interior live oak (*Quercus wislizenii*), and yerba santa (*Eriodictyon californicum*). Our plots were located primarily on Boomer soils series. These are very deep, well drained soils that formed in material weathered from metavolcanic rock. We identified 51 species in our 1m^2 plots at the Tower fire line, 19 of which were nonnative. The most common nonnative species on the Tower fire line was foxtail fescue (*Vulpia myuros)*.

The Shasta Divide fuel break was constructed in 1985 by bulldozers and prescribed burning. The fuel break has been periodically maintained by prescribed burning and hand crews. The Shasta Divide fuel break is located primarily in an oak woodland vegetation type dominated by canyon live oak (*Quercus chrysolepis*), black oak (*Quercus kelloggii*), and whiteleaf manzanita (*Arctostaphylos viscida*). We identified 56 species in our 1m^2 plots at the Shasta Divide fuel break, 10 of which were nonnative. The most common nonnative species on the Shasta Divide fuel break was foxtail fescue.

Shasta Divide fuel break, Whiskeytown National Recreation Area

The Whiskey Creek shaded fuel break was created in 2001 and 2003 by selective thinning and prescribed burning. Fuels were masticated and remain on the ground within the fuel break. The Whiskey Creek shaded fuel break is located in a chaparral habitat dominated by whiteleaf manzanita, black oak, and chamise. Our plots were located primarily on Boomer soils at this site, which are very deep, well drained soils that formed in material weathered from metavolcanic rock.

We identified 56 species in our 1m^2 plots at the Whiskey Creek fuel break, 8 of which were nonnative. The most common nonnative species on the Whiskey Creek shaded fuel break was barren brome (*Bromus sterilis*).

Whiskey Creek fuel break,
Whiskeytown National Recreation Area

The Whiskey Creek and Shasta Divide fuel breaks had lower mean relative nonnative cover (7% and 12%, respectively) than most other sites in our study (18%) including the Tower fire line (39%). Relative nonnative cover was higher on the fuel break than in the adjacent wildland at all three sites in the Whiskeytown National Recreation Area, and this effect differed among fuel breaks (Figure 3-8).

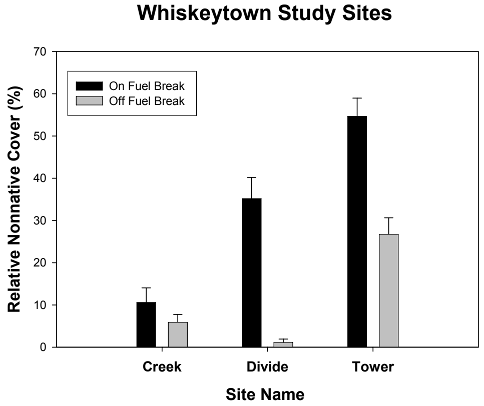

Figure 3-8. ANOVA found a significant interaction between position on and off the fuel break and site (N=173, df=2, 167, F=11.743, *P*<0.001). Error bars represent + 1 SE.

Calf Canyon Fuel Break, Bakersfield BLM and San Luis Obispo CDF

The Calf Canyon fuel break is located near the town of Santa Margarita in San Luis Obispo County. This fuel break is managed by the Bakersfield District of the Bureau of Land Management (BLM), and maintained by the San Luis Obispo Unit of the California Department of Fire and Forestry (CDF). This fuel break was first constructed in 1965 using bulldozers, and has been maintained periodically by hand crews. The areas adjacent to the fuel break burned during the 2002 Highway 58 fire.

Calf Canyon fuel break,
San Luis Obispo CDF and BLM.

Calf Canyon is a chamise dominated chaparral habitat. Other shrub species we observed at Calf Canyon included wedgeleaf ceanothus (*Ceanothus cuneatus*) and black sage. Our plots at Calf Canyon were located primarily on Cieneba soils. These are very shallow, somewhat excessively drained soils that formed in material weathered from granitic rock.

Calf Canyon had the second highest species richness of our 24 study sites; we identified 97 species in our 1m^2 plots at Calf Canyon, 21 of which were nonnative. The most common nonnative species was cheatgrass (*Bromus tectorum*).

The Calf Canyon fuel break had higher mean relative nonnative cover (30%) than the mean (18%) of 24 sites in our study. Nonnative plants were found in 100% of our 1m^2 plots on Calf Canyon fuel break, and in 76% of plots outside the fuel break. Nonnative plant cover was significantly higher on the Calf Canyon fuel break than in the adjacent wildland (Figure 3-9).

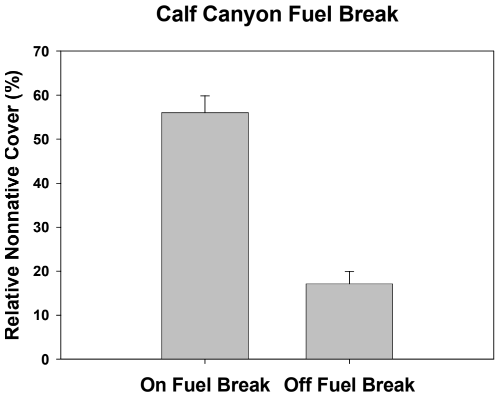

Figure 3-9. ANOVA found significant differences in relative nonnative abundance on the Calf Canyon fuel break compared with adjacent wildlands (N=60, df=1, 58, F=55.639, *P*<0.001). Error bars represent + 1 SE.

Sequoia and Kings Canyon National Park

We studied three fuel breaks at Sequoia and Kings Canyon National Parks, the Shepard Saddle fire line, the Lookout Point fire line, and the Lewis Creek fire line. All of our plots in Sequoia and Kings Canyon were located primarily on soils of the Holland series. These are very deep, well drained soils that formed in material weathered from granitic rock.

The Shepard Saddle fire line is located near Sequoia National Park's southwestern boundary near the town of Three Rivers in Tulare County. This fire line was constructed in 1960 by bulldozers, and has not been maintained. Areas in the vicinity of this fire line were burned during the 1996 Kaweah fire. Unlike most other areas in Sequoia National Park, the Shepard Saddle fire line is occasionally subject to grazing. The Shepard Saddle fire line includes black oak woodlands and chaparral habitats.

The most common nonnative species on the Shepard Saddle fire line was soft chess (*Bromus hordeaceus)*. We observed 80 species in our 1m^2 plots on Shepard Saddle, including 20 nonnative species.


Shepard Saddle fire line in
Sequoia National Park

The Lookout Point fire line is located in the Mineral King area of Sequoia National Park in Tulare County. This fire line was constructed in 1997 by hand crews to contain the Redwood fire. The Lookout Point fire line is located in oak woodland and chaparral habitats, dominated by canyon live oak (*Quercus chrysolepis*) and indian manzanita (*Arctostaphylos mewukka*). The most common nonnative species on the Lookout Point fire line was cheatgrass. We observed 42 species in our 1m^2 plots at Lookout Point, including three nonnative species.

The Lewis Creek fire line is located in the Cedar Grove area of Kings Canyon National Park, Fresno County. This fire line was constructed in 1981 by hand crews, in preparation for a prescribed burn. Portions of the Lewis Creek fire line were burned in the 1980 Lewis Creek fire. The Lewis Creek fire line is located in a chaparral habitat, dominated by whiteleaf manzanita, wedgeleaf ceanothus, and birchleaf mountain mahogany (*Cercocarpus betuloides*). The most common nonnative plant found on the Lewis Creek fire line was cheatgrass. We observed a total of 55 species in our 1m^2 plots at Lewis Creek, three of which were nonnative.

Shepard Saddle had much higher relative nonnative cover (39%) than either the Lookout Point or Lewis Creek fire lines (6% and 12% respectively). Relative nonnative plant cover was significantly higher on the Shepard Saddle and Lookout fire lines than in the adjacent wildland areas. However, there was no difference in relative nonnative plant cover on the Lewis Creek fire line compared with adjacent wildlands (Figure 3-10).

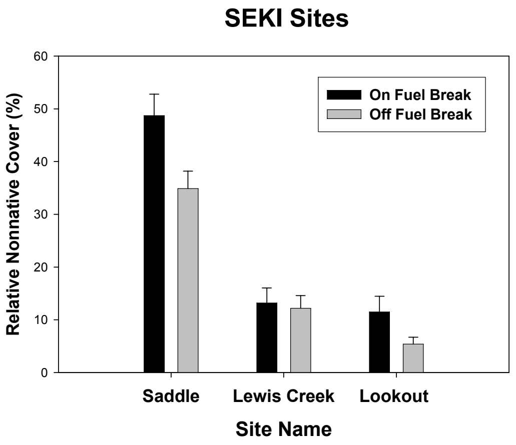

Figure 3-10. ANOVA found significantly higher relative nonnative abundance on the Shepard Saddle and Lookout Point fire lines compared with adjacent wildlands, but this pattern did not emerge on the Lewis Creek fire line (interaction between site and position on fuel break, N=173, df=2, 167, F=41.113, *P*<0.001). Error bars represent + 1 SE. Significance assessed with Bonferroni adjusted *P* value of 0.015 for 3 post-hoc comparisons.

Sierra National Forest

We studied two fuel breaks in the Sierra National Forest, the Burrough Mountain fuel break and the Cascadel Point fuel break. The Burrough Mountain fuel break is located in the Sierra National Forest near the town of Toll House in Fresno County. The Cascadel Point fuel break is located east of the town of North Fork in Madera County.

The Burrough Mountain fuel break was first constructed in 1935, and has been maintained regularly through clearing and prescribed burning. This fuel break is located in mixed oak woodland. The most common tree species we observed included interior live oak, black oak, and California buckeye (*Aesculus californica*). Our plots on the Burrough Mountain fuel break were located on soils from the Ahwahnee, Chaix, and Holland series. These are deep, well to somewhat excessively well drained soils formed in material weathered from igneous rock such as granite and granodiorite.

The Burrough Mountain fuel break had the highest site level species diversity of any of our study sites. We detected over 100 species in our 1m^2 plots at Burrough Mountain. Twenty of these species were nonnative. The most common nonnative plant we encountered at this site was tocalote (*Centaurea melitensis*).

Burrough Mountain fuel break,
Sierra National Forest

The Cascadel Point fuel break is not currently maintained, although prescribed burning was conducted in the vicinity of the fuel break in 1980. The Cascadel Point fuel break is located within a mule deer winter range habitat area and is currently excluded from cattle grazing.

The fuel break is located in a mixed oak woodland, characterized by black oak (*Quercus kelloggii*), ponderosa pine (*Pinus ponderosa*), canyon live oak (*Quercus chrysolepis*), and whiteleaf manzanita (*Arctostaphylos viscida*). Our plots at Cascadel Point were located primarily on soils of the Holland series. These are very deep, well drained soils that formed in material weathered from granitic rock.

The most common nonnative plant in our plots on the Cascadel Point fuel break was field hedge parsley (*Torilis arvensis*). We recorded 80 species in our 1m^2 plots on the Cascadel Point fuel break, 20 of which were nonnative.

Cascadel Point fuel break,
Sierra National Forest

The Burrough Mountain fuel break had higher mean relative nonnative cover (23%) than the mean (18%) of 24 sites in our study, while the Cascadel Point fuel break had slightly lower mean relative nonnative cover (17%). Nonnative plants occurred in 100% of the plots on the Burrough Mountain fuel break, and 53% of plots in the adjacent wildland. Nonnative plants occurred in 75% of the plots on the Cascadel Point fuel break, and 56% of plots in the adjacent wildland.

Nonnative plant cover was significantly higher on both the Burrough and Cascadel Point fuel breaks than in the adjacent wildlands, and there were also significant differences between fuel breaks (Figure 3-11).

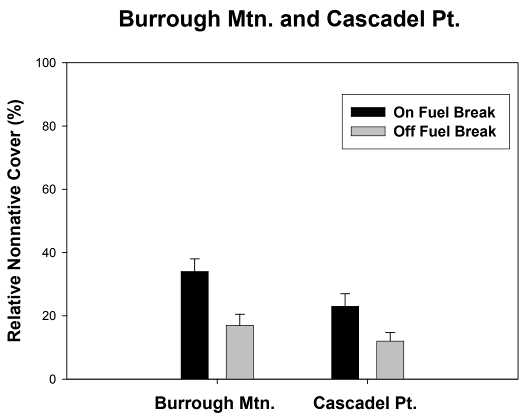

Figure 3-11. ANOVA found significant differences between fuel breaks (N=110, df=1, 106, F=4.674, *P*=0.033), and with position on or off fuel break (N=110, df=1, 106 F=18.772, *P*<0.001). Error bars represent + 1 SE.

Aguanga Fuel Break, Cleveland National Forest

The Aguanga fuel break is located in the Cleveland National Forest, near the town of Oak Grove in San Diego County. This fuel break was constructed in 1974 by hand crews, mechanical thinning, and prescribed fire. It has been maintained on an approximately five year rotation by hand crews and prescribed burning. Portions of the fuel break were most recently prescribed burned in 2003.

Aguanga fuel break, Cleveland National Forest

The Aguanga fuel break is located in a chaparral vegetation type, dominated by chamise, red shank, and cupleaf ceanothus (*Ceanothus greggii*).

The most common nonnative species on the Aguanga fuel break was red brome. We identified 80 species in our 1m^2 plots at this site, 9 of which were nonnative. The Aguanga fuel break had lower mean relative cover (9%) than the mean (18%) of 24 sites in our study. Nonnative plants occurred in 80% of plots on the Aguanga fuel break, and 40% of plots in the adjacent wildland.

Relative nonnative cover was significantly higher on the Aguanga fuel break than in the adjacent wildland area (Figure 3-12).

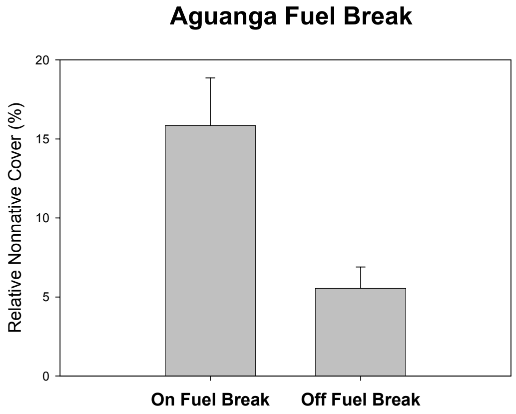

Figure 3-12. ANOVA found significant differences in relative nonnative abundance on the Aguanga fuel break compared with adjacent wildlands (N=60, df=1, 58, F=14.016, $P<0.001$). Error bars represent + 1 SE.

Pilot Grove Fuel Break, Mendocino National Forest

The Pilot Grove fuel break is located in the Mendocino National Forest near Clear Lake in Lake County. This fuel break was constructed in 1960 by bulldozers, and has been maintained by prescribed burning on an approximately five-year rotation. The area surrounding this fuel break was burned during the 1996 Forks fire.

Pilot Grove fuel break,
Mendocino National Forest

The Pilot Grove fuel break includes a range of plant communities, including ponderosa pine forest, black oak woodlands, and chaparral habitats dominated by chamise. Portions of the fuel break were historically seeded with grasses, including Harding grass (*Phalaris aquatica)*. Our plots on the Pilot Grove fuel break were located primarily on soils from the Neuns series. These are moderately deep, well drained soils that formed in slope alluvium and colluvium from metamorphosed igneous and sedimentary rocks.

We identified 78 species in our 1m^2 plots at Pilot Grove, 17 of which were nonnative. The most common nonnative species on the Pilot Grove fuel break was foxtail fescue. Nonnatives were detected in 80% of the quadrats on the Pilot Grove fuel break, and only 20% of those outside the fuel break. The Pilot Grove fuel break had slightly lower mean relative nonnative cover (15%) than the mean (18%) of 24 sites in our study. Nonnative plant cover was significantly higher on the Pilot Grove fuel break than in the adjacent wildland off of the fuel break (Figure 3-13).

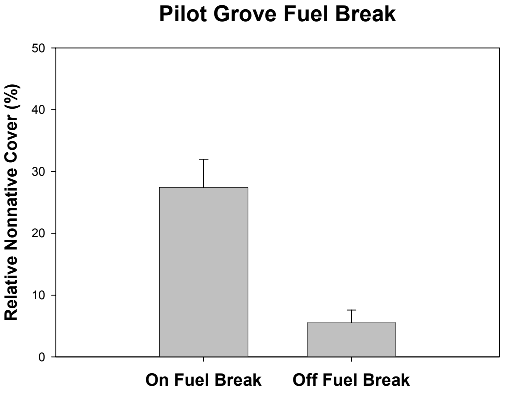

Figure 3-13. ANOVA found significant differences in relative nonnative abundance on the Pilot Grove fuel break compared with adjacent wildlands, (N=70, df= 1, 68, F=29.807, $P<0.001$). Error bars represent + 1 SE.

Rouse Ridge Fuel Break, San Bernardino National Forest

The Rouse Ridge fuel break is located east of the town of Hemet, Riverside County, in the San Bernardino National Forest. This fuel break was constructed in 1984 by bulldozers and prescribed burning. Portions of the fuel break were prescribed burned again during 2002 and 2003.

Rouse Ridge fuel break,
San Bernardino National Forest

The Rouse Ridge fuel break is located primarily in a chaparral vegetation type dominated by chamise, California buckwheat, and birchleaf mountain mahogany (*Cercocarpus betuloides*). Soils on the Rouse Ridge fuel break were primarily of the Chawanakee and Goulding series. Both series are shallow, somewhat excessively drained soils. The Chawanakee is formed in material weathered from granitic rock, while the Goulding series is formed in material weathered from metavolcanic or metasedimentary rocks.

We identified 81 species in our $1m^2$ plots at Rouse Ridge, 16 of which were nonnative. The most common nonnative species on the Rouse Ridge fuel break was cheatgrass.

Nonnative species occurred in 65% of plots outside the fuel break, and 90% of plots on the fuel break. The mean relative nonnative cover at the Rouse Ridge study site (31%) was higher than the mean (18%) of 24 sites in our study. Nonnative plant cover was significantly higher on the Rouse Ridge fuel break than in the adjacent wildland (Figure 3-14).

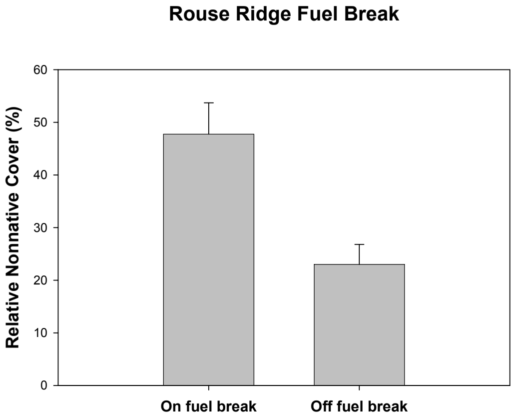

Figure 3-14. ANOVA found significant differences in relative nonnative abundance on the Rouse Ridge fuel break compared with adjacent wildlands (N=60, df=1, 58, F=12.195, *P*=0.001).
Error bars represent + 1 SE.

Sierra Pelona Fuel Break, Angeles National Forest

The Sierra Pelona fuel break is located in the Angeles National Forest east of the City of Santa Clarita, Los Angeles County. The Sierra Pelona Fuel Break was constructed in the 1960s by bulldozers. The fuel break has been annually maintained by cattle grazing, and is periodically prescribed burned.

Sierra Pelona fuel break,
Angeles National Forest

The Sierra Pelona fuel break occurs in oak woodland and chaparral type plant communities, dominated by scrub oak (*Quercus berberidifolia*), canyon live oak, chamise, and California buckwheat. Our plots on the Sierra Pelona fuel break were located on the Gaviota series. These consist of shallow, well drained soils that formed in material weathered from hard sandstone or meta-sandstone. The most common nonnative species we observed on the Sierra Pelona fuel break was cutleaf filaree (*Erodium cicutarium).* We identified 71 species in our $1m^2$ plots at the Sierra Pelona fuel break, 16 of which were nonnative.

Nonnative species were found in 75% of plots in the wildland area, and 100% of plots on the fuel break. The Sierra Pelona fuel break had higher relative cover of nonnative plant species (31%) than the mean (18%) of 24 sites in our study.

Relative nonnative plant cover was significantly higher on the Sierra Pelona fuel break than in the adjacent wildland (Figure 3-15).

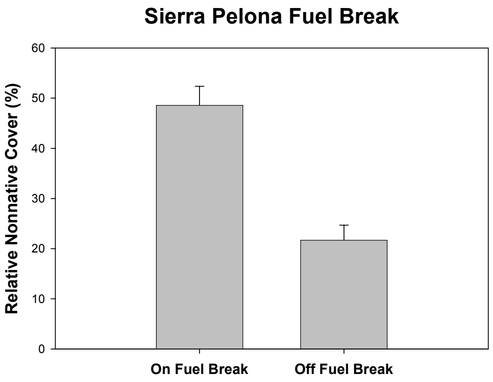

Figure 3-15. ANOVA found significant differences in relative nonnative abundance on the Sierra Pelona fuel break compared with adjacent wildlands (N=60, df=1, 58, F=25.518, *P*<0.001).
Error bars represent + 1 SE.

Blacks Ridge Defensible Fuel Profile Zone, Lassen National Forest

The Blacks Ridge Defensible Fuel Profile Zone (DFPZ), a shaded fuel break, is located in the Eagle Lake Ranger District of the Lassen National Forest, near the town of Little Valley in Lassen County.

Blacks Ridge DFPZ,
Lassen National Forest

This shaded fuel break was constructed as part of the Herger-Feinstein Quincy Library Group Forest Recovery Act, Bill HR 858, passed in 1997. The entire Blacks Ridge DFPZ is planned to occupy almost 3642 hectares (ha) (9000 acres), including thinning and group selection treatments. As of 2003 when we collected data, much of this DFPZ had not yet been constructed. We collected data on two portions of the DFPZ, where almost 101 ha (250 acres) had been treated to reduce fuels using mechanical thinning and prescribed burning between 2002 and 2003.

The Blacks Ridge DFPZ is located in a ponderosa pine forest. Other common species we observed in our plots at the Blacks Ridge DFPZ included mountain mahogany (*Cercocarpus ledifolius*), mahala carpet (*Ceanothus prostratus*), and mule's ear (*Wyethia mollis*). Our plots on the Blacks Ridge DFPZ were located on Trojan and Holland soils. Trojan soils are very deep, well drained soils that formed in colluvium and residuum derived from volcanic rocks or from schist and argillite. Holland soils are very deep, well drained soils that formed in material weathered from granitic rock.

We identified 60 species in our 1m^2 plots at Blacks Ridge DFPZ, three of which were nonnative. The most common nonnative plant we found was cheatgrass. Nonnative species were found in 18% of plots in the untreated wildland area, and only 8% of plots within the DFPZ. The Blacks Ridge DFPZ had the third lowest relative cover of nonnative plant species (1.6%) of 24 sites in our study.

Nonnative plant cover was not statistically different in the treated area of the Blacks Ridge DFPZ compared to the adjacent wildland (Figure 3-16).

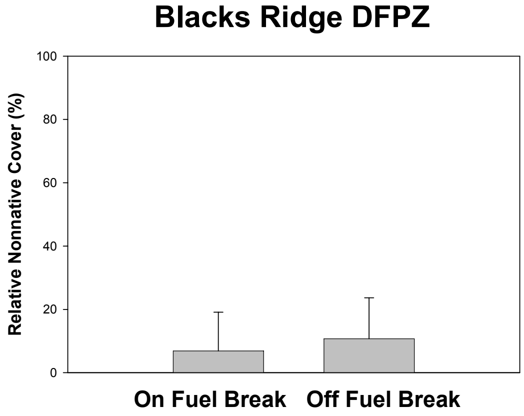

Figure 3-16. ANOVA found no difference in relative nonnative abundance on the Blacks Ridge DFPZ compared with adjacent wildlands (N=80, df=1, 78, F=25.518, *P*=0.1430). Error bars represent + 1 SE.

Sierra Madre Ridge Fuel Break, Los Padres National Forest

The Sierra Madre Ridge fuel break is located in the Los Padres National Forest, southwest of the Cuyama Valley, in Santa Barbara County. This fuel break was constructed in 1964 by bulldozers. The fuel break has been maintained regularly, initially through the use of herbicides and mechanical clearing, and more recently through prescribed burning.

Sierra Madre Ridge fuel break,
Los Padres National Forest

The Sierra Madre Ridge fuel break is located in a scrub oak habitat, dominated by Tucker's oak (*Quercus john-tuckeri*), and scrub oak. The most common nonnative species on the Sierra Madre Ridge fuel break was cheatgrass. Our plots were located on Aramburu and Lodo soils. The Aramburu series are moderately deep, well drained soils that formed in material weathered from shale or sandstone. The Lodo series consists of shallow, somewhat excessively drained soils that formed in material weathered from hard shale and fine grained sandstone.

We identified 80 plant species in our 1m^2 plots at the Sierra Madre Ridge, 11 of which were nonnative. Nonnative species occurred in 20% of plots outside the fuel break and 100% of plots within the fuel break. The Sierra Madre Ridge fuel break had slightly higher relative nonnative cover (22%) than the mean (18%) of 24 sites in our study.

Nonnative plant cover was significantly higher on the Sierra Madre Ridge fuel break than in the adjacent wildland (Figure 3-17).

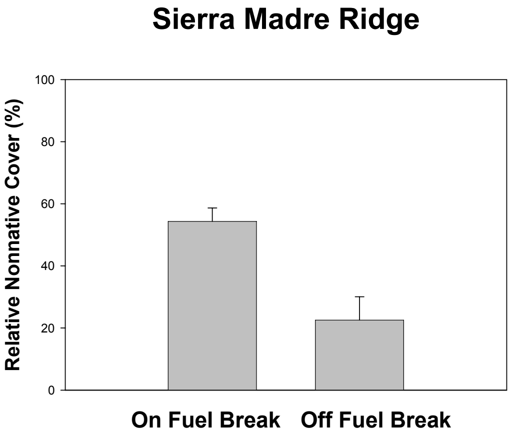

Figure 3-17. ANOVA found significantly higher relative nonnative abundance on the Sierra Madre Ridge fuel break compared with the adjacent wildland (N=60, df=1, 58, F= 133.226, *P*<0.001). Error bars represent + 1 SE.

Palos Ranches Fuel Break, Sequoia National Forest and BLM

This fuel break is located west of the town of Wofford Heights in Kern County. The fuel break consists of two separate portions, the Shirley portion and the Palos Ranches portion, constructed and managed by separate agencies, the USDA Forest Service and the Bureau of Land Management. The Shirley portion is located within the Sequoia National Forest. This portion of the fuel break was constructed in 1977 by mechanical thinning. The fuel break is located in a mixed conifer forest dominated by incense cedar, white fir, and black oak. The only nonnative plant found on the Shirley portion of the fuel break was cheatgrass.


Palos Ranches fuel break, BLM

The Palos Ranches portion of the fuel break is located on land managed by the Bakersfield District of the Bureau of Land Management. This portion of the fuel break was constructed by bulldozers and hand crews in 1998 and 2001 for use during a prescribed burn. The Palo Ranches portion of the fuel break is located in a chaparral habitat, dominated by wedgeleaf ceanothus, birchleaf mountain mahogany, and greenleaf manzanita (*Arctostaphylos patula*). The most common nonnative species on the Palos Ranches portion of the fuel break was cheatgrass.

Soils on both portions of the Palos Ranches fuel break were predominately Walong series. The Walong series consists of moderately deep, well drained soils that formed in material weathered from granitic rocks.

We identified 85 species in our 1m^2 plots on the entire Palos Ranches fuel break, including both the Palos Ranches and Shirley portions. Eight of these species were nonnative. Nonnative species were found in 50% of our plots outside the fuel break and 70% of our plots within the treated area. The Palo Ranches fuel break had slightly lower relative nonnative cover (16%) than the mean (18%) of 24 sites in our study.

Nonnative plant cover was significantly higher on the Palo Ranches fuel break than in the adjacent wildland (Figure 3-18).

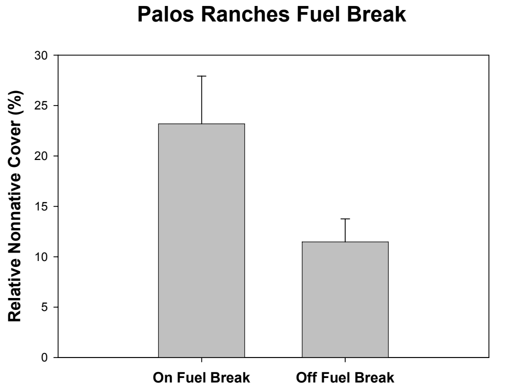

Figure 3-18. ANOVA found significant differences in relative nonnative abundance on the Palos Ranches fuel break compared with adjacent wildlands (N=60, df=1, 58, F=5.094, *P*=0.028).
Error bars represent + 1 SE.

Antelope Border Defensible Fuel Profile Zone, Plumas National Forest

The Antelope Border Defensible Fuel Profile Zone (DFPZ), a shaded fuel break, is located in the Plumas National Forest in the vicinity of the Antelope Recreation Area, Plumas County. This fuel reduction project was implemented as part of the Herger-Feinstein Quincy Library Group Forest Recovery Act, HR 858, passed in 1997. The entire Antelope Border DFPZ consists of 34 units, varying in size from 5 to 50 ha (11 to 127 acres). For this study we collected data on units 11 and 12, totaling about 40 ha (100 acres) in size. These units were constructed in 2001 using mechanical thinning and prescribed burning.

Antelope Border DFPZ,
Plumas National Forest

The Antelope Border DFPZ is located in a ponderosa pine forest. Other common species we observed included antelope bitterbrush (*Purshia tridentata*) and mahala carpet. Soils on the Antelope Border DFPZ were from the Chaix and Cagwin series. The Chaix series consists of moderately deep, somewhat excessively drained soils that formed in material weathered from acid intrusive igneous rock, mainly granite or granodiorite. The Cagwin series consists of moderately deep, somewhat excessively drained soils that formed in material weathered from granite.

The most common nonnative plant we encountered in our study plots at the Antelope Border DFPZ was cheatgrass. We identified 59 species in our 1 m^2 plots at the Antelope Border DFPZ, three of which were nonnative. Nonnative species occurred in 26% of our plots outside the fuel break and only 4% of our plots within the treated area.

The Antelope Border DFPZ had much lower relative nonnative cover (2%) than the mean (18%) of 24 sites in our study. Relative nonnative plant cover tended to be higher outside of the Antelope Border DFPZ (*P*=0.076), (Figure 3-19).

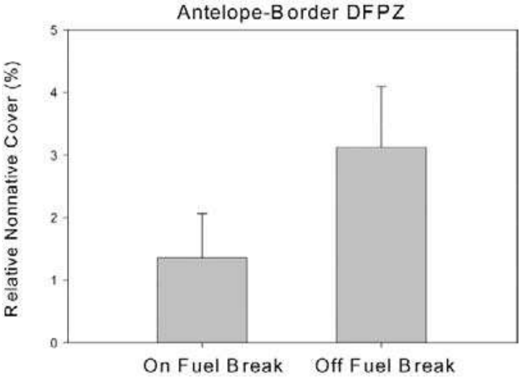

Figure 3-19. ANOVA found no significant differences in relative nonnative abundance within the Antelope Border DFPZ compared with adjacent untreated areas (N=80, df=1, 78, F=3.237, *P*=0.076). Error bars represent + 1 SE.

Fallen Leaf Lake Shaded Fuel Break, Lake Tahoe Basin Management Unit

The Fallen Leaf Lake shaded fuel break is located within the Lake Tahoe Basin Management Unit of the USDA Forest Service, near Lake Tahoe in El Dorado County. This shaded fuel break was constructed in 1995 by mechanical thinning and prescribed burning. The Fallen Leaf Lake shaded fuel break is located at an elevation of 2000 meters, the highest of any of our study sites. This site also had the greatest duff depth (57 cm) of any area we sampled.

Fallen Leaf Lake shaded fuel break, Lake Tahoe Basin Management Unit

The Fallen Leaf Lake shaded fuel break is located in a mixed coniferous forest. Dominant trees species include white fir, canyon live oak, incense cedar, and Jeffrey pine. Soils at this fuel break were predominately from the Meeks series, a deep, well or somewhat excessively drained soil that formed in material weathered from glacial outwash.

We did not find nonnative plants in any of our $1m^2$ plots at Fallen Leaf Lake. We identified 21 native species at the Fallen Leaf fuel break.

Oregon Fire Line, Shasta Trinity National Forest

The Oregon fire line is located in the Shasta Trinity National Forest near the town of Weaverville in Trinity County. This fire line was constructed by bulldozers in 1980 to suppress the Oregon fire.

Oregon fire line, Shasta Trinity National Forest

The Oregon fire line is located in an oak woodland, dominated by Oregon white oak (*Quercus garryana*). Other common species found in the vicinity of the Oregon fire line include grey pine (*Pinus sabiniana*) and greenleaf manzanita. Soils at the Oregon fire line were from the Musserhill series. The Musserhill series consists of moderately deep, well drained soils formed in materials weathered from weakly consolidated conglomerate.

We identified 60 species in our 1m^2 plots at the Oregon fire line, 11 of which were nonnative. The most common nonnative plant we found on the Oregon fire line was field hedge parsley.

The Oregon fire line had slightly higher mean relative nonnative cover (19%) than the mean (18%) of 24 sites in our study. Nonnative species occurred in 78% of plots outside the fire line and 90% of plots within the fire line.

Nonnative plant cover was significantly higher on the Oregon fire line than in the adjacent wildland (Figure 3-20).

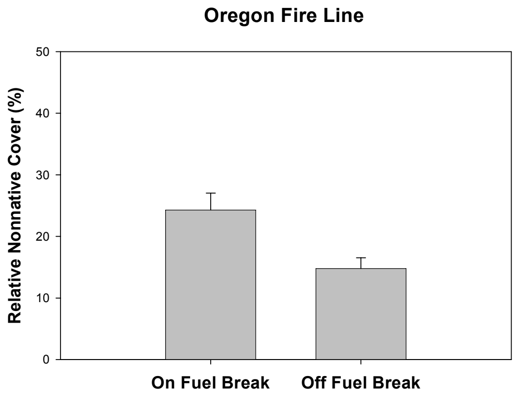

Figure 3-20. ANOVA found significant differences in relative nonnative abundance within the Oregon fire line compared with adjacent untreated areas (N=70, df=1, 68, F=7.190, *P*=0.009). Error bars represent + 1 SE.

McKenzie Ridge Fuel Break, Sequoia National Forest

The McKenzie Ridge fuel break is located in the Sequoia National Forest, west of Grant Grove in Kings Canyon National Park, Fresno County. This fuel break was constructed in the 1960s by mechanical thinning. It has been periodically maintained by prescribed burning, thinning, and discing. Portions of the McKenzie Ridge fuel break were burned in the 2001 Highway fire. The fuel break is located in a mixed conifer forest, dominated by incense cedar, ponderosa pine, and black oak. Our plots on McKenzie Ridge were found in Holland and Jocal soil series. The Holland series consists of very deep, well drained soils that formed in material weathered from granitic rock. The Jocal series consists of deep and very deep, well drained soils formed in material weathered from metasedimentary rocks.

We identified 58 species in our 1m^2 plots at McKenzie Ridge, 10 of which were nonnative. The most common nonnative plant we found on the McKenzie Ridge fuel break was cheatgrass. Nonnative species occurred in only 5% of plots outside the fuel break and 31% of plots within the fuel break. The McKenzie Ridge fuel break had much lower relative nonnative plant cover (4%), than the mean (18%) of 24 sites in our study.

Relative nonnative plant cover was significantly higher in plots on the McKenzie Ridge fuel break than outside of the fuel break (Figure 3-21).

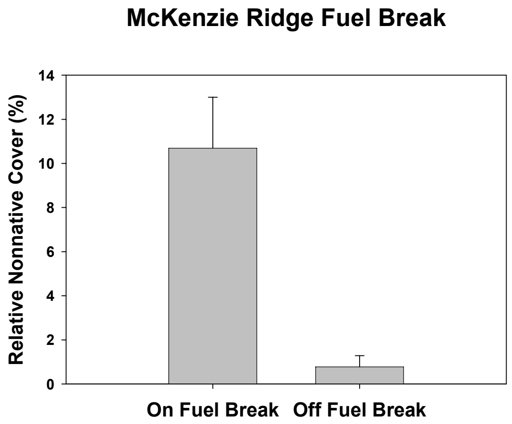

Figure 3-21. ANOVA found significant differences in relative nonnative abundance on the McKenzie Ridge fuel break compared with adjacent untreated areas (N=81, df=1, 79, F=42.771, *P*<0.001). Error bars represent + 1 SE.

DISCUSSION

The 24 fuel breaks described in this chapter occurred across a wide range of vegetation types, soil series, elevations, and climates. Each site had a unique history, including various dates of construction, different construction and maintenance regimes, varying fire histories, and different land use histories. Despite this variation, we found that 19 of the 24 fuel breaks had significantly higher relative nonnative cover than the adjacent wildland areas. The six fuel breaks where nonnative cover was similar on the fuel break and in the adjacent wildland were the Blacks Ridge DFPZ, the Antelope Border DFPZ, the Lewis Creek fire line, the Cascadel Point fuel break, and the Gasquet shaded fuel break. These sites had several common characteristics (Table 3-2). None of them were constructed by bulldozers, and they had either never been maintained or had very long (i.e. 20 year) maintenance rotations. All of these sites, except the Lewis Creek fire line, had significantly deeper duff depths on the fuel break than the mean (11 cm) of all sites studied.

Table 3-2. Characteristics of fuel breaks where relative nonnative cover did not differ between plots on the fuel break and plots in the adjacent wildland area.

[A range of values is given where individual transects at the same site vary. NA, not applicable, is given for maintenance frequency of fuel breaks that have not yet been maintained. Cm, centimeter]

Site Name	Construction Method	Maintenance Frequency	Age (years)	Vegetation Type	Number of Fires	Duff Depth (cm)
Blacks Ridge	Mechanical	NA	0-1	Coniferous Forest	0	21.6
Antelope Border	Mechanical	NA	1	Coniferous Forest	0	17.0
Lewis Creek	Hand Crews	20 yrs	21	Chaparral	0-2	7.1
Cascadel Point	Hand Crews	20 yrs	80	Oak Woodland	2-3	17.9
Gasquet	Mechanical	NA	7	Oak Woodland	0-1	21.0

In addition to sharing common features, these sites also differed from each other in several ways. They included three of the four vegetation types we identified, and they had experienced a range of fire histories.

It is likely that a number of factors, including construction method and maintenance history as well as propagule availability and chance may explain the lack of an association between nonnative abundance and position relative to the fuel break that we observed at these sites.

Continued monitoring would help determine if a pattern of increasing nonnative abundance appeared over time on these fuel breaks. Time since construction was strongly associated with nonnative abundance when we evaluated all of the fuel breaks together (See Figure 1-7 from Chapter 1).

Cheatgrass was the most common nonnative species at eight of our study sites, and was both the most abundant and frequent species across all of our sites. This result supports the findings of others that cheatgrass is both widespread and common in California (Bossard and others, 2000).

Foxtail fescue was the most common nonnative at three of the sites, red brome was the dominant nonnative at two sites, and field hedge parsley was the most common nonnative at two sites. The other nine study sites had different dominant nonnative species. The lack of one dominant nonnative at all sites suggests that fuel breaks may create conditions favorable to a number of different nonnative plant species or that local and site-specific factors may dictate differences between nonnatives in fuel breaks. The colonization of a fuel break by a particular species may reflect which species has a nearby seed source or is able to disperse into the treated area.

Most of the common nonnatives encountered in this study are known to respond favorably to disturbance. Four of the five most common nonnatives were annual grasses from the genus *Bromus.* These annual grasses have been found to readily colonize disturbed sites across a wide range of environments (Bossard and others, 2000). These grasses have also been found to alter fuel conditions in the habitats they invade, and contribute to changes in fire behavior and frequency to the detriment of the native plant community (D'Antonio & Vitousek 1992). The establishment of these species in fuel breaks may have serious implications for native plant communities and fire regimes in the areas they invade (Brooks and others, 2004).

Text Box 3-1: Summary of Site Specific Findings:

- Individual sites differed greatly in nonnative cover, fire history, and environmental variables.
- Nonnative cover was higher within fuel treatments than adjacent wildlands at 19 of our 24 study sites.
- Sites without significant differences in nonnative cover in and out of fuels breaks were characterized by higher duff depths, construction methods other than bulldozing, and were newly constructed or had very infrequent maintenance.
- Cheatgrass was the most common nonnative plant species at 8 of our study sites.
- A number of different species assumed dominance at the other 16 sites, suggesting that many nonnative species may be well adapted to take advantage of the conditions provided by fuel treatments.

Chapter Four: Summary

Some litter cover and overstory canopy were retained on the Whiskey Creek fuel break in Whiskeytown National Recreation Area.

We found that fuel breaks have the potential to promote the establishment and spread of nonnative plants. However, fuel breaks with more canopy and ground cover may be less likely to be invaded. Varying construction methods to retain more litter cover, minimize the exposure of bare ground, and retain some canopy cover might reduce nonnative germination and establishment on fuel breaks. Increasing the time between fuel break maintenance also could allow ground and canopy cover to increase and also lower the probability of nonnative invasion.

Even in relatively uninvaded vegetation types such as coniferous forests, the use of bulldozers significantly increased the abundance of nonnative plants. Bulldozers have large blades specifically designed to remove surface soil layers, and may be more likely to introduce nonnative seeds into fuel breaks by disrupting soil seed banks and transporting seeds between sites.

Bulldozers were used to construct this fuel break in the Mendocino National Forest.

We found that nonnative cover decreased with distance from the fuel break, suggesting that fuel breaks act as sources of nonnative plant seeds during the invasion of adjacent areas. Wildland areas adjacent to fuel breaks were more likely to be invaded by nonnative species when the wildlands had been subject to recurrent fires. Nonnative plant abundance on fuel breaks and in adjacent wildlands continued to increase with fuel break age.


Recent burn adjacent to the Calf Canyon fuel break maintained by the San Luis Obispo Unit of CDF

Native species may also be promoted by fuel breaks, particularly native annual forbs and grasses. We found that native and nonnative diversity were significantly correlated. Many native species, particularly annual forbs, require periodic disturbance to persist in natural ecosystems. The best management regime for maintaining native plant diversity is likely one that restores natural disturbance processes of the frequency, intensity, and duration with which native species evolved. However, these disturbances may also promote nonnative plants. Land managers will have to weigh the benefits of maintaining natural disturbance regimes to native plant communities against the potential risks of promoting nonnative invasives.


Native grasses were abundant on this fuel break in the Sierra National Forest.

We found significant differences in relative nonnative cover and nonnative species richness among vegetation types. Vegetation type has been found to be among the most important factors influencing nonnative plant abundance, either because of the life history characteristics of the dominant plant community or because of other factors such as elevation land use and disturbance history (Keeley 2000).


The Oso Ridge fuel break, and other coastal scrub sites, supported high numbers of nonnative plants.

Despite the strong influence of vegetation type on nonnative abundance and species richness, we found that a number of variables, including fuel break construction method, distance to the fuel break, fire number, and grazing still had significant effects on nonnative abundance when evaluated within individual vegetation types separately. This suggests that although important, vegetation type alone does not determine the abundance of nonnatives. We found that fuel breaks appear to promote nonnative abundance in all vegetation types, and this pattern may be compounded by more numerous fires or by grazing.

The 24 fuel breaks we sampled had unique histories, including various dates of construction, different construction and maintenance regimes, varying fire histories, and different land use histories. Despite this variation, we found that 19 of the 24 sites had significantly higher relative nonnative cover within fuel breaks than in adjacent wildland areas.

At most sites, such as the Tower fire line, there was a significant increase in nonnative abundance on the fuel break.

Cheatgrass was the most common nonnative species at eight of our study sites. Cheatgrass was both the most abundant and frequent species across all of our sites, suggesting that this species is widespread and common in California. However, the other sixteen study sites had twelve different dominant nonnative species. The lack of one dominant nonnative at all sites suggests that fuel breaks may create conditions favorable to a number of different nonnative plant species or that local conditions may dictate nonnative occurrence. The colonization of a fuel break by a particular species may reflect which species has a nearby seed source or is able to disperse into the treated area.

Cheatgrass was the most common nonnative species at our sites.

This study was observational, and there were many environmental and anthropogenic factors for which we could not control. Research using controlled, replicated experiments will be necessary to fully understand the mechanisms that influence nonnative plant establishment within pre-fire fuel manipulation projects and invasion into adjacent wildland areas. Here we have identified potentially important variables influencing patterns of nonnative abundance with respect to fuel breaks and suggested ways that the probability of nonnative invasion might be minimized. If these methods are strategically implemented as part of a long term fuel reduction program, it may be possible to both achieve fuel management goals and reduce the probability of nonnative plant invasion on fuel breaks and in surrounding wildland areas.

Oso Ridge fuel break,
Casper's Wilderness Park

Summary of our findings:

- Fuel breaks may promote nonnative and native plants.
- Fuel breaks with more canopy and ground cover may be less likely to be invaded.
- Nonnative plants are more abundant adjacent to older fuel breaks and in areas that have experienced more numerous fires.
- Native species may also be associated with fuel breaks, particularly native annual forbs and grasses.
- Cheatgrass was the most common nonnative plant species at eight of our study sites.
- A number of different species assumed dominance at the other 16 sites, suggesting that many nonnative species may be well adapted to take advantage of the conditions provided by fuel breaks.

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**Rocky Mountain
Research Station**

General Technical
Report RMRS-GTR-98

September 2002

Mistletoes of North American Conifers

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Abstract

Geils, Brian W.; Cibrián Tovar, Jose; Moody, Benjamin, tech. coords. 2002. **Mistletoes of North American Conifers**. Gen. Tech. Rep. RMRS–GTR–98. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 123 p.

Mistletoes of the families Loranthaceae and Viscaceae are the most important vascular plant parasites of conifers in Canada, the United States, and Mexico. Species of the genera *Psittacanthus*, *Phoradendron*, and *Arceuthobium* cause the greatest economic and ecological impacts. These shrubby, aerial parasites produce either showy or cryptic flowers; they are dispersed by birds or explosive fruits. Mistletoes are obligate parasites, dependent on their host for water, nutrients, and some or most of their carbohydrates. Pathogenic effects on the host include deformation of the infected stem, growth loss, increased susceptibility to other disease agents or insects, and reduced longevity. The presence of mistletoe plants, and the brooms and tree mortality caused by them, have significant ecological and economic effects in heavily infested forest stands and recreation areas. These effects may be either beneficial or detrimental depending on management objectives. Assessment concepts and procedures are available. Biological, chemical, and cultural control methods exist and are being developed to better manage mistletoe populations for resource protection and production.

Keywords: leafy mistletoe, true mistletoe, dwarf mistletoe, forest pathology, life history, silviculture, forest management

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Mistletoes of North American Conifers

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Preface

The mistletoes are serious disease agents affecting forests in all three countries represented by the North American Forestry Commission (NAFC 2002): Canada, Mexico, and the United States of America. For this reason, the Commission through its Insect and Disease Study Group has asked us to prepare a practical guide for field foresters. This publication provides basic information on the species of mistletoes, their hosts, distributions, effects, methods of evaluation, and management. This work updates and expands the several pages dedicated to mistletoes in the previous guide produced for the NACF (Davidson and Prentice 1967). This book covers the mistletoes (Loranthaceae and Viscaceae) that parasitize conifer hosts and occur in North America (Canada, United States, and Mexico). A similar management synopsis but from a different perspective is available for the mistletoes of eucalypts in Australia (Reid and Yan 2000).

The literature on mistletoes is large (over 5,700 articles on North American mistletoes) but widely scattered for some topics and rare for other topics. We intend this synoptic review as a guide to useful references for addressing management concerns from biological conservation to wood fiber production. Because many references have been already cited by Hawksworth and Wiens (1996) for the dwarf mistletoes, we give emphasis to general reviews, recent publications, and information on other mistletoes. An extensive, searchable, annotated bibliography (and other information) is available at the Mistletoe Center (2002). To facilitate use of this guide, we provide a glossary for specialized terms (see appendix D) and post the text online.

Many chapters in this book were first drafted by F. G. Hawksworth and D. Wiens as they were preparing botanical monographs for *Phoradendron* and for *Arceuthobium* (published as Hawksworth and Wiens 1996). Although information in this book has been selected, revised, and updated, the present authors and technical editors acknowledge Hawksworth and Wiens as the original source for many passages of text.

The systematics of *Psittacanthus*, *Phoradendron*, and *Arceuthobium* are the active subjects of current research; taxonomic revisions of these genera are expected in the near future. This book is not a systematics and taxonomic review of these mistletoes; no new species names or combinations are proposed. The nomenclature used in this book for mistletoes is adapted from several sources including taxonomic publications by Hawksworth, Wiens, and others (see Hawksworth and Wiens 1996), the International Plant Names Index (Plant Names Project 1999), the VAST database (Missouri Botanical Garden 2002), and the National PLANTS database (USDA, NRCS 2001).

The taxonomy of many host groups is also subject to uncertainty, disagreement, and revision. The names of many hosts cited in the literature are no longer accepted, and the proper name for a population in question may not be apparent. The host taxonomy accepted here follows the Flora of North America (Flora of North America Committee 1993) for Canada and the United States and Perry (1991) for Mexico. These sources also provide valuable host information including description, synonymy, and distribution. Nomenclatures for taxa not represented in these sources (and some authorities) are from the International Plant Names Index (Plant Names Project 1999).

Because this book has international readership in several languages (English and Spanish), we usually refer to plants by their scientific name. To accommodate those not familiar with these names, we provide appendix B, relating scientific and vernacular names for trees species; and we refer to common genera in the text as “pines” for *Pinus* and “dwarf mistletoes” for *Arceuthobium*. The formal nomenclature for mistletoes including authority, publication, and common synonyms is given for each mistletoe before its description.

The technical editors are grateful to the many supporters, contributors, reviewers, and editors who helped to prepare and publish this guide (see appendix C). We thank C. G. Shaw and Jerome Beatty, USDA Forest Service, Washington Office, for their helpful support to this project. We also thank the members of the NAFC, Insect and Disease Study Group for encouraging and supporting this work. The NAFC (2002) is a commission of the Food and Agriculture Organization of the United Nations and consists of the national forest agencies of Canada, the United States, and Mexico. Specialists from the represented countries meet in study groups to exchange technical assistance on insects and diseases, tree improvement, silviculture, fire management, and other topics.

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September 2002

Author Profiles

Frank G. Hawksworth died in 1993 after starting this project and a monographic review of the genus *Arceuthobium*. He had been Project Leader and Supervisory Plant Pathologist with the Rocky Mountain Research Station in Fort Collins, CO. Beginning with his doctoral studies at Yale University, Dr. Hawksworth dedicated his professional life to the single question, “What is mistletoe?” He described numerous species (most with Del Wiens), authored over 275 articles on dwarf mistletoes, and compiled an extensive library on mistletoes of the world. He is commemorated by *Arceuthobium hawksworthii*.

Delbert Wiens is retired Professor of biology, University of Utah, Salt Lake City. He received a Ph.D. degree from the Claremont Graduate School, CA for his work on the taxonomy of *Phoradendron*. Dr. Wiens has investigated numerous aspects of plant biology including systematics, biogeography, cytology, reproductive biology, and mimicry. He has a particular interest in the Loranthaceae and Viscaceae and the flora of Africa and Southeast Asia. Dr. Wiens recently completed a popular book on the mistletoes of Africa and continues exploring the world.

John A. Muir is a registered professional Forester by the Province of British Columbia and serves as the Provincial Forest Pathologist for the Ministry of Forests, Victoria, B.C. Dr. Muir earned a Bachelor and Master degrees in forest pathology from the University of British Columbia; he has a Ph.D. degree in plant pathology from the University of California, Berkeley. His current activities include development of forest practices and regulations for diseases and development of models and decision aids for dwarf mistletoes and other pathogens. His work supports innovative disease management practices such as genetic resistance and intensive cultural techniques to enhance growth and sustainability of young forests.

Simon F. Shamoun is a research scientist with the Canadian Forest Service, Pacific Forestry Centre and adjunct professor at the University of British Columbia and at the University of Victoria. Dr. Shamoun obtained a Bachelor of Science degree in forestry from the University of Mosul, Nineveh, Mesopotamia (Iraq); Master of Science degree in plant pathology from North Carolina State University; and a Ph.D. degree in plant pathology from the University of Arkansas. His current research focuses on management of competing vegetation, forest weeds, and dwarf mistletoes using fungal pathogens. He is investigating the population structure and genetic diversity of several candidate biological control agents and their target plants.

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Ignacio Vázquez Collazo is a Research Investigator at the Centro de Investigaciones del Pácifico Centro in Uruapan, Michoacán, Mexico. He has published numerous articles on the biology, effects, and management of both dwarf mistletoes and leafy mistletoes in central Mexico.

Pesticide Precautionary Statement

This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

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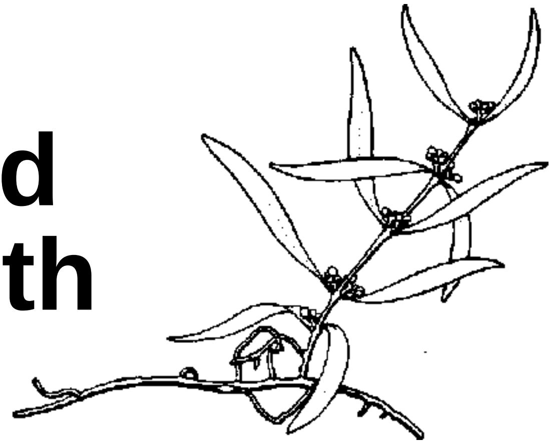
Chapter 1

Loranthaceae and Viscaceae in North America



Mistletoes of Canada, Mexico, and the United States

The mistletoes are a diverse group in the order Santales of shrubby, usually aerial, parasitic plants with fruits possessing a viscid layer (Kuijt 1968, 1969a). They are widely distributed geographically and as a group have a broad host range on conifers and other woody plants (Calder 1983). Many mistletoes are specially adapted for avian pollination and dispersal, and several avian species make extensive use of these resources (Kuijt 1969a, Watson 2001). The mistletoes are damaging pathogens of trees; and in many parts of the world are serious forest pests (Hawksworth 1983, Knutson 1983). General information on mistletoes is available at Calder and Berhhardt (1983), Cházaro and others (1992), Geils (2001a, 2001b), Gill and Hawksworth (1961), Kuijt (1969a), Mistletoe Center (2002), Nickrent (2002), Sinclare and others (1987), and Vega (1976).

The principal families of mistletoe are the Loranthaceae and Viscaceae (Calder 1983). The Eremolepidaceae, Misodendraceae, and several genera of Santalaceae could also be included as "mistletoes," but these interesting parasites do not occur on North American conifers (Kuijt 1969a, 1988, Wiens and Barlow 1971). The loranthaceous and viscaceous mistletoes had been considered sub-families within the Loranthaceae but are now recognized as distinct, related families (Barlow 1964). There are several anatomical, embryological, and chromosomal differences between the two families (Kuijt 1969a, Wiens and Barlow 1971), but a practical difference is that the flowers in the Viscaceae are small and inconspicuous, whereas those in the Loranthaceae are large, colorful, and possess a calyculus (see Venkata 1963). The Viscaceae occur in tropical and temperate zones of the Northern Hemisphere; the Loranthaceae are generally tropical (Barlow 1983). The two families overlap in Mexico (Cházaro and Oliva 1987a, 1987b, 1988a).

The mistletoes of conifers in the New World are *Cladocolea*, *Struthanthus*, *Psittacanthus*, *Dendropemon* (Loranthaceae) plus *Arceuthobium*, *Phoradendron*, and *Viscum* (Viscaceae) (table 1-1). Scharpf and others (1997) review these genera and list the other mistletoes that infect conifers elsewhere. The most important genera to North American forestry are *Arceuthobium*, *Phoradendron*, and *Psittacanthus*. Field guides or keys for the identification of these mistletoes include: Bello (1984), Bello and Gutierrez (1985), Hawksworth and Scharpf (1981), Scharpf and Hawksworth (1993), Standley (1920), Tropical Agriculture Research and Training Center (1992), and Unger (1992).

The genus *Cladocolea* Tiegh. includes at least 23 little-studied mistletoes mostly of Central and Southern Mexico (Cházaro 1990, Kuijt 1975a). Plants are erect or vine-like shrubs (fig. 1-1); most species are parasites of oaks or other broadleaf trees. These mistletoes cause little damage to their hosts; their greatest importance is scientific, as rare species in a curious genus. The species reported to infect conifers (table 1-2) are:

- *Cladocolea cupulata* Kuijt [Journal Arnold Arboretum 56(3):285–286, 1975]
- *C. microphylla* (Kunth) Kuijt [Journal Arnold Arboretum 56(3):313–317, 1975]

Mistletoes of the genus *Struthanthus* Mart. are climbing vines to several meters long (fig. 1-2). These mistletoes ("mata palo" or "tripa de pollo") include 50 to 60 species from Mexico to Argentina (Bello 1984, Cházaro and Oliva 1988a, Kuijt 1964, 1975b). The *Struthanthus* mistletoes typically have broad host ranges that occasionally include a few conifers. The genus *Struthanthus* is a taxonomically chaotic and difficult group (Kuijt 1969a); applied names should be accepted with caution. The species reported to infect conifers (table 1-2) are:

- *Struthanthus deppeanus* (Schldt. & Cham.) Blume [Systema Vegetabilium 7:1731, 1830]
- *S. interruptus* (Kunth) Blume [Systema Vegetabilium 7:1731, 1830]
- *S. palmeri* Kuijt [Canadian Journal Botany 53(3):252. 1975]
- *S. quericola* (Schltdl. & Cham.) Blume [Systema Vegetabilium 7:1731, 1830]

Table 1-1—Mistletoes of North American conifers.

Family	Genus	Distribution in North America	Conifer hosts in North America
Loranthaceae			
	Cladocolea	Mexico	*Pinus*
	Struthanthus	Mexico	*Pinus, Taxodium*
	Psittacanthus	Mexico	*Abies, Pinus*
Viscaceae			
	Arceuthobium	Canada, Mexico, United States	*Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga*
	Phoradendron	Mexico, United States	*Abies, Calocedrus, Cupressus, Juniperus, Taxodium*
	Viscum	Canada, United States	*

*In North America, *Viscum* occurs as an introduced species only on angiosperms; elsewhere *Viscum* infects *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, and *Juniperus*.

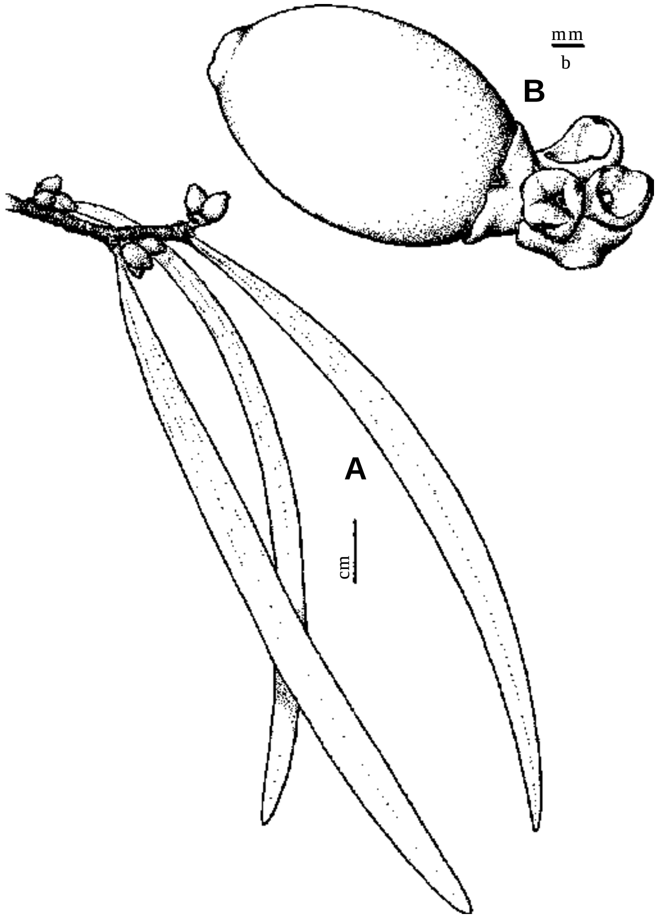


Figure 1-1—*Cladocolea cupulata*, **A** habit, pistillate plant and **B** fruit and supporting structure (three fruits removed). Illustration courtesy of Job Kuijt, edited from figure 9 in Journal Arnold Arboretum. 56(3): 285.

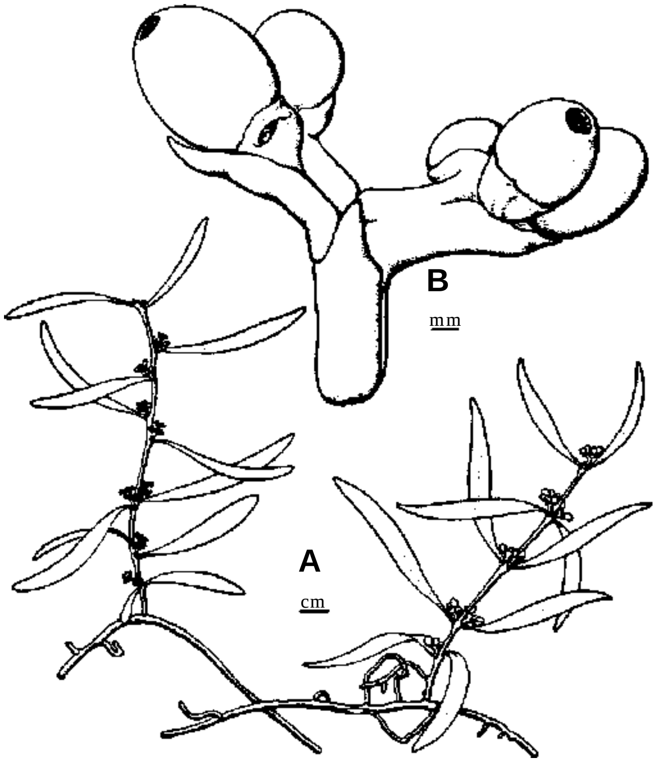


Figure 1-2—*Struthanthus palmeri*, **A** a habit, staminate plant and **B** fruit and supporting structure. Illustration courtesy of Job Kuijt, edited from figures 6 and 7 in Canadian Journal of Botany 53:252.

Table 1-2—*Cladocolea* and *Struthanthus* occurrence on conifers in Mexico.

Mistletoe	Distribution	Hosts	Reference
Cladocolea cupulata	Jalisco	*Pinus jaliscana* *P. lumholtzii*	Cházaro and others (1992)
Cladocolea microphyllus	Michoacán	*Pinus leiophylla*, *P. montezumae*, *P. pseudostrobus*	Bello Gonzalez (1984)
Struthanthus deppeanus	Chiapas, Oaxaca, Puebla, Veracruz	*Pinus patula*	Cházaro and Oliva (1988a)
Struthanthus interruptus	Michoacán	*Pinus lawsonii*	Bello Gonzalez (1984)
Struthanthus palmeri	Sonora	*Taxodium distichum* var. *mexicanum*[c]	Kuijt (1975b)
Struthanthus quericola		*Pinus* sp.	Cházaro and Oliva (1988a)

Note: These mistletoes are principally parasites of hardwoods over most of their distribution; this table presents only reports of the mistletoe on a conifer host and their joint distribution.

[a] Reported as *Struthanthus microphyllus*; determination by Kuijt (personal communication)

[b] Reported as *Struthanthus venetus*; determination by Kuijt (personal communication).

[c] Reported as *Taxodium mucronatum.*

Struthanthus palmeri (fig. 1-2) is found as far north as 60 km south of Nogales, AZ, and may be the most northern of the New World Loranthaceae (Kuijt 1975b). *Struthanthus* mistletoes cause little economic damage and are most important for scientific interest.

The genus *Psittacanthus* consists of 75 to 80 species, distributed from Mexico to Argentina on a wide range of angiosperm and gymnosperm hosts. In contrast to most of the other mistletoes of Mexico, the flowers are large and conspicuous-red, yellow, or orange (Cházaro and Oliva 1988a). Although about 10 species occur in Mexico, only four are parasites of fir or pine. These mistletoes are widely distributed but seriously damaging in only a few locations. The biology and management of these mistletoes are discussed in chapter 2.

The genus *Phoradendron* includes about 250 species, exclusive to the New World in tropical or temperate zones. Hosts include several genera of conifers, many broadleaf trees and shrubs, and other mistletoes. In some areas, *Phoradendron* mistletoes can be quite common and cause serious damage to conifers (Hawksworth and Scharpf 1981). The *Phoradendron* species on conifers are described in chapter 3.

The dwarf mistletoes, genus *Arceuthobium*, consist of 42 species of North and Central America, Europe, Asia, and Africa (Hawksworth and Wiens 1996). These mistletoes are restricted to conifers and usually quite damaging to their host. Descriptions, hosts, and distributions of 40 taxa are presented in chapter 4; damage, effects, and importance in chapter 5; survey methods in chapter 6; and management in chapters 7 and 8.

Two other genera of mistletoes are worthy of mention here. The European mistletoe, *Viscum album* L, was introduced to California by Luther Burbank about 1900 (Hawksworth and others 1991), and a recent introduction was discovered in 1988 for British Columbia (Muir 1989). Although subspecies of *Viscum album* are able to infect fir, spruce, pine, Douglas-fir, and juniper native to North America, *Viscum album* in Canada and the United States is only reported on broadleaf trees (Barney and others 1998). This mistletoe is not considered a threat to natural conifer stands in North America. Two additional species of mistletoes on conifers have been collected from Hispaniola in the Caribbean (Kuijt, personal communication). *Dendropemon constantiae* Krug & Urban is an uncommon species usually found on *Pinus occidentalis*; and *D. pycnophyllys* Krug & Urban is a common species, apparently restricted to pine hosts.

Although many mistletoe genera share host species in common, there are only a few examples of two genera of mistletoe infecting the same tree (Hawksworth and Wiens 1996). *Abies concolor* is coinfected by *Arceuthobium abietinum* and *Phoradendron pauciflorum* in California. *Pinus engelmannii* is coinfected by *A. vaginatum* subsp. *vaginatum* and *Psittacanthus macrantherus* in Durango, Mexico. *Pinus pseudostrobus* is coinfected by *A. globosum* subsp. *grandicaule* and *Psittacanthus macrantherus* in Michoacán, Mexico.

Economic and Ecological Importance

Mistletoes have long been held by many peoples as special. Their sacred, mythical role in numerous cultures is documented by Frazer (1930) in his classic study of magic and the golden bough. Mistletoes are an inspiration for art (Becker and Schmoll 1986); their haustoria produce woodroses. In traditional, agricultural societies, mistletoes provide fodder, dyes, and drugs. Mistletoes are used for holiday decoration and models for new pharmaceuticals. A few North American mistletoes are narrow endemics threatened with extinction. Rolston (1994) describes the values of such species and why they ought to be preserved. Most mistletoes, however, have

Key to Genera of Mistletoes in North America

1. Flowers with a calyculus, usually large and showy (Loranthaceae) 2
    2. Flowers less than 1 cm long, light green; leaves less than 5 cm long and 2 cm wide 3
        3. Inflorescence a determinate spike of monads .... *Cladocolea*
        3. Inflorescence generally indeterminate, dioecious .... *Struthanthus*
    2. Flowers 3–5 cm long, yellow or reddish; leaves 5–8 cm long and over 2 cm wide .... *Psittacanthus*
1. Flowers without a calyculus, less than 3 mm long, same color as the shoots; plants leafless or with leaves less than 5 cm long or 2 cm wide (Viscaceae) 4
    4. Fruit elongated and bicolored; seeds explosively dispersed (one exception); leafless; parasitic on pine, Douglas-fir, spruce, larch, fir, or hemlock .... *Arceuthobium*
    4. Fruit round, uniformly colored pink, reddish, or white; seeds dispersed by birds; leafless or with well-developed leaves, parasitic on juniper, cypress, incense-cedar, bald-cypress or fir .... *Phoradendron*

wide distributions, are locally abundant, and significantly alter the environment (Watson 2001). These mistletoes are important agents of disease, disturbance, and evolution. As pathogens, mistletoes affect host physiology (Knutson 1983, Kolb 2002). The results of tree disease are brooming, dieback, reduced growth, survival, and reproduction and increased susceptibility to other diseases and injuries. The consequences of an infestation are both economic and ecological. Mistletoes are forest pests for the commercial losses they cause and are influential symbionts for the many and complex interactions they affect. Assessing mistletoe importance revolves around two questions: how much (extent and abundance) and what effects.

Because mistletoes have major resources impacts (such as on timber yield), information is compiled regionally to describe their incidence and severity. North America consists of Canada, the continental United States of America, and the Republic of Mexico (fig. 1-3). North American mistletoes are found in most of the major coniferous forests and parasitize pine, fir, spruce, Douglas-fir, larch, hemlock, juniper, cypress, incense-cedar, and bald-cypress (table 1-1). The significant conifers not parasitized are arborvitae (*Thuja*), redwood (*Sequoia*), and giant sequoia (*Sequoiadendron*). The only mistletoes in Canada are dwarf mistletoes, but these occur across the country from Newfoundland to British Columbia. The most important are in eastern spruce bogs (Magasi 1984), central jack and lodgepole pine forests (Brandt and others 1998), and coastal hemlock forests (Alfaro 1985). Both *Phoradendron* and *Arceuthobium* occur in the United States. Although *Phoradendron* mistletoes are widely distributed across the Southern and Western States, the species that infect conifers are most common in the Western–Southwestern portion of the country (from western Texas to California, Colorado, and Oregon). *Phoradendron* mistletoes are abundant and damaging in some locations, but we know of no regional estimates of their incidence and severity. The dwarf mistletoes occur in the Northeastern States, Northern Lake States, Western States, and southeastern Alaska (see Forest Health Protection 2002). Drummond (1982) reports the infested area as 14 percent for the black spruce type in the Northern Lake States; 22 percent for the Rocky Mountain Douglas-fir type; 34 percent of the Rocky Mountain ponderosa pine type; 40 percent of the lodgepole pine type; and 22 percent of the commercial host type in Pacific states. Mistletoes including *Psittacanthus*, *Phoradendron*, and *Arceuthobium* are the principal cause of forest disease across Mexico. Mistletoes are most abundant in the cool or temperate coniferous forests and are found on more than 10 percent of the forest area (Hawksworth 1983). The forest area infected varies by State—Durango 15 percent, Nayarit 10 percent, Sonora 9 percent, Chihuahua 8.5 percent, Baja California 7 percent, Zacatecas 24 percent, Sinaloa 10 percent, and Jalisco 12 percent (Caballero 1968, 1970). Although the actual extent of infested area on a regional basis changes little from year to year, various definitions and data sources are used. These generate somewhat different estimates that are in broad agreement that mistletoes are common in some areas.

From an economic perspective, the effects of mistletoe infestation are described by Hawksworth (1993). Relevant to timber production, mistletoes reduce growth, yield, and quality and increase operation and protection costs for planning, harvesting, regeneration, and fuel management. Mistletoes are a concern in recreation areas for increased hazard from broom breakage (Hadfield 1999) and increased expense in vegetation management (Lightle and Hawksworth 1973).

From an ecological perspective, the effects of mistletoe infestations are complex because there are numerous criteria and relationships that might be considered relevant in a given situation. Allen and Hoekstra (1992) suggest describing ecological phenomena from alternative viewpoints or “criteria” of the population, species, community, landscape, and ecosystem. For a diseased tree, mistletoe infection means reduced competitive status and reproduction fitness (but see van Ommeren and Whitham 2002). The symbiotic relation between host and mistletoe has numerous population genetic and coevolutionary consequences that cannot be properly categorized as positive or negative (see Atsatt 1983, Norton and Carpenter 1998). Other species in addition to a host also are connected to the mistletoe by herbivory, pollination, use of the witches’ broom, or other relations. Watson (2001) recognizes mistletoes as keystone resources in many communities. Canopy effects are especially significant. Crown deformation and tree death affect composition of trees that compose the forest canopy and the structure of that canopy (Reid and others 1995). Numerous species, landscape, and ecosystem processes are consequently influenced—there are winner and losers, increases and decreases. Many indirect and long-term interactions involving mistletoes exhibit chaotic behaviors; a range of outcomes are likely rather than a single one determined (see Gleick 1988). The relevant fact is that mistletoes are often an important ecological and evolutionary agent driving that system (Holling 1992).

Management Strategies

The mistletoe literature indicates not only that mistletoes have important effects but also that infestations can be affected by management intervention to change their spread and intensification. Effective

Figure 1-3—North America, Canada, United States of America, and Mexico with political subdivisions.

Canadian Provinces, Territories and abbreviations

Province-Territory	Abbreviation
Alberta	Alta.
British Columbia	B.C.
Manitoba	Man.
New Brunswick	N.B.
Newfoundland	Nfld
Northwest Territories	N.W.T.
Nova Scotia	N.S.
Ontario	Ont.
Prince Edward Island	P.E.I
Quebec	Que.
Saskatchewan	Sask.
Yukon Territory	Y.T.

Mexican States and abbreviations

Mexican state	Abbreviation
Aguascalientes	Ags.
Baja California	B.C.
Baja California Sur	B.C.S.
Colima	Col.
Coahuila	Coah.
Chiapas	Chis.
Distrito Federal	D.F.
Durango	Dgo.
Guerrero	Gro.
Guanajuato	Gto.
Hidalgo	Hgo.
Jalisco	Jal.
Michoacan	Mich.
Morelos	Mor.
México	Edo de Mex.
Nayarit	Nay.
Nuevo León	N.L.
Oaxaca	Oax.
Puebla	Pue.
Quintana Roo	Q. Roo
Querétaro	Qro.
Sinaloa	Sin.
San Luis Potosí	S.L.P.
Sonora	Son.
Tabasco	Tab.
Tlaxcala	Tlax.
Tamaulipas	Tamps.
Veracruz	Ver.
Yucatán	Yuc.
Zacatecas	Zac.

U.S. states and abbreviations

Province-Territory	Abbreviation
Alabama	AL
Alaska	AK
Arizona	AZ
Arkansas	AR
California	CA
Colorado	CO
Connecticut	CT
Delaware	DE
Dist. of Columbia	DC
Florida	FA
Georgia	GA
Idaho	ID
Illinois	IL
Indiana	IN
Iowa	IA
Kansas	KS
Kentucky	KY
Louisiana	LA
Maine	ME
Maryland	MD
Massachusetts	MA
Michigan	MI
Minnesota	MN
Mississippi	MS
Missouri	MO
Montana	MT
Nebraska	NE
Nevada	NV
New Hampshire	NH
New Mexico	NM
New Jersey	NJ
New York	NY
North Carolina	NC
North Dakota	ND
Ohio	OH
Pennsylvania	PA
Rhode Island	RI
South Carolina	SC
South Dakota	SD
Tennessee	TN
Texas	TX
Utah	UT
Vermont	VT
Virginia	VA
Washington	WA
West Virginia	WV
Wisconsin	WI
Wyoming	WY

intervention is both purposeful and persistent. Tkacz (1989) describes an approach called Integrated Resource Management used in the Southwestern Region, USDA Forest Service, that incorporates forest insect and disease considerations into a planning, implementing, and monitoring process. Many other organizations have comparable management systems. Common elements of these systems include (1) formulation of objectives, (2) review of the expected performance of alternatives, (3) selection and implementation, and (4) monitoring and reaction. Holling and Meffe (1996) warn of the dangers from attempting rigid control in natural resource management; they advocate an adaptive process for complex environments with changing objectives and management options. Although management in mistletoe-infested stands has not always been successful for various reasons (Conklin 2000), management processes and techniques are available with the potential for producing desirable results.

A simplistic review of one management strategy that once dominated conifer forestry is instructive. A prevailing objective on public forests in the 20th century was sustained economic production of timber. Foresters knew that dwarf mistletoes were obligate parasites that died when the host tree was cut and had limited capability of spread (Weir 1916b). The preferred control technique was clearcutting in large blocks to remove the mistletoe and retard reinfestation (Stewart 1978). Where employed, it worked. A challenge to forest pathologists arose when objectives were expanded to include wildlife and aesthetic values, and treatments required or produced infrequent, selective removal that left infected trees. At least in the American Southwest, dwarf mistletoe infestations were not fading away (Conklin 2000, Maffei and Beatty 1988). Other control techniques based on biological, chemical, genetic, and silvicultural approaches were needed (Scharpf and Parmeter 1978, Muir 1993).

Hawksworth (1978) and Parmeter (1978) describe the epidemiological bases for control of dwarf mistletoes that can be extended with modification to other mistletoes. For technical and management reasons, silvicultural approaches have been used more commonly than chemical or biological control or genetic selection. Although there has been some success with chemical controls, phytotoxicity and need for reapplication have limited this approach (Adams and others 1993, Lichter and others 1991, Scharpf 1972). The concepts of control with biological agents are well developed (DeBach 1964), and use of insects and fungi on mistletoes has been considered (Cházaro and others 1992, Julian 1982, Mushtaque and Balock 1979). There is evidence for inherited variation in host resistance to infection by at least the dwarf mistletoes. Genetic selection may provide regeneration alternatives (Ringnes and others 1996). Silvicultural approaches include pruning, sanitation, species replacement, and other techniques that rely on cutting trees. As with chemical, biological, and genetic approaches, cultural methods must be adapted to fit the mistletoe and host combination in the context of specific management objectives and constraints.

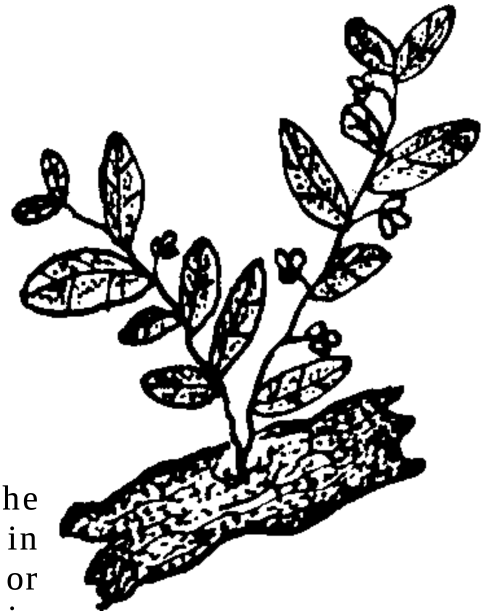
Assessment and monitoring are essential elements of a strategy for managing mistletoes. Mistletoe infestations initially develop slowly but accelerate rapidly and cause significant departure from typical stand development. These facts suggest that early intervention provides greater flexibility and that a good model of stand response is useful for predicting what a treatment might produce in 20 to 40 years. Although the Dwarf Mistletoe Impact Model (Forest Health Technology Enterprise Team 2002) is primarily intended for assessing silvicultural alternatives, it (and other models) can be modified or developed for evaluating tactics of deploying biological agents or genetically selected stock (Robinson and others 2002).

The mistletoes of North American conifers range from obscure species in remote locations to major forest pests. Management varies from intensive timber production to biological conservation. Although these mistletoes can have significant impacts on forest conditions, they are also subject to management influence through various methods that alter rates of spread and intensification. Knowing which methods are appropriate and effective requires an understanding for each kind of mistletoe: its life history, hosts, distribution, effects, and ecology.

I. Vázquez Collazo
B. W. Geils

Chapter 2

Psittacanthus in Mexico



The *Psittacanthus*, parrot-flower, is the only genus of the family Loranthaceae that is significant to conifer forestry in North America. These mistletoes do not occur in Canada or the United States; and in Mexico, they are only important in central and southern portions. *Psittacanthus* also occurs in Central America (rarely on conifers) and other regions of the tropical New World where these mistletoes achieve their greatest diversity and abundance on numerous hardwoods. Plants are showy (fig. 2-1), become quite large, and are locally abundant. They are damaging to conifers, but they also provide special resource values. Because there are few studies for *Psittacanthus* on conifers (for example, Vázquez 1993a) and the taxonomy is confused, information on these mistletoes is sparse and difficult to interpret. This chapter reviews *Psittacanthus* on conifers with regard to life cycle, description, damage, importance, and management.

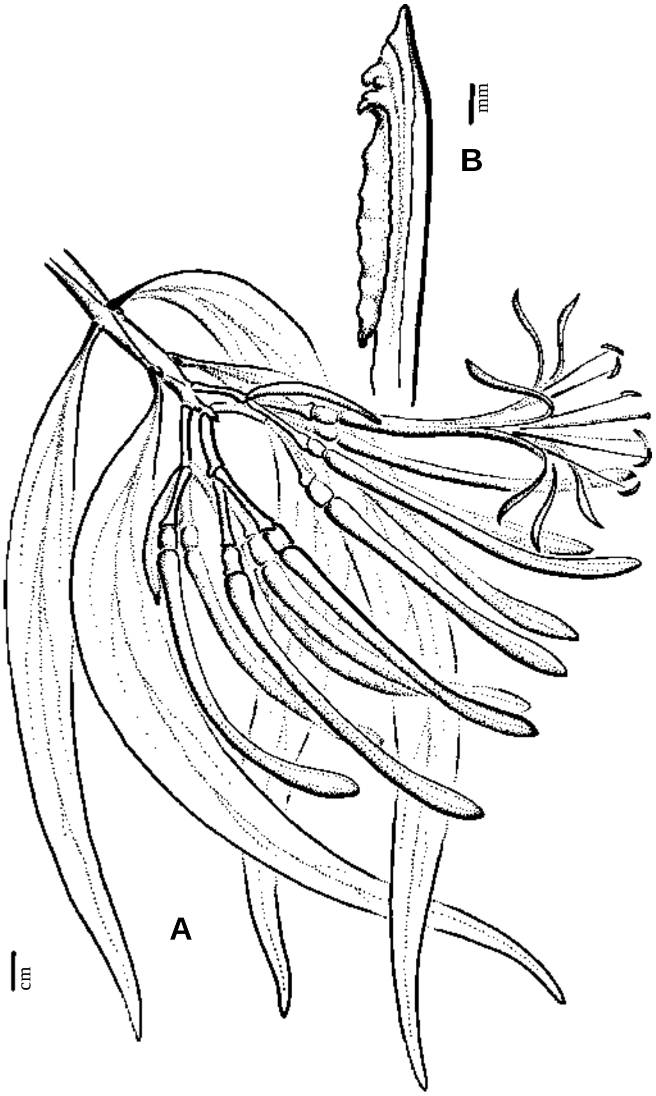


Figure 2-1—*Psittacanthus angustifolius*, **A** habit, leaves and flowers and **B** tip of petal. Illustration courtesy of Job Kuijt, edited from figure 10 in Annals Missouri Botanical Garden. 74:524.

General Life Cycle

The life cycle of *Psittacanthus* is divided into the fundamental processes of dispersal and development separated by inoculation and germination. Although some seeds are dispersed to the lower branches of an infested host by gravity, *Psittacanthus* is typically dispersed by birds feeding on fruits and defecating on branches. Incubation and production of the first flowers require several years. Once established, however, the infection is perennial, and the mistletoe produces a large haustorium with many long branches. Although *Psittacanthus* does photosynthesize, it is a parasite, and when it becomes large, it seriously interferes with host growth and reproduction.

Some of the *Psittacanthus* features that enhance bird-dispersal are time and duration of maturation, fruit size and attractiveness, adaptations for passage through the digestive tract, adhesion, and rapid germination after being voided (see Kuijt 1969a). Watson (2001) reviews the literature on coevolution of mistletoes and associates. Salas (1988) reports a study of *Psittacanthus* dispersal by birds at three sites in Michoacán (table 2-1). He observes that only eight out of 162 captured birds (4.9 percent, two crescent-chested warblers, a single Audubon's warbler, and two Bullock's orioles) carried mistletoe seeds in their feathers. Typical dispersal of *Psittacanthus* is for a passerine bird to feed on the fruit, fly to another tree, and void the seed to a suitable branch for infection. As with other mistletoes, those factors that influence bird abundance, distribution, and feeding behavior also affect the mistletoe's dispersal, population dynamics, host relations, and evolution (Lopez and Ornelas 1999).

Vázquez (1989) summarizes a 5-year study of *Psittacanthus calyculatus* on *Pinus douglasiana* in Michoacán. Additional data from that study are reported here (fig. 2-2) with observations of annual phenology (table 2-2). Bello (1984) provides photographs of an establishing seed, young plant, developing haustorium, and severely infested tree. *Psittacanthus* fruits are large (2.0 by 2.5 cm), and seeds have a sticky (viscous) layer that easily adheres them to a branch. When the basal portion of a mature seed makes contact, the seed germinates, opens its large cotyledons, and establishes an infection. Then 5 months later, the first true leaves are produced. Vegetative growth with more leaves and branches continues throughout the first year. Although shoot growth is determinate, the plant branches dichotomously expand its total length over the first 3 years at a rate of 30 cm per year. In May of the fourth year, shoot terminals begin producing flower buds. Full flowering is reached in 6 months; pollination occurs in November and December. The usual pollinators for most species are thought to be hummingbirds; but Freeman and others (1985) suggest passerine birds are the principal pollinators of *P. calyculatus* in Sinaloa. Senescing flowers are shed from November through March of the fourth year. Fruit maturation requires about 1 year and occurs from November to February of the fifth year. A generation therefore requires on average about 5 years to complete. Mature plants continue to flower and grow each year with an annual phenology that varies by host and elevation. On *Pinus douglasiana* at 1,700 m above sea level, full flowering occurs in November; on *P. pseudostrobus* at 2,400 m, flowering is delayed 3 months. Although an infection begins as a small plant growing *on* a host branch, it can

Table 2-1—Dispersal of *Psittacanthus calyculatus* at three sites in Michoacán, Mexico, for three guilds of bird species.

Guild	Species	Site Canoa alta	 Capácuaro	 Cicapien
Insectivore				
	a Flycatcher	X	-	-
	Audubon's warbler	X	X	X
	Hermit warbler	-	-	X
	Common yellowthroat	X	-	-
	Black and white warbler	-	X	-
	Painted redstart	X	-	X
	Gray-sided chickadee	-	-	X
	Olive warbler	-	X	X
	Bushtit	-	X	X
	White-breasted nuthatch	-	-	X
	Warbling vireo	X	-	-
	Hutton's vireo	-	-	X
	Crescent-chested warbler	X	-	X
	Wilson's warbler	-	-	X
Omnivore				
	Bullock's oriole	X	X	X
	Gray silky-flycatcher	X	-	X
	American robin	-	X	X
Granivore				
	Rufous-capped brush-finch	-	X	X
	Black-headed grosbeak	-	X	X

Source: Salas (1988).

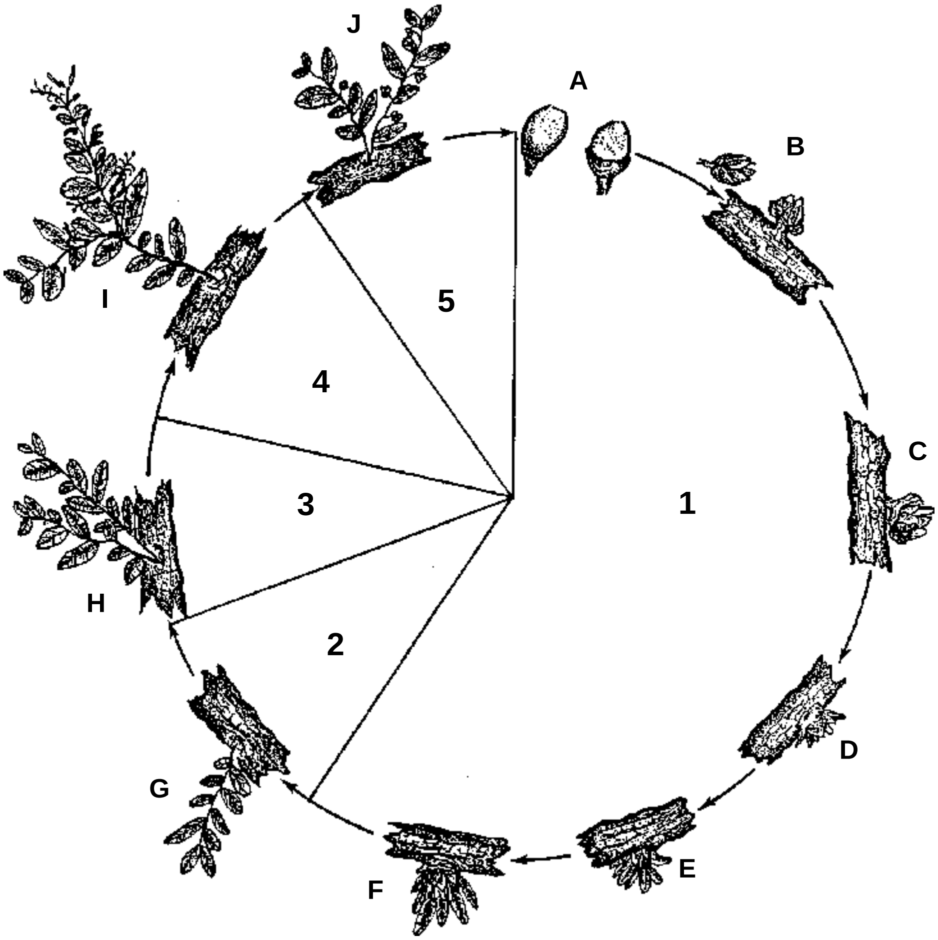


Figure 2-2—Life cycle of *Psittacanthus calyculatus*, from observations by Vázquez (1989) over a 5-year period. Year 1: A October, fruit matures; B November, infection; C November, cotyledons appear, D April, leaf buds appear; E October, leaves sprout; F October, leaves develop. Year 2: G continued vegetative growth. Year 3: H additional shoots develop. Year 4: I November, flowering. Year 5: J November, fruits mature.

Table 2-2—Phenology of *Psittacanthus calyculatus* on *Pinus douglasiana.*

	Month [a]											
Stage [b]	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**June**	**July**	**Aug.**	**Sept.**	**Oct.**	**Nov.**	**Dec.**
V1	X	X	-	-	-	-	-	-	-	-	-	-
V2	X	X	X	-	-	-	-	-	-	-	-	-
V3	X	X	X	X	X	X	X	X	X	-	-	-
FL1	X	X	X	X	X	X	X	X	-	-	-	-
FL2	X	X	-	-	-	-	-	-	-	-	-	-
FL3	X	X	-	-	-	-	-	-	-	-	-	-
FR1	X	X	X	X	-	-	-	-	-	-	-	-
FR2	X	X	X	X	X	X	X	X	X	X	X	X
FR3	X	X	X	X	-	-	-	-	-	-	-	-

[a] Month during which stages of life cycle are evident.

[b] V1 = early vegetative, V2 = full vegetative, V3 = final vegetative, FL1 = early flowering, FL2 = full flowering, FL3 = final flowering, FR1 = early fruiting, FR2 = full fruiting, FR3 = final fruiting.

ultimately *replace* the entire terminal portion of the host branch. With the vegetative growth of a single plant and sexual reproduction generating new plants, an infestation can eventually take over most of a tree's crown. Vázquez (1986) suggests a four-class system for rating infestation severity.

Kuijt (1967, 1970) describes the interesting anatomy and morphology of seedlings, seedling establishment, and the haustorium of *Psittacanthus*. Seedlings and the haustorium have several particular features that help construct a phylogeny for the genus (Kuijt 1983). The haustorium in *Psittacanthus* becomes quite large and is even harvested as a specialty product (see below).

Description of Genus

Psittacanthus
Mistletoe, parrot-flower, muérdago verdadero

Shrubby parasites of trees and other woody plants; stems brittle, erect, cylindrical or square, frequently ridged; epicortical root absent, primary haustorium often large; phyllotaxy opposite or whorled, leaves large (maximum 1 m in length), leathery or fleshy, green, persistent, opposite; leaf blade cordate, obovate, oval or lanceolate; leaf apex pointed; floral bracts short and stout; flower bisexual, six-partite, with a tubular perianth, 3 to 8 cm long, yellow, red, or orange, smooth; stamens dimorphic, as numerous as perianth lobes; anthers rarely more than 6 mm; ovary inferior, one-chambered; fruit berry, elliptical, green initially, developing into black or dark brown seed; endosperm lacking or apparently so (Standley 1920 but see Kuijt 1983).

Psittacanthus is endemic to the New World and ranges from Mexico to Argentina (Cházaro and Oliva 1988b). According to Reséndiz and others (1989), *Psittacanthus* is found in 25 Mexican States, absent only from Aguascalientes, Coahuila, Chihuahua, Hidalgo, Nuevo León, Tamaulipas, and Distrito Federal. Although *Psittacanthus* is distributed throughout Mexico, it is most common in the Central and Southern regions. Most species of *Psittacanthus* have broad host ranges on numerous woody hardwoods; some include conifers among their hosts. On conifers, *Psittacanthus* is limited to the cool temperate forests where conifers occur. The elevational distribution in Mexico ranges from 800 m on *Pinus oocarpa* to 3,300 m on *P. rudis*.

The taxonomy of *Psittacanthus* is quite confused; a comprehensive, monographic treatment would greatly benefit our understanding of the genus. Because of misidentification or subsequent taxonomic revision, numerous reports and publications refer to mistletoes using names that do not properly apply; sufficient information to identify the subject mistletoe is seldom given. These taxonomic difficulties are being overcome with projects such as Flora Mesoamericana (2002). Managers and researchers can reduce the confusion in the future by filing voucher specimens with a recognized herbarium for identification and future reference.

Standley (1920) initially describes only seven species of *Psittacanthus* for Mexico; Reséndiz and others (1989) later recognize 14 species for the country. Host data are frequently absent or sparse (genus only) on herbarium labels, but Reséndiz and others (1989) compile available data for Mexico from numerous collections. They report as hosts of *Psittacanthus* more than 50 genera of angiosperms and conifers, including trees, shrubs, and cactus. The primary angiosperm hosts are *Quercus*, *Acacia*, *Juglans*, *Ficus*, *Populus*, *Salix*, *Prunus*, *Prosopis*, *Annona*, *Bursera*, *Citrus*, *Nerium*, *Olea*, *Crataegus*, *Bacharis*, *Fraxinus*, *Eucaliptus*, *Persea*, *Cassuarina*, *Pseudosmondingium*, *Arbutus*, *Ulmus*, *Liquidambar*, *Psidium*, *Spondia*, *Phitecellobium*, *Amphipterigium*, *Pyrus*, *Mimosa*, and *Cydonia*. No monocots are known to be parasitized. *Psittacanthus* throughout its range is reported for conifers mostly on pine (table 2-3). In Mexico, the most common *Psittacanthus* species on conifers are *P. calyculatus* and *P. macrantherus* (Bello and Gutierrez 1985). Mathiasen and others (2000c) first report *P. angustifolius* on pine in Southern Mexico; this and other species (for example, *P. pinicola*) may be more widely distributed than apparent from the literature.

Description of Species

Only several species of *Psittacanthus* are reported as parasites of conifers in Mexico. Because of taxonomic uncertainty and the recent discovery of a new species for Mexico, we include in addition to frequently reported mistletoes several other species known or suspected to infect conifers in Mexico.

1. *Psittacanthus americanus*

Psittacanthus americanus (Mart.), Flora 13:108, 1830.
=*Loranthus americanus* L

Description. Shrub 1 m tall; shoots erect and spreading, square or more or less angular, smooth; leaves fleshy, ovate, elliptical, rounded, 6 to 10.5 cm long by 3 to 6.5 cm wide, apex very obtuse; petiole short; perianth 6 cm long, bright red or orange; fruit berry, 0.8 by 1.0 cm, green initially, developing into reddish brown (Bello and Gutierrez 1985, Standley 1920).

Discussion. Vázquez and others (1986) refer to *Psittacanthus americanus* as abundant on *Pinus leiophylla*, *P. teocote*, and *P. montezumae* at sites in Michoacán. Standley (1920) adds Guerrero, and Bello and Gutierrez (1985) add Chiapas and Veracruz to the distribution. Reséndiz and others (1989) describe the species as having the smallest elevational range of the Mexican species. Kuijt (personal communication), however, reserves the name *Psittacanthus americanus* for a mistletoe of the Lesser Antilles that is not found in North or Central America. The collections of *Psittacanthus americanus* from Mexico should be reexamined.

2. *Psittacanthus angustifolius*

Psittacanthus angustifolius Kuijt, Ann. Missouri Bot. Gard. 74:523–525, 1987.

Description. Stems sharply angular; leaves paired, narrow, thin, 17 by 2.5 cm, base acute, apex attenuate; petiole to 5 mm long; inflorescences terminal, of four to six triads (groups of three); triad peduncles about 1 cm long, lowest with bracts to 2 cm long; bud stout, straight or somewhat curved; petals orange, 7.5 to 8 cm long, petal apices 4 mm wide, blunt, each with a

Table 2-3—Conifer hosts of *Psittacanthus* as reported in examined literature.

Host species	Reference
Abies religiosa	Bello (1984), Bello and Gutierrez (1985)
Cupressus sp.	MartÌnez 1983
Pinus caribaea var. *hondurensis*	Kuijt (1987), Mathiasen and Howell (2002)
Pinus douglasiana	Bello (1984), Bello and Gutierrez (1985), Vázquez (1989)
Pinus lawsonii	Bello (1984)
Pinus leiophylla	Bello (1984), Bello and Gutierrez (1985), Gibson (1978), Vázquez (1989), Vázquez and Pérez (1989), Vázquez and others (1982, 1985, 1986)
Pinus maximinoi	Mathiasen and others (2000b)
Pinus michoacana	Bello (1984), Bello and Gutierrez (1985)
Pinus montezumae	Vázquez (1989), Vázquez and Pérez (1989), Vázquez and others (1982, 1985, 1986)
Pinus oocarpa	Mathiasen and others (2000b)
Pinus oocarpa var. *ochoterenia*	Mathiasen and others (2000c)
Pinus pseudostrobus	Bello (1984), Gibson (1978)
Pinus tecunumanii	Melgar and others (2001)
Pinus teocote	Bello (1984), Bello and Gutierrez (1985), Vázquez and Pérez (1989), Vázquez and others (1982, 1985, 1986)

fleshy ligule-like median crest extending inwards (see fig. 2-1); anthers 6 mm long (Kuijt 1987).

Discussion. Kuijt (1987) only reports the host as pine, but the reported host range now includes *Pinus caribaea* var. *hondurensis*, *P. oocarpa*, *P. oocarpa* var. *ochoterenia*, *P maximinoi*, *P. tecunumanii*, and *Psidium guineese* (Mathiasen and Howell 2002, Mathiasen and others 2000b, Mathiasen and others 2000c, Melgar and others 2001). The mistletoe is known from Nicaragua, Belize, Honduras, Guatemala, and Mexico (Chiapas). Although the mistletoe appears to be more common and damaging in Central America (Mathiasen and others 2000c), it has only recently been described, and new populations are being discovered. With its wide host range, it may be more common in southern Mexico than presently reported.

3. *Psittacanthus calyculatus* (*sensu lato*)

Psittacanthus calyculatus (DC.) G. Don, Gen. Syst. 3:415, 1834.
Psittacanthus rhynchanthus (Bentham) Kuijt, Ann. Missouri Bot. Gard. 74:529, 1987
=*P. chrismarii*

Description. Shrub 1.0 by 1.5 m tall, herbaceous initially but becoming woody; stems green, quadrangular or ridged when young; leaves dark green, 5 to 14 cm long by 1.4 by 6 cm wide, leathery, lanceolate or elliptical to ovate, smooth; leaf blade asymmetric, margin undulating, with long attenuate apex and cuneate base, venation pinnate and prominent; inflorescence terminating the shoot; flower buds strongly incurved, 4 cm long, tip acute, base dilated, on peduncles up to 2 cm long, bracts fused to cup-like structure, in triads, perianth 3 to 5 cm long, red to orange, smooth; stamens as numerous as perianth lobes; fruit berry, 2.5 cm long by 2 cm wide, glabrous, with flaring calyculus (Bello and Gutierrez 1985, Hernandez 1991). Bello (1984) and Cházaro and Oliva (1988a) provide brief descriptions and illustrations.

Kuijt (1987) recognizes two similar taxa of *Psittacanthus* initially described as *Loranthus calyculatus* and *L. rhynchanthus*. He applies the name *P. calyculatus* to the Mexican species (Puebla and Morelia) in which the mature, unopened bud is nearly straight with a blunt tip, and the name *P. rhynchanthus* to a lowland, Mesoamerican (to Venezuela) species in which the bud is distinctively curved and beaked. He describes a number of additional characteristics that distinguish the two, such as symmetrical leaves 8 by 4 cm for *P. calyculatus* and asymmetrically curved, larger leaves 12 by 4 cm for *P. rhynchanthus*. Kuijt (1987) does not mention any host preference differences, but given the southern and lowland distribution of *P. rhynchanthus*, we suspect the more common parasite of conifers in Mexico is *P. calyculatus*. These differences, however, can only be resolved by examination of voucher specimens in light of Kuijt's interpretation of the type material.

Discussion. Bello (1984) lists the conifer hosts of *Psittacanthus calyculatus* as *Abies religiosa*, *Pinus douglasiana*, *P. lawsonii*, *P. leiophylla*, *P. michoacana*, *P. pseudostrobus*, and *P. teocote*. Vázquez here adds *Pinus montezumae*, *P. herrerai*, *P. pringlei*, and *P. rudis* and describes this as the species with the most number of conifer hosts, largest distribution, and most importance. Bello and Gonzales (1985) locate the mistletoe (without host distinction) as from Tamaulipas to Jalisco, Chiapas, Yucatan, Oaxaca, Valley of Mexico, Guanajuato, Morelia, and Michoacán. Freeman and others (1985) add Sinaloa, and Hernandez (1991) adds Tlaxcala. The mistletoe in Michoacán is widespread, mostly found in the subhumid temperate zones, from 1,300 to 2,750 m (Bello and Gonzales 1985). In natural stands of *P. leiophylla* and *P. pseudostrobus* in Michoacán, Gibson (1978) observes the mistletoe has a patchy distribution and some sites are severely infested. Vázquez (1989) describes the life cycle and phenology of this mistletoe. Vázquez (1994b) and Vázquez and others (1986) discuss control.

4. *Psittacanthus macrantherus*

Psittacanthus macrantherus Eichl., Mart. Flora Brasilense. 5(2):26, 1868.

Description. Shrub 1.0 m tall; shoots stiff, brown, cylindrical, glabrous; leaves 6 to 7.5 cm long, fleshy, elliptical, obovate, margin entire, apex obtuse, base attenuate; perianth 5.5 to 6.5 cm long, yellow or orange, large; anthers 18 mm long, as numerous as perianth lobes; fruit berry, green, glabrous (Bello and Gutierrez 1985, Standley 1920).

Discussion. Bello and Gutierrez (1985) only identify the hosts as pine and fir; but Vázquez (here) describes the pine hosts as *Pinus engelmannii*, *P. herrerai*, *P. lawsonii*, *P. lumholtzii*, *P. oocarpa*, and *P. pseudostrobus*. The mistletoe occurs locally in the Sierra de San Pedro Nolasco, Jalisco (Cházaro 1989b), Oaxaca and Michoacán (Bello and Gutierrez 1985), and Sinaloa (Gentry 1946). It ranges in elevation from 1,300 to 2,200 m. It is the second most important *Psittacanthus* on conifers in Mexico.

5. *Psittacanthus pinicola*

Psittacanthus pinicola Kuijt, Ann. Missouri Bot. Gard. 74:525–529, 1987.

Description. Stems terete, becoming fissured and black with age; leaves symmetrical, in irregular whorls of three 11 by 2.5 cm, elliptical to lanceolate; apex rounded, base tapered; inflorescences lateral, axillary, often on older leafless stems, an umbel of two or three dyads (groups of two); petals 4 cm long, red with yellow-green tip, orange in middle, ligulate at base; buds inflated at ovary to 5 mm, tapering to slender, curved tip at 1.5 mm; anther 3 to 4 mm long (Kuijt 1987, includes two illustrations).

Discussion. This attractive mistletoe is distinguished by the combination of parasitism on pine (*Pinus caribaea*) and inflorescences composed of pairs of flowers. The species is known from Central America at elevations below 650 m; it appears not to cause serious damage (Mathiasen and Howell 2002). Although we are aware of no collections from Mexico, other mistletoes (namely *Arceuthobium hondurense*) have recently been found to have widely disjunct distributions from Honduras to Mexico.

6. *Psittacanthus schiedeanus*

Psittacanthus schiedeanus (Schltdl. & Cham.) Blume, Sys. Veg. 7(2):1730, 1830.

Description. Shrub large, to 50 cm; stems, sharply quadrangular and four-winged until large lenticels develop; nodes flattened; haustorium very large; leaves bluish-green, 20 cm long by 8 cm wide; leaf blade asymmetric, ovate 6 to 16 by 1.4 by 4.5 cm; apex attenuate; petiole distinct and stout; venation pinnate; inflorescence terminal, leafless, forked; flowers 6.5 to 8 cm long in bud, on peduncles 1.5 to 2 cm long, perianth orange, 3 to 5 cm long, segments linear, separated to base, recurved; stamens dimorphic, very slender; fruit berry, 1.5 cm long by 1 cm wide (Bello and Gonzales 1985, Standley 1920). Bello (1984), Cházaro and Oliva (1988a), and Hernandez (1991) provide illustrations. Kuijt (1967) describes seedling structure and development in great and illustrated detail.

Discussion: The hosts most commonly reported for *Psittacanthus schiedeanus* are oaks and other hardwoods (Bello 1984, Lopez and Ornelas 1999). Vázquez and others (1982) name *Pinus leiophylla*, *P. montezumae*, and *P. teocote* as important, damaged hosts in Michoacán. Collections from Honduras (EAP) extend the hosts to include *P. oocarpa*. Standley (1920) reports this mistletoe as occurring in Central America and Mexico from Veracruz to Michoacán and Oaxaca. Hernandez (1991) describes its distribution in Tlaxcala, and it is collected from Chiapas (Flora Mesoamericana 2002).

Damage and Effects on Host

Damages produced by *Psittacanthus* to pine hosts include reductions of diameter increment, cone production, and seed viability. Vázquez and others (1982, 1985) report a series of studies from Michoacán to determine the effects of *Psittacanthus* to *Pinus leiophylla*, *P. montezumae*, and *Pinus teocote*.

Vázquez and others (1982, 1985) observe that the reduction in diameter increment for trees infected by *Psittacanthus* varies by host species and size class. The diameter increment of infected *Pinus leiophylla* trees is only 10 percent of uninfected trees (0.7:7.0 mm per year). The diameter increments of infected *P. montezumae* and *P. teocote* are both 47 percent of uninfected trees of the species, although the two species grow at different absolute rates (0.2:5.3 mm and 0.7:1.5 mm per year, respectively). Increment losses are greatest in the 20-cm diameter class for *P. leiophylla* and *P. montezumae* and in the 40-cm class for *P. teocote*. Reduction in diameter increment can also be expressed as loss in productivity or volume. Reduced volume production by infected *P. leiophylla* corresponds to half the annual productivity of 127 trees per ha or 0.0186 m^3 per tree per year. Infected *P. montezumae* lose the equivalent of 0.0843 m^3 per tree per year; infected *P. teocote* lose 0.0150 m^3 per tree per year. In terms of growth, *P. montezumae* is the species most severely impacted.

Vázquez (1986) uses a four-class rating system (table 2-4) to stratify *Psittacanthus*-infected trees by disease severity and to assess the effects on reproductive potential (Vázquez and Pérez 1989). They observe that severely infected trees of *Pinus montezumae* and *P. teocote* fail to produce cones, and *P. leiophylla* produces 23.8 percent fewer cones. Moderately infected trees of *P. montezumae* produce 37.5 percent fewer cones, and moderately infected *P. teocote* produce 19.4 percent fewer cones. No reduction in cone production is noted for moderately infected *P. leiophylla* or lightly infected trees of any species. They also note an effect on seed germination. Seeds from severely infected *P. leiophylla* exhibit only a 67 percent germination rate. Seed germination from moderately infected trees is reduced 25 percent for *P. montezumae* and 5 percent for *P. teocote*. In terms of reproductive loss, *P. montezumae* is the species most severely impacted.

Economic and Ecological Importance

Although *Psittacanthus* is established as a widespread and damaging parasite of conifers in Mexico, it is also important for medicine, crafts, and wildlife

Table 2-4—Four-class rating system for evaluating severity of diseases caused by *Psittacanthus.*

Disease index	Infection class	Percent of crown infected
0	uninfected	0
1	light	1–30
2	moderate	31–60
3	severe	61–100

(Cházaro and others 1992). Vázquez and others (1982, 1985) and Vázquez and Pérez (1989) document the impacts of *Psittacanthus* on conifer growth and reproduction. Martinez (1983) reports that 3,396 ha of *Pinus lumholtzii*, *P. montezumae*, *P. leiophylla*, *Cupressus*, *Quercus*, and *Alnus* in Jalisco, Mexico, and Michoacán are infested by *Psittacanthus*. Over most of its extensive range, however, *Psittacanthus* appears to occur as small patches of a few infected trees. Traditional medicines are produced from the mistletoe; Browner (1985) identifies some of these uses in Oaxaca. The large haustorium of an old *Psittacanthus* infection causes distorted growth of the host branch into an interesting form resembling a rose or similar flower after the mistletoe tissue is removed. Artisans use these woodroses to produce lamp stands and other decorative, craft items (Cházaro and others 1992). These mistletoes are also used and are important to numerous birds for nectar and fruit (Freeman and others 1985, Lopez and Ornelas 1999, Salas 1988).

Management Strategies

The *Psittacanthus* mistletoes are easily detected, obligate parasites, with long life cycles, and slow rates of spread and intensification. Because of these attributes, economic control is generally feasible. Chemical and silvicultural methods are used for mistletoe control; some biological control occurs naturally but has not been developed as management tool (Cházaro and others 1992, Hernandez 1991).

Biological Control

The principal insects that feed on *Psittacanthus* belong to the order Homoptera, including scale insects *Coccus*, *Saccharicoccus*, *Gascardia*, and *Aenidomytilus*, and the aphid *Macrosiphum* (Vázquez and others 1986). These homopterans feed exclusively on plant sap, infesting leaves, branches, flowers, and fruits. A heavy infestation weakens and may eventually kill a host mistletoe plant. *Macrosiphum* has the best potential as a biological control agent because aphids are excellent vectors of viruses (Horst 2002), which are themselves agents of biological control.

Vázquez and others (1986) report isolating the fungi *Alternaria*, *Ceratocystis*, and *Fumago* from *Psittacanthus*. The disease caused by *Alternaria* (see García 1977, Horst 2002) in *Psittacanthus* produces leaf spot of older leaves and blight of young branches. The fungus spreads quickly during wet periods and induces concentric dark lesions, which lead to extensive necrosis of mistletoe leaves and shoots. Because *Ceratocystis* causes much damage and is readily cultured, it has a good potential as a biological control agent. *Fumago* causes blights and sooty molds; these fungi are very common in tropical and subtropical agriculture around the world. The development of *Fumago* is promoted by the secretions of some Homopterans (aphids and scales). The resulting disease and infestation can produce reactions in the host plant similar to symptoms caused by mistletoe itself; severe leaf infestations reduce photosynthesis and therefore growth (García 1977, Horst 2002).

Chemical Control

Few studies for chemical control of *Psittacanthus* on conifers are published (for example, Vázquez 1994b). Vázquez and others (1986) describe an experiment in Michoacán on *Psittacanthus calyculatus* and *P. americanus* infecting *Pinus leiophylla*. They report 1-month and 6-month evaluations of commercial application of four herbicides: two 2,4-D derivatives (Esterón and Fitoamina), one pyridine (Gramoxone), and one urea derivative (Karmex). At neither observation time did Karmex appear to damage the mistletoe. At 1 month, Gramoxone appears to provide excellent control with high mortality rate (80 percent) of fruits, leaves, and branches and slight transient phytotoxicity in the pine. At 6 months, however, the mistletoe treated with Gramoxone recovers and produces new vigorous buds, flowers, and fruits. Therefore, Gramoxone only causes a temporary delay in mistletoe development. At 1 month, Fitoamina causes severe damage, 40 percent defoliation, to mistletoe leaves and tender buds but has less effect on the mistletoe fruits. At 6 months, Fitoamina affects 80 percent of the mistletoe with defoliation, leaf spotting, and fruit deformity. At 6 months, Esterón causes complete defoliation of the mistletoe and failure to set fruit. The 2,4-D derivative herbicides are the more effective chemical control agents, but their use must be consistent with local regulations.

Silviculture

Several silvicultural practices are useful for controlling *Psittacanthus* in severely infested stands. The appropriateness of a given method depends on numerous factors, including stand type and location, infection intensity, management objectives, and constraints. Sanitation, intermediate thinning, shelterwood, and clearfelling are available techniques. Sanitation consists of removing severely infected trees and leaving light and moderately infected trees. Periodic examinations are made to monitor disease intensification; trees are removed as they become heavily infected. Sanitation is usually conducted at the time of intermediate thinnings, but if intensification is rapid relative to the thinning cycle, early removal may be considered. During shelterwood regeneration cuts, mistletoe-infected trees are generally removed and not used as seed trees. Lightly infected, genetically superior trees are occasionally retained to provide seed and then removed after 5 years. Where more than 75 percent of trees are infected and most are severely infested, clearfelling is usually employed for stand regeneration. Replacement with species less damaged or resistant to mistletoe infection can be considered.

As with all mistletoes, the first decision on control is whether it is appropriate given the management objectives of the stand, values produced in the stand, and available options for treatment.

B. W. Geils
D. Wiens
F. G. Hawksworth

Chapter 3

Phoradendron in Mexico and the United States

The generally familiar mistletoes are the leafy *Phoradendron* that typically infest hardwood trees and are placed at doorways for winter celebrations. Several of these mistletoes, however, more resemble the dwarf mistletoes by their apparently leafless stems and presence on conifers; but their large, fleshy berries that are attractive to birds clearly identify them as *Phoradendron*, “the tree thief.” For several reasons, the conifer-infecting *Phoradendron* (the group reviewed here) have not gotten the level of attention from forest managers that the *Arceuthobium* have. *Phoradendron* most typically cause slight damage to junipers in Southwestern woodlands. But these mistletoes include a number of different species, range from Oregon to Mexico, infect a variety of hosts, and provide an interesting model of host–parasite interactions.

Along with the other mistletoes, the taxonomy, biology, physiology, and ecology of the *Phoradendron* are reviewed by Gill and Hawksworth (1961) and Kuijt (1969a). Foresters have long been interested in the *Phoradendron* on incense cedar (Meinecke 1912).

Picture guidebooks are available by Walters (1978) for the Southwest and by Scharpf and Hawksworth (1993) for the Pacific States. General summaries of information including control are provided by Hawksworth and Scharpf (1981), Hernandez (1991), and Vega (1976). The taxonomy of the *Phoradendron* on conifers was first monographed by Trelease (1916) and then revised by Wiens (1964). Confusion over the position and ranking of several taxa (Hawksworth 1979) and recent evidence from molecular systematics (Ashworth 2000) suggest the group requires another taxonomic monograph.

Life History and Biology

The *Phoradendron* have a typical mistletoe life cycle characterized by bird dispersal of sticky seeds, internal parasitism of a woody host, and aerial shoots for flower and fruit production. *Phoradendron* biology, reproduction, and parasitism have received intense study from ecological and evolutionary perspectives.

Life Cycle

The most detailed but still comprehensive study and review of a *Phoradendron* life cycle is that by Felix (1970a) for the mistletoe on *Abies concolor*. A number of bird species feed on the mistletoe fruits and disperse seeds by excreting or regurgitating them. The most important birds for effective dispersal include cedar waxwings, euphonias, silky flycatcher, bluebirds, thrushes, robins, and solitaires (see Sutton 1951, Gill 1990). Seeds pass quickly, and because birds perch in trees, seeds are deposited at suitable sites for infection (often the top or warm side of a potential host, commonly one already infected). Germinating seeds produce a radicle, holdfast, and penetrate the host branch usually near a needle (Ruhland and Calvin 2001). The endophytic system consists of longitudinal strands and sinkers (Calvin and others 1991, Felix 1970a). Once aerial shoots are produced, the *Phoradendron* does photosynthesize, but it is a parasite (see below) not a simple epiphyte. Plants are either male or female. Although Dawson and others (1990a) report a male-bias and provide hypotheses why there might be such a bias, Daughtery and Mathiasen (1999) find the sex ratio is one to one. Flower production and reproduction is typical, except that natural hybridization occurs but rarely (Wiens and Dedecker 1972). Fruits are produced several years after infection; older plants produce more and larger fruits (Dawson and Ehleringer 1991, Dawson and others 1990a, 1990b). Although the shapes of shoots and leaves of *Phoradendron* might mimic their host, the biology behind the appearance is unclear (Atsatt 1993b). Endophytic systems are perennial, but plants of all ages are subject to mortality by extreme low temperatures (Wagener 1957).

Host–Parasite Physiology

The physiology of *Phoradendron* is generally reviewed by Fisher (1983), Knutson (1983), and Kolb (2002) as typical for most mistletoes (but different from that of the dwarf mistletoes). Many details of the nitrogen, carbon, and water relations of the "xylem-tapping" *Phoradendron juniperinum* are elucidated in a series of recent ecophysiology studies (Ehleringer and others 1986, Marshall and Ehleringer 1990, Marshall and others 1993, 1994). The mistletoes do fix some carbon but get much from their host; mistletoes transpire a lot of water (all from their host); and they get a lot of nitrogen from the host, as the inevitable consequence of the physiological relation (Marshall and others 1994). Lei (1997) concludes that heavy mistletoe infection increases host-plant water stress and reduces vigor, viability, and reproductive success of the host in favor of the mistletoe. McHenry (1934) reports that *Phoradendron* at the Grand Canyon kills juniper. Hawksworth and Wiens (1966) indicate that junipers may also form witches' broom in response to infection.

Host–Parasite Ecology

Numerous authors have studied the effects of *Phoradendron* parasitism on population dynamics and interactions with other species. Hreha and Weber (1979) compare pinyon dwarf mistletoe (*Arceuthobium divaricatum*) and juniper mistletoe (*Phoradendron juniperinum*) at the South Rim of the Grand Canyon, reporting more infection in bigger (older) trees, a lack of infestation in recently burned (young) areas, and general stability in the populations. They consider the pinyon dwarf mistletoe the more detrimental because it more readily kills its host. Juniper mistletoe often has a patchy distribution, with some trees heavily infested. Gregg (1991) concludes the critical difference between infested and uninfested sites is the need for a dependable moisture supply to maintain the high demand of infected trees. Moisture stress in firs infected by *Phoradendron* is associated with reduced resistance and increased successful attack by the fir engraver (Felix 1970a, Ferrell 1974). Gehring and Whitham (1992) report that on droughty sites, juniper severely infested by mistletoe have lower rates of beneficial mycorrhiza infection, and female junipers are more seriously affected than male junipers. Another three-way, conditional interaction is described by van Ommeren and Whitham (2002) for juniper, mistletoe, and their avian dispersers. Although mistletoe has a negative impact on the health of infected trees, mistletoe provides a more dependable food source than juniper for the shared avian dispersers of each species' seeds. By considering dispersal and reproductive success in the interaction model, they conclude that the net effect of mistletoe parasitism, depending on populations, shifts between favoring the mistletoe to favoring the juniper.

The *Phoradendron* also exhibit a curious phenomenon whereby a mistletoe is parasitized by another mistletoe of the same or different species (Hawksworth and Wiens 1966, Wiens and Calvin 1987). Although several of the conifer-infecting *Phoradendron* may be infected by other *Phoradendron* mistletoes (Felix 1970b), the occurrence is too rare to effect a significant biological control.

Description of Genus

Phoradendron
Mistletoe, injerto

Shrubby parasite of trees and other woody plants (fig. 3-1), woody at base, glabrous or hairy; shoots cylindrical, green or less often reddish, 20 cm in height, nodes constricted, lacking epicortical roots; phyllotaxy opposite or decussate; inflorescence a spike; perianth generally three-parted and persistent; anthers small, sessile and bilocular; fruit a berry, 3 to 6 mm, single color of white, pink, or reddish. A genus of about 200 species in temperate and tropical America. Type species: *Phoradendron californicum* Nuttall.

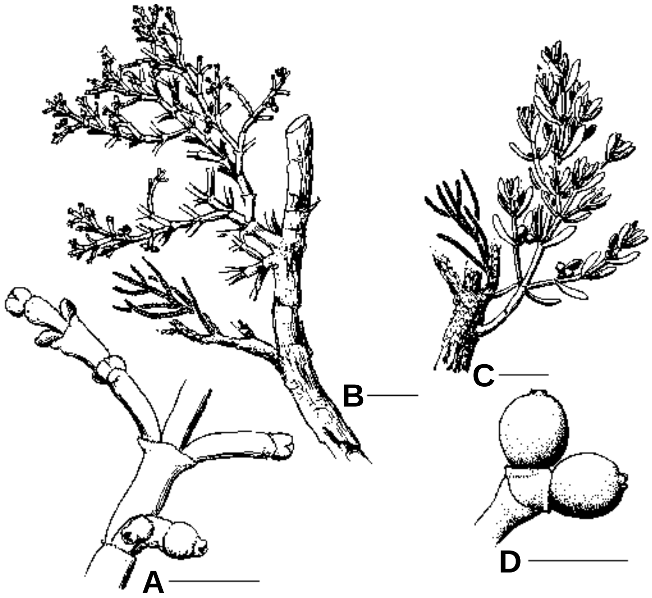


Figure 3-1—*Phoradendron* (all scales represent 5 mm). **A**, *P. juniperinum* on host; **B**, *P. juniperinum* with young fruit; **C**, *P. densum* on host; **D**, young fruits of *P. densum.* Adapted from Hitchcock and others (1964), p. 99, drawing by J.R. Janish. Our **C** and **D** originally labeled as *P. bolleanum* in figure, but accompanying text suggests figure represents *P. bolleanum* var. *densum* (Torr.) Fosberg, which we recognize as *P. densum.*

The genus *Phoradendron*, the largest genus of mistletoes, is in serious need of definitive taxonomic study. Trelease (1916) is the first monographic study of the genus, but Wiens (1964) revises many of Trelease's taxa that occur on conifers (see table 3-1). This taxonomy is further reconsidered by Hawksworth and Wiens (1993a, 1993b) for the flora of California, Nevada, and Arizona. Other floristic treatments with keys and illustrations include Hitchcock and others (1964) for the Pacific Northwest, McMinn (1939) for California, Standley (1920) for Mexico, and Wiggins (1980) for Baja California. Kuijt (1996) questions the significance and interpretation of many of the traditional morphological features used for the taxonomy of *Phoradendron*. Ashworth (2000) provides much insight to the relations among these mistletoes using techniques of molecular systematics.

Most of the taxa of *Phoradendron* that parasitize conifers are in the section *Pauciflorae* as described by Wiens (1964). Ashworth (2000) reports that these taxa (see table 3-1), delimited by morphological features, also form a single, related cluster based on molecular features. *Phoradendron rhipsalinum* is also a parasite of conifers but is apparently more closely related to a number of *Phoradendron* that typically infect hardwoods. A few other *Phoradendron* reportedly occur on conifers, but these are either rare cases or possibly misidentifications. Usual conifer host genera are *Abies*, *Calocedrus*, *Cupressus*, *Juniperus*, *Taxodium* (table 3-2). Martínez (1948) illustrates *Phoradendron velutinum* on *Pinus leiophylla* in Pueblo, but this is a rare host for a mistletoe with a wide host range, and we know of no other reports on pines.

In 1990, Wiens and Hawksworth drafted a further revision of *Phoradendron* section *Pauciflorae* that has never been completed and published (copy on file at Flagstaff Laboratory, Rocky Mountain Research Station). In that draft, they proposed recognizing seven new species on American conifers and raising to specific rank a previously submerged taxon not now generally accepted at that level. Although we do not describe any new species in this publication, we do suggest here that there may be differences in some populations that warrant recognition at the specific level. We leave it to other taxonomists using morphological and molecular techniques to judge these opinions. Specimens for these "ined" taxa are assembled for deposition at the U.S. National Herbarium.

Table 3-1—Taxonomic history of *Phoradendron* that parasitize conifers.

Trelease (1916)	Wiens (1964)	Accepted here
P. bolleanum Eichler *P. tequilense* n. sp.	*P. bolleanum* subsp. *bolleanum*	*P. bolleanum* (Seem.) Eichl.
P. capitellatum Torrey n. sp.	*P. capitellatum* Torr. ex Trel.	*P. capitellatum* Torr. ex Trel.[a]
P. densum Torrey n. sp. *P. guadalupense* n. sp.[c] *P. saltillense* n. sp.	*P. bolleanum* subsp. *densum* (Torr.) Wiens, comb. nov.	*P. densum* Torr. ex Trel.[a,b] *P. saltillense* Trel.[d]
P. juniperinum Engelmann *P. ligatum* n. sp.	*P. juniperinum* subsp. *juniperinum*	*P. juniperinum* Engelm. ex A. Gray[a,b]
P. libocedri Howell	*P. juniperinum* subsp. *libocedri* (Engelm.) Wiens, comb. nov.	*P. libocedri* (Engelm.) T.J. Howell[b]
P. longifolium Eichler	*P. longifolium* Eichler ex Trel.	*P. longifolium* Eichler ex Trel.
P. minutifolium Urban	*P. minutifolium* Urban	*P. minutifolium* Urban
P. pauciflorum Torrey	*P. bolleanum* subsp. *pauciflorum* (Torr.) Wiens, comb. nov.	*P. pauciflorum* Torr.[a,b]
		P. rhipsalinum Rzed.[e]

[a] Name used in Hawksworth and Wiens (1993a).
[b] Name used in Hawksworth and Wiens (1993b).
[c] Wiens (1964) indicates this taxon probably now extinct.
[d] Referred to by Hawksworth and Cibrián (1985) as *P. densum* subsp. *saltillense* (Trel.) Wiens.
[e] Taxon first recognized in 1972.

Description of Species

1. *Phoradendron bolleanum*
Bollean Mistletoe

Phoradendron bolleanum (Seem.) Eichl., Mart. Fl. Bras, v. II. 134.

Description. Plants 20 to 30 cm high, reddish; internodes 10 to 20 mm long; leaves spatulately linear-elliptical, 8 to 22 mm long and 1 to 4 mm wide, sessile, apex acute reddish, densely hairy; mature fruit is about 4 mm diameter, white to straw-colored (Trelease 1916, Cházaro and Oliva 1987b with illustration). This mistletoe is usually characterized by its bright reddish to brown color; however, some all-green populations have been found in central Chihuahua (Hawksworth and Cibrián 1985).

Hosts. Usual hosts are *Juniperus* and *Arbutus*. This is the only *Phoradendron* on *Arbutus* (*A. arizonica* and *A. xalapensis*); the closely related *Arctostaphylos* (*A. pungens*) is also rarely infected. Vega (1976) lists the hosts of "*Phoradendron bolleanum*" as not only *Juniperus* and *Arbutus* (*A. unedo*) but also *Quercus*,

Table 3-2—Host range and distribution of *Phoradendron* on conifers.

Phoradendron	Principal hosts	Mexico	United States
P. bolleanum	*Juniperus, Arbutus*	X	-
P. capitellatum	*Juniperus*	X	-
P. densum	*Juniperus, Cupressus*	X	X
P. juniperinum	*Juniperus, Cupressus*	X	X
P. libocedri	*Calocedrus*	X	X
P. longifolium	*Quercus, Pinus*	X	-
P. minutifolium	*Juniperus*	X	-
P. pauciflorum	*Abies*	X	X
P. rhipsalinum	*Taxodium, Quercus*	X	-
P. saltillense	*Juniperus, Cupressus*	X	-
	Total number of species	10	4

Pinus, and *Abies*. Given that he lists the distribution for this mistletoe to include Baja California, we suspect he is including *P. pauciflorum* and other *Phoradendron* under this name. *Cupressus benthami* is an unusual host in the pine–cypress woodlands of Veracruz (Cházaro 1989a).

Distribution. Mexico (Chihuahua, Durango, Hidalgo, Jalisco, Nayarit, Querétaro, Sonora, Sinaloa, Veracruz, and Zacatecas). Common in Sierra Madre Occidental, and Zacatecas to central Chihuahua (Hawksworth and Cibrián 1985). Cházaro (1989a) records *Phoradendron bolleanum* on *Cupressus* (*C. benthami*) in Veracruz. This is the most widespread *Phoradendron* on conifers in Mexico. Known elevational range is from 1,900 to 2,500 m. The mistletoe on junipers in eastern New Mexico, western Texas, and northern Coahuila are considered another taxa.

Discussion. *Phoradendron bolleanum* is a widespread and diverse mistletoe with a complicated taxonomic history. We are attempting here to include only reports of *P. bolleanum* subsp. *bolleanum* and populations resembling the type on juniper from the Sierra Madre Occidental and parasitizing both *Juniperus* and *Arbutus*. We describe other taxa under *P. densum* and *P. pauciflorum*.

Phoradendron bolleanum is unusual for mistletoes of section *Pauciflorae senus* Wiens (1964) in that it commonly parasitizes both gymnosperms and angiosperms (Hawksworth and Wiens 1966). Trelease (1916) questions whether one species of mistletoe would occur on such unrelated host genera; and without experimental evidence, the question is still open. However, no morphological grounds for a taxonomic separation of the populations on the two hosts have been found. Although infections of *Juniperus* and *Arbutus* frequently occur together, we have seen many situations from Chihuahua to Jalisco where only one host is infected, even though the other is present. For example, *P. bolleanum* has been found in Jalisco on *Arbutus* only, even though *Juniperus* occurs in the same areas (M. Cházaro B., personal communication). This suggests that there may be two host races of the mistletoe, one primarily parasitic on *Juniperus* and one on *Arbutus*. The areas where both types of hosts are infected may represent instances of sympatry of the two races. Carefully controlled, crossinfection experiments are needed to determine the status of the host populations of this mistletoe.

Various authors have attempted to sort out the systematic relations among taxa of *Phoradendron bolleanum* complex. Wiens (1964) revised the previous work by Trelease and Fosberg but later revised himself in floral treatments for Texas (Wiens 1970), Arizona (Hawksworth and Wiens 1993a), and California (Hawksworth and Wiens 1993b). Further changes by Hawksworth and Wiens are contemplated in an uncompleted draft. Ashworth (2000) identifies several sister groups for taxa of the complex: *P. bolleanum* subsp. *bolleanum* groups with *P. minutifolium*, *P. densum* and *P. pauciflorum* (both previously considered as subspecies of *P. bolleanum*) group together.

2. *Phoradendron capitellatum*
Hairy Mistletoe

Phoradendron capitellatum Torr. ex Trel., Genus *Phoradendron* 25, pl 17, 1916.

=*Phoradendron bolleanum* var. *capitellatum* (Torr. Ex Trel.) Kerney & Peebles

Description. Plants 30 to 80 cm tall, yellow–green; internodes 5 to 15 mm long, pendulous with age; leaves 6 to 14 mm long and 2 to 3 mm wide, densely hairy with stellate trichomes; flowers December to February; mature fruit is about 3 mm in diameter, pinkish–white (Hawksworth and Scharpf 1981with color picture and 1993a).

Hosts. Known hosts are *Juniperus deppeana*, *J. pinchotii*, *J. monosperma*, and *J. osteosperma*. It usually occurs at elevations below *Phoradendron juniperinum*, but the two species are sometimes sympatric and rarely even on the same host tree.

Distribution. United States (Arizona, New Mexico) and Mexico (Chihuahua, Sonora). This mistletoe has a restricted distribution and is known only in central and southeastern Arizona (nine counties), southwestern New Mexico (Grant, Hidalgo, Luna), northeastern Sonora, and northwestern Chihuahua (Hawksworth and Cibrián 1985). Hawksworth and Scharpf (1981) map its distribution in the United States and into Mexico. Known elevational range is 800 to 1,700 m.

Discussion. This highly distinctive parasite of junipers is characterized by its small, densely stellate–pubescent leaves. It is the only leafy mistletoe known to occur on junipers in Arizona and is poorly known. Ashworth (2000) finds that *Phoradendron capitellatum* is the most divergent taxa within the *Pauciflorae*, although there is some support for a sister group with *P. juniperinum*.

3. *Phoradendron densum*
Dense mistletoe

Phoradendron densum Torr. ex Trel., Genus *Phoradendron* 27, 1916.

=*Phoradendron bolleanum* var. *densum* (Torr. ex Trel.) Fosberg,

=*Phoradendron bolleanum* subsp. *densum* (Torr. ex Trel.) Wiens

Description. Plants 10 to 30 cm high, green (fig. 3-1); internodes 6 to 17 mm long; leaves 10 to 20 mm long and 2 to 4 mm wide, glabrous, sessile, apex obtuse; mature fruit is about 4 mm in diameter, white to straw-colored. (Hawksworth and Scharpf 1981with color photo, Hitchcock and others 1964 with illustration).

Hosts. *Cupressus arizonica, C. bakeri, C. goveniana, C. macnabiana, C. macrocarpa* (rare), *C. sargentii, Juniperus californica, J. monosperma, J. occidentalis, J. osteosperma, J. pinchotii.* The mistletoe is reported on *Pinus monophylla* at Mt. Pinos (Ventura, California) by McMinn (1939), but this has not been confirmed.

Distribution. United States (Arizona, California, Oregon) and Mexico (Baja California). The mistletoe ranges from southern Oregon (Klamath and Jackson) throughout California to the lower elevations of the Sierra San Pedro Mártir in Baja California, Mexico, and with outlying populations in central Arizona on *Cupressus* (Coconino, Yavapai, Maricopa, and Gila). Trelease (1916) reports *Phoradendron densum* from Sonora, and the Forest Pathology Herbarium-Fort Collins, CO, holds collections as well from Coahuila and Nuevo Leon, although these collections may more properly belong under *Phoradendron saltillense.*

The population in the Sierra San Pedro Mártir infects *Juniperus californica* but not *Cupressus,* which occurs at higher elevations (Hawksworth and Wiens 1966). The reciprocal situation occurs in Arizona; the mistletoe infects cypress but not junipers, even though junipers are widely distributed and abundant in the State. Hawksworth and Scharpf (1981) provide a distribution for Oregon, California, and Arizona. Known elevational range is 200 to 2,300 m.

Discussion. Ashworth (2000) illustrates the close systematic relationships among the taxa of section *Pauciflorae senu* Wiens. Her work, however, also brings out the taxonomic difficulty among *Phoradendron bolleanum, P. densum,* and the various taxa at one time or other considered subspecies of these (see table 3-1). For the reviewer (such as here), the problem is determining to which taxa various reports of hosts and distribution refer. Based on their descriptions and distributions, Hawksworth and Wiens (1993a, 1993b) restrict their interpretation of *P. densum* to include only certain populations from Oregon to Baja California on juniper and cypress and from central Arizona on cypress. Many of the mistletoes on either cypress or juniper from the Sierra Madre Oriental are now referred to *Phoradendron saltillense.* From eastern New Mexico, western Texas, and northern Coahuila (Wiens 1964), it is now referred to Hawksworth's mistletoe (see below). Several other populations usually referred to either *P. bolleanum* or to *P. densum* also have differences in morphology, life history, hosts, and distribution, so that they may warrant recognition at the specific level. Considering the difficulty of classifying these mistletoes using traditional criteria, molecular techniques (for example, Ashworth 2000) should be considered.

The population of *Phoradendron* on various junipers in western Texas, southern New Mexico, and Coahuila has been referred to as *Phoradendron bolleanum* subsp. *hawksworthii* (Wiens 1970) and *Phoradendron hawksworthii* (Hawksworth 1979, Hawksworth and Cibrián 1985, Hawksworth and Scharpf 1981). Although the name *Phoradendron hawksworthii* Wiens is accepted by the PLANTS database (USDA, NRCS 2001), it is not yet a validly published name and remains "ined." The Hawksworth's mistletoe plants are about 10 to 25 cm tall, dark green, with internodes 6 to 12 mm long. Leaves are 6 to 25 mm long, 2 to 2.5 mm wide and slightly hairy. The mature fruit is white and about 4 mm in diameter. The hosts are *Juniperus ashei, J. deppeana, J. flaccida, J. monosperma,* and *J. pinchotii.* This mistletoe is common throughout western Texas (Brewster, Culbertson, Edwards, Hudspeth, Presido, Terrell, Val Verde) and occurs in southern New Mexico (Dona Ana, Lincoln, Otero, Socorro?) and northern Coahuila (Sierra del al Encantada). [Note: the population collected from northwest of Carrizozo, NM, in 1969 could not be relocated and may be extinct.] The Hawksworth's mistletoe resembles *P. saltillense* but is distinguished by several features (table 3-3). Hawksworth's mistletoe is not sympatric with *P. capitellatum,* which also occurs on junipers in southern New Mexico. Hawksworth's mistletoe, however, is sympatric with *P. juniperinum* and may even infect

Table 3-3—Comparison of Hawksworth's mistletoe and *Phoradendron saltillense*.

Character	Hawksworth's mistletoe[a]	*Phoradendron saltillense*
leaf width	narrow, 2 mm or less	wide, more than 3 mm
leaf transection	upper surface flattened, lower rounded	dorsoventrally flattened
tip of mature leaf	abrupt, with point 0.2–0.3 mm or with the scar of such a point	never developing a point
internode length[b]	short, 6–12 mm, mean 9 mm	long, 6–17 mm, mean 11 mm
segments per staminate inflorescence	usually only one segment	typically two segments

[a] *Phoradendron densum* populations in western Texas and southern New Mexico.
[b] Internode length is correlated with total plant size.

the same tree; but Hawksworth's mistletoe usually extends to lower elevations than the distribution of *P. juniperinum*. Both *P. juniperinum* and Hawksworth's mistletoe appear to induce a witches' broom formation on its host (Hawksworth and Wiens 1966, D. Conklin, personal communication).

4. *Phoradendron juniperinum*
Juniper mistletoe

Phoradendron juniperinum Engelm. ex A. Gray, Mem. Am. Acad. N. S. iv. 59, 1849.

Description. Plants 20 to 40 cm tall, globose, green to yellow–green, glabrous; internodes 5 to 10 mm long; leaves reduced to minute scales; mature fruit is about 4 mm in diameter, pinkish–white colored (Hawksworth and Wiens 1993a, 1993b, Hichcock and others 1964 with illustration).

Hosts. Common hosts are *Juniperus californica*, *J. deppeana*, *J. pinchotii*, *J. flaccida*, *J. monosperma*, *J. occidentalis*, *J. osteosperma*, and *J. scopulorum*. *Cupressus arizonica* is commonly parasitized in central Chihuahua, but this tree is rarely infected in Texas (Hawksworth and Cibrián 1985), Arizona (Hawksworth and Wiens 1966), and New Mexico (Linnane 1987). Other rare hosts are *C. bakeri* in California (Hawksworth and Wiens 1966), *Chamaebatiara millefolium* (Rosaceae) in Arizona (Hawksworth 1952), and *Pinus monophylla* (Hawksworth 1979). Vega (1976) adds *Juniperus mexicanus* as a host.

Distribution. United States (Oregon, California, Nevada, Utah, western Colorado, Arizona, New Mexico, and western Texas) and Mexico (Baja California, Chihuahua, Durango, Sonora). It occurs in the Chisos Mountains in Big Bend National Park, Texas (Brewster), but is not yet known in adjacent Coahuila, Mexico. A collection in the Forest Pathology Herbarium-Fort Collins, CO, includes a single collection by J.R. Weir (no date) from Oakley, ID (Cassia) with a *Juniperus osteosperma* infected by *Phoradendron juniperinum*. Bunderson and others (1986) attempt to predict the distribution on the mistletoe from environmental site factors. Hawksworth and Scharpf (1981) provide a distribution map. Known elevational range is 1,000 to 2,600 m.

Discussion. The taxon described by Trelease (1916) as *Phoradendron ligatum* for its constricted scales is now included under *P. juniperinum* (Wiens 1964). This distinctive leafless species is the most widespread *Phoradendron* on conifers. *Phoradendron juniperinum* is geographically sympatric with *P. capitellatum* in Arizona, with Hawksworth's mistletoe in New Mexico, and with *P. densum* in California. In fact, natural hybrids of *P. juniperinum* x *P. densum* that appear to be sterile F1 plants have been found in the Inyo and San Bernardino Mountains in California (Wiens and DeDecker 1972). Vasek (1966) observes that *P. juniperinum* usually does not parasitize *Juniperus californica,* and *P. densum* usually does not parasitize *J. osteosperma*. *Phoradendron juniperinum* forms a sister group with *P. libocedri*, but there is also some evidence in support of another sister group with *P. capitellatum* (Ashworth 2000).

Phoradendron juniperinum is a widespread and common mistletoe on junipers in many of the Western States. It is the subject of numerous studies on ecophysiology (see below). Several curious observations (Hawksworth and Wiens 1966) on *P. juniperinum* include rarely occurring massive witches' brooms and parasitism by *Phoradendron villosum* subsp. *coryae* (normally on oak).

5. *Phoradendron libocedri*
Incense–cedar mistletoe

Phoradendron libocedri (Engelm.) T.J. Howell, Fl. N.W. Amer. 1:608, 1902.

=*Phoradendron juniperinum* Engelm. ex Gray var. *libocedri* Engelm.

=*Phoradendron juniperinum* Engelm. ex Gray subsp. *libocedri* (Engelm.) Wiens

Description. Plants 20 to 80 cm tall, woody only at base, older plants pendulous, green; internodes 10 to 29 mm long; leaves reduced to minute scales; pistillate inflorescences usually with one segment and two flowers (occasionally more); mature fruit 4 mm in diameter, pinkish white to straw colored (Hawksworth and Wiens 1993b).

Hosts. On *Calocedrus decurrens*. There is one collection by Platt and Felix (Dodge Ridge, Tuolumne, CA, 1968) of *Phoradendron libocedri* on *Abies concolor*. They report only a single fir tree was infected in a stand where the mistletoe was common on the associated incense cedar. Weir (*5995* from Del Norte CA in 1917) is a *Chamaecyparis lawsoniana* with a single infection of *P. librocedri*; he reports infected incense cedar are nearby.

Distribution. United States (California, Oregon, Nevada) and Mexico (Baja California). The main range of the mistletoe is from southern Oregon (Jackson, Josephine, Klamath) through the Cascade and Sierra Nevada Ranges to southern California. The population in Nevada (Douglas) is near the California border. Isolated known occurrences are in northern Oregon (Jefferson, Warm Springs Indian Reservation) and on San Benito Peak in the South Coast Range in Monterey County, California. It also occurs in the Sierra Juarez and Sierra San Pedro Mártir in Baja California (Wiggins 1980). Although the mistletoe has a wide range, it is not very common (McMinn 1939). Hawksworth and Scharpf (1981) provide a picture of an infested incense cedar and a distribution map. Known elevational range is 400 to 2,500 m.

Discussion. *Phoradendron libocedri* had been considered a subspecies of *P. juniperinum* (Wiens 1964) but is here recognized again at the specific level (Trelease 1916). *Phoradendron libocedri* and *P. juniperinum* are sympatric in the Sierra Nevada, but each remains restricted to it own host; *P. libocedri* has longer internodes and is more pendulous (mimicking its host? see Ashworth 2000). The two taxa, however, do form a very close sister group (Ashworth 2000). Meinecke (1912) describes the swellings and burls caused by *Phoradendron libocedri* and speculates on the age and parasitism of the mistletoe.

6. *Phoradendron longifolium*

Phoradendron longifolium Eichler ex Trel. Genus *Phoradendron* 53, 1916.

Description. Plants becoming generally woody; internodes 15 to 30 mm long; leaves linear, 32 to 84 mm long by 6 to 9 mm wide, apex rounded to acute; fruit 3 to 4 mm diameter, lightly puberulent (Wiens 1964, Bello 1984 with illustration, Bello and Gutierrez 1985).

Hosts. Usually *Quercus* but also *Alnus*, *Pinus pseudostrobus*, *P. michoacana* (Bello Gutierrez 1985).

Distribution. Mexico (Durango, Tamaulipas, Hidalgo, Mexico, Oaxaca).

Discussion. Wiens (1964) places *Phoradendron longifolium* in section *Calyculatae* but admits little material was available for morphological comparisons to other *Phoradendron*. Ashworth (2000) reports *P. longifolium* forms a sister group with *P. galeottii* with which it shares several morphological features, but not time of flowering, which Wiens uses as a taxonomic character. Although *P. longiflorum* occurs in pine woodlands of central Mexico, we have no information on how common or damaging it is.

7. *Phoradendron minutifolium*

Injerto de páraro

Phoradendron minutifolium Urban Bot. Jahrb. Syst 23, Beibl. 57:2, 1897

Description. Plants 30 to 80 cm tall, dull green; internodes 4 to 12 mm long; leaves 3 to 5 mm long and 1 to 1.5 mm wide, resembling scales, glabrous; spike one-jointed; mature fruit is about 4 mm in diameter, pinkish–white colored (Hernandez 1991 with illustration, Trelease 1916).

Hosts. *Juniperus deppeana* (Acosta and others 1992). Other juniper species are probably hosts, but our host collections are only identified as *Juniperus* sp. Depending on how populations in Colima and Jalisco are classified, also on *Cupressus*.

Distribution. Mexico (Chihuahua, Coahuila, Durango, Puebla, Tlaxcala, Veracruz). The mistletoe is most common in Tlaxcala (Hernández 1991) and Veracruz and in the Sierra Madre Occidental in southern Chihuahua and Durango. An apparently extreme outlier occurs in northern Coahuila in the Sierra del Carmen (across from Big Bend, TX). Depending on how populations on *Cupressus* are classified, also in Colima and Jalisco. Known elevational range is 2,000 to 2,750 m.

Discussion. *Phoradendron minutifolium* in Coahuila is sympatric with *Phoradendron saltillense* on juniper; the two mistletoes sometimes even coinfect the same tree. *Phoradendron minutifolium* and *P. bolleanum* subsp. *bolleanum* form a close sister group (Ashworth 2000).

A population of *Phoradendron* that appears similar to *P. minutifolium* occurs on *Cupressus* in the nearby vicinities of El Sauz and Terrero, Sierra de Mammitlan and Cerro Grande in Colima and Jalisco. Although these mistletoe are referred by the name *Phoradendron olivae* (Cházaro 1990, Cházaro and others 1992), we are unable to confirm that this name has been validly published, but the holotype is reported to be a collection by Wiens, Cházaro, Hawksworth, and Olivo (*7051*, 1 August 1989) deposited at IBUG (Universidad de Guadalajara). The hosts are variously identified as *Cupressus benthami* and *C. lusitanica*. The plants on *Cupressus* are larger and more open-formed because of longer internodes (15 to 25 mm) and smaller leaves (only 1 to 2 mm long). The mistletoes of *Cupresssus* have a distribution far to the west and south of those on *Juniperus*. Additional study of these mistletoes is needed.

8. *Phoradendron pauciflorum*

Fir mistletoe

Phoradendron pauciflorum Torr., Pacif. Rail. Rep. iv. 134.

=*Phoradendron bolleanum* (Seem.) Eichl. var. *pauciflorum* (Torr.) Fosberg

=*Phoradendron bolleanum* (Seem.) Eichl. subsp. *pauciflorum* (Torr.) Wiens

Description. Plants 20 to 40 cm high, green; internodes 10 to 21 mm long; leaves with short petiole, 5 to 30 mm long and 5 to 8 mm wide, glabrous; leaf apex obtuse; mature fruit is about 4 mm wide, pinkish white to straw colored (Hawksworth and Scharpf 1981 with color picture, Hawksworth and Wiens 1993a, 1993b).

Hosts. *Abies concolor* is usually the only host, although autoparasitism has been reported (Felix 1970b). It rarely parasitizes *Cupressus arizonica* var. *montana* in the Sierra San Pedro Mártir, Baja California, Mexico, where this tree is associated with infected *Abies* (Hawksworth and Wiens 1966).

Distribution. United States (Arizona, California) and Mexico (Baja California). This mistletoe is common in the central and southern Sierra Nevada (Calaveras) south to the Sierra San Pedro Mártir in Baja California, Mexico (Wiggins 1980). An extreme disjunct occurs in southern Arizona (Pima) in the

Santa Catalina and Rincon Mountains. Hawksworth and Scharpf (1981) provide a distribution map. Known elevational range is 1,400 to 2,600 m.

Discussion. This species was previously submerged under *Phoradendron bolleanum* (table 3-1) and confused with *P. densum* (Wiens 1964). Felix (1970a) provides a detailed study of the biology of *P. pauciflorum* including information on reproduction and dispersal, shoot growth, endophytic system, branch mortality, mistletoe mortality, effects on host, associated species, and epiparasitism.

A population of an unnamed *Phoradendron* occurs on the rare *Abies durangensis* in Chihuahua, Durango, and Jalisco. This mistletoe on fir is sometimes sympatric with *P. bolleanum*, but has yellow-green, linear leaves with an acuminate apex. The populations include a few widely scattered localities in the Sierra Madre Occidental; all the *A. durangensis* populations that we have visited in Durango are parasitized by this mistletoe.

9. *Phoradendron rhipsalinum*

Phoradendron rhipsalinum Rzed., Cact. Suc. Mex 17:102, 1972.

Description. Plants 2 to 4 m long, pendulous, bright green; leaves 4 to 6 cm long and 4 to 5 mm wide, glabrous; mature fruit yellow–green, 1.5 mm in diameter (Bello 1984 with illustration, and Bello and Gutierrez 1985 with picture and detailed description).

Hosts. *Taxodium distichum* var. *mexicanum*. *Quercus castanea* is also infected (Bello 1984, Bello and Gutierrez 1985).

Distribution. Mexico (Guanajuato, Jalisco, Mexico, Michoacán). Known elevational range is 1,600 to 2,300 m in pine-oak woodlands to subtropical matorral.

Discussion. This is one of the most distinctive Mexican mistletoes. Its 4 to 6 cm long “strap–like” leaves make it unusual. It forms huge pendulous masses hanging from the bald-cypress trees that look from a distance like masses of Spanish moss. Ashworth (2000) concludes this mistletoe does not fit with the other parasites of conifers in the section *Pauciflorae* but appears more closely related to *P. brachystachyum* rather than *P. bolleanum* as suggested by Kuijt (1996). It causes severe mortality to bald-cypress, for example in the vicinity of Zamora, Jalisco. Although approximately 120 species of mistletoe occur in Mexico, this is the only species described by a Mexican botanist (Cházaro and others 1992).

10. *Phoradendron saltillense*

***Phoradendron saltillense* Trel. Genus** *Phoradendron* 27, 1916.

=*P. bolleanum* subsp. *densum* (Torr.) Wiens, pro parte.

Description. Plants moderately long and stout; internodes 10 to 20 mm, papillate-hispid; leaves narrowly oblong, 20 to 30 mm long by 2 to 3 mm wide, sessile, apex acute; spike 50 to 60 mm long, with single joint and pistillate two-flowered (Trelease 1916, Standley 1920).

Hosts. *Cupressus arizonica, C. benthami, Juniperus deppeana, J. flaccida, J. monosperma*, and *J. saltillense.*

Distribution. Mexico (Coahuila, Nuevo Leon, San Luis Potosi, Puebla). Known elevational range is 1,850 to 2,850 m. This mistletoe is common the Sierra del Carmen, northern Coahuila, and it may occur in the Chisos Mountains, Texas. Hawksworth and Cibrián (1985) lists *P. densum* subsp. *saltillense* (Trel.) Wiens on *Cupressus arizonica* in Coahuila and on *Juniperus* in the Sierra Madre Oriental from Coahuila to Zacatecas.

Discussion. *Phoradendron saltillense* is first described by Trelease (1916), accepted by Standley (1920), submerged under *Phoradendron bolleanum* subsp. *densum* by Wiens (1964), and recognized here as a validly published name. It is separated from *P. densum* populations in Arizona by more than 1,000 km, but near to Hawksworth’s mistletoe in the Sierra del Carmen. It is distinguished from Hawksworth’s mistletoe by several morphological features (table 3-3). *Phoradendron saltillense* is sympatric in Nuevo Leon and Coahuila with populations of an unnamed *Phoradendron* that have longer, narrower, thinner leaves and a more open branching habit; these two contrasting mistletoes may even occur in the same tree.

Importance

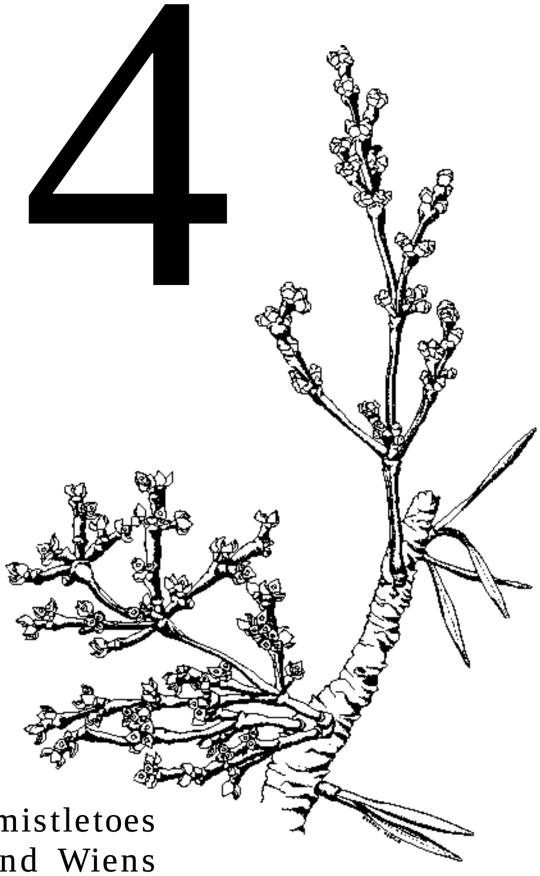
Although the *Phoradendron* mistletoes that infect conifers are widely distributed in the Western United States and in Mexico on a number of common and valuable hosts, their importance is mostly on a local basis and for special uses. In the United States, *Phoradendron* are most important in California on incense cedar and true fir in certain areas and important broadly across the Southwest (California to Texas) on junipers. In Mexico, *Phoradendron* (all species) are found throughout the Republic, but only recognized as a forest plague on about 4,000 ha in Jalisco, Mexico, and Michoacán (Martinez 1983). Hawksworth and Cibrián (1985), however, add that *Phoradendron* are damaging to junipers in the north (Sierra Madre Occidental, Oriental, and del Carmen). Although *Phoradendron* are a minor issue on a few forest species (see Felix 1970a, Meinecke 1912), they can be a serious concern in some recreation and other high-value sites (Frankel and others 1989, Linnane 1987). These mistletoes have a high nutritional value as animal forage (Urness 1969) and are utilized as such (Cházaro and Oliva 1988b, Gallina 1988). *Phoradendron* mistletoes are also consumed by humans as a stimulating beverage (Whiting 1950) and as a traditional medicine for childbirth and several ailments (Cházaro and Oliva 1988a, Moore 1979, Whiting 1950). A strong caution, however, is appropriate. Various compounds from *Phoradendron* and other mistletoes are being investigated for their pharmacological potential, but many of these compounds are present in toxic dosages to humans (Turner and Szczawinski 1991). Although it is the more leafy *Phoradendron* mistletoes on hardwoods that are usually harvested commercially for winter-festival greenery, the conifer mistletoe can still be enjoyed for attracting numerous, colorful birds (Sutton 1951).

Management Strategies

Phoradendron mistletoes seldom cause sufficient damage in an area that control is required; but where management objectives indicate that mistletoe control is justified, cultural methods are available. Although there are insects that feed on these mistletoes (Burke 1975) and fungi that caused disease (Horst 2002, Scharpf and Hawksworth 1966), there are no biological control programs for the *Phoradendron*. Chemical control has been tested using various herbicides (Quick 1963) and ethephon (Adams and others 1993), but none are recommended. We know of no genetic improvement programs to develop conifer resistance to *Phoradendron* mistletoes. Cultural methods are briefly discussed by Frankel and others (1989), Hawksworth and Scharpf (1981), and Hernandez (1991). Operations include regenerating with a nonhost tree, thinning trees to improve vigor and tolerance of the infestation, and sanitation by removing infected trees or branches or removing aerial shoots. Pruning infected branches is often sufficient; where the loss of infected branches cannot be accepted, the aerial shoots can be just knocked off. Removing the shoots does not eliminate the mistletoe infection but does reduce its reproduction and damage. Shoots will reappear after several years. Covering infected branches with tarpaper or creosote has not proven either attractive or effective. Perhaps the best way for discouraging additional bird-dispersal of mistletoe seeds is with branch pruning or shoot removal (since it is often the mistletoe fruits that initially attract the birds). Given the modest damage and slow rate of increase of these mistletoes, these methods are usually sufficient.

F. G. Hawksworth
D. Wiens
B. W. Geils

Chapter
4



Arceuthobium in North America

The biology, pathology, and systematics of dwarf mistletoes are recently and well reviewed in Hawksworth and Wiens (1996). That monograph forms the basis for the text in this and chapter 5 and should be consulted for more information (for example, references, photographs, and distribution maps). In addition to extracting the information that would be most relevant to forest managers and arborists, we here include new references on hosts, distributions, and ecology. The synonymy in this chapter is neither formal nor complete; rather, we provide additional names used in previous, significant literature (such as Gill 1935, Hawksworth and Wiens 1972, Kuijt 1955).

General Life Cycle

The life cycle of dwarf mistletoe is distinctive because of two features—obligate parasitism (shared with all mistletoes) and hydrostatically controlled, explosive dispersal (with one exception). The details of cytology, anatomy, embryology, genetics, and evolution that underlie these features are described by Hawksworth and Wiens (1996) and Kuijt (1960a, 1960b, 1969a).

Especially for dwarf mistletoes with their reduced morphologies, differences in reproductive phenology and host specificity are taxonomically decisive (Hawksworth and Wiens 1996). The life histories of several dwarf mistletoes are well studied (Gilbert 1984, 1988, Hawksworth 1961, 1965, Scharpf and Parmeter 1982, Strand and Roth 1976).

Life History

Dwarf mistletoe life history comprises four stages: dispersal, establishment, incubation, and reproduction (fig. 4-1). Dispersal begins when a mature fruit discharges its seed into ballistic flight. Establishment includes the time from the seed lodging at a safe-site until the parasitic relationship is initiated. Several years of incubation pass while an extensive, endophytic system develops under the host’s bark. The reproductive stage continues with repeated, intermittent production of aerial shoots and flowers and continued expansion of the endophytic system. Reproduction ends with the death the mistletoe plant; this usually does not occur until the host itself dies. Various physical and biological factors affect the temporal and spatial unfolding of these processes into population consequences and afford an opportunity for management intervention.

Dispersal—Mistletoe dispersal is effected by the hydrostatic contraction of a mature fruit that propels a single, small seed upon ballistic flight to either a location where a host may be inoculated (safe-site) or elsewhere. Unlike other mistletoes that are primarily dispersed by birds consuming mature fruits and defecating viable seeds, the dwarf mistletoes rely almost exclusively on this ballistic mechanism. Birds and mammals are important, however, for the rare, long-distance dissemination of seeds to new infection centers (Nicholls and others 1984). The exception is *Arceuthobium verticilliflorum*, which is found in widely spaced pine forests of Mexico. This species has nonexplosive fruits twice the size of other dwarf mistletoes and is predominately dispersed by birds.

The special morphological and anatomical features that facilitate dispersal include the supporting structure for the fruit (pedicel) and characteristic, sticky, viscin cells (Wilson and Calvin 1996, Hawksworth and Wiens 1996). When the fruit matures, the pedicel elongates and water pressure increases. With separation of the fruit from the pedicel, the seed is ejected at nearly 24 m per second (Hinds and Hawksworth 1965) and tumbles in a short ballistic flight until it lands upon and sticks to a surface. The shape of the ballistic trajectory is influenced by height above the ground, pedicel–fruit orientation, seed shape and weight, discharge velocity, and gravity (Hawksworth 1961). Dwarf mistletoe seeds have a mass of 2 to 3 mg; wind affects the flight, but seeds fall to their destination within seconds. Although maximum horizontal displacement may reach 16 m, 10 m is a more typical, free-flight distance (see Escudero and Cibrián 1985). Most seeds are displaced horizontally only 2 to 4 m and deposited lower in the crown; some seeds, however, are shot

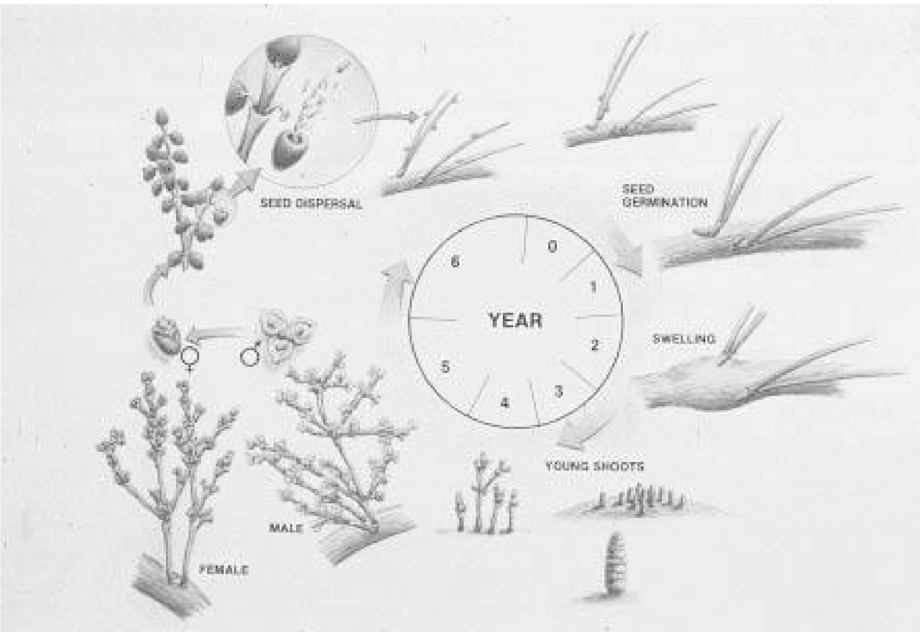


Figure 4-1—Generalized life cycle of a typical dwarf mistletoe. Illustration courtesy of W. R. Jacobi.

higher into the crown to effect vertical spread (Hawksworth and Geils 1985, Richardson and van der Kamp 1972, Shaw and Hennon 1991, Wicker and Hawksworth 1991). Because of variation in crown density, foliage display, and mistletoe position, the rate of seed interception within any tree crown is highly variable. Only about 40 percent of seeds are intercepted by any tree crown; 60 to 80 percent of seeds are retained in the crown from which they originated (reinfection); of those that escape, 90 percent may be intercepted by an adjoining tree (contagion) (Hawksworth 1965, Smith 1985).

After their ballistic flight, seeds continue to move by gravity or rarely by birds and mammals (Nicholls and others 1984). The viscin coating helps the seed adhere to any surface it strikes, including host foliage. After the initial interception, this viscin imbibes water, swells, loosens, and permits the seed to slide down the needle (see Hawksworth and Wiens 1996 for illustrations). If the needle points upward, the seed lodges on a twig at the base of a needle (a good safesite); otherwise, the seed slides off and relocates in the crown or falls to the ground. Most infections, but not all, occur on young branch wood (Sproule 1996a). Although only a few seeds reach safesites (less then 10 percent, according to Hawksworth 1965), large numbers of seeds are produced on heavily infected trees (Hawksworth 1965, Smith 1977, Wicker 1967a). Although it seems inefficient, for short range spread and intensification this dispersal mechanism is effective enough for dwarf mistletoes to have persisted since the Miocene, adapted to nearly a hundred host species, and spread throughout the conifer forests of North America.

Establishment—The physical process of dispersal brings the mistletoe seed within millimeters of establishing a new infection; biological growth completes the establishment phase. Although the embryo of some tropical species begins growth soon after dispersal, most temperate mistletoes do not resume growth (germinate) until the following spring when light, moisture, and temperature are suitable (Gill and Hawksworth 1961, Lamont 1983, Scharpf 1970, Wicker 1974).

Genetic factors, predation, and environmental conditions reduce the number of viable seeds; field germination varies from 7 to 90 percent (Hawksworth and Wiens 1996). The chlorophyllous endosperm helps maintain the embryo and permits growth of the hypocotyl (see Deeks and others 2001). If the germinating seed rests on a host shoot with thin bark and its growth encounters a needle base, it then develops an external holdfast structure and penetration wedge that grows into the host cortex (Scharpf and Parmeter 1967). From the penetration wedge, fine strings of mistletoe tissue — the endophytic system — ramifies throughout the host cortex and eventually becomes embedded in xylem as “sinkers” (Cibrián and others 1980, Calvin and Wilson 1996, Hunt and others 1996). With the establishment of the endophytic system, the parasitic nutritional relation is initiated. Although little is know about the mechanisms of host resistance (see chapter 7), a high degree of host specificity and inherited variation in susceptibility suggest that physiological compatibility is required for an infection to become established (Kolb 2002).

Incubation—The endophytic system expands within the cortex and becomes embedded in the xylem for a number of years before aerial shoots are produced (incubation period). The endophytic system both encircles the infected branch and grows along it. The nature of distal–proximal growth depends upon the dwarf mistletoe species and point of origin. When a species such as *Arceuthobium douglasii* infects the host’s apical meristem, a systemic infection is established whereby the growth of the endophytic system keeps up with the growth of the host shoot. In other cases, growth of the endophytic system is limited, and a localized (nonsystemic) infection establishes. In nonsystemic infections, the infected branch develops a distinct fusiform swelling (except by a few host species). The incubation period extends from 2 to 12 years depending on mistletoe species and environmental conditions (Hawksworth and Wiens 1996). Typically, incubation periods range from 3 to 4 years.

Even after aerial shoots are produced, the endophytic system continues to grow (Calvin and Wilson 1996). Pathological effects of the mistletoe infection become evident as infected branches develop persistent witches’ brooms, and the upper crown thins and dies. Although a single, systemic infection can eventually develop into a large witches’ broom, most severe pathological effects result from multiple infections. Rarely, the endophytic system grows into the bole and establishes a main stem infection that persists as long as the host lives. Branch infections usually occur in the lower crown. These parasitized branches do not readily self-prune but are subject to breakage (especially large brooms in brittle hosts) and consumption by fire (brooms tend to be low and are highly flammable). Infections in the upper crown are lost as crown-dieback in severely diseased trees progresses.

Reproduction—Dwarf mistletoes are dioecious plants that only reproduce from seeds borne on shoots (see Gilbert 1988). Although dwarf mistletoe shoots have chlorophyll, they have no photosynthetic significance. Their function is primarily reproductive and secondarily in water regulation and synthesis of growth compounds (Wilson and Calvin 1996). Shoots range in size from several millimeters to 0.5 m, but most species are 2 to 10 cm tall. Generally, 1 to 2 years elapse from shoot appearance to the initial flowering. Several flower crops (range one to five) are usually produced, and shoots many be retained for 2 to 7 years. Meiosis may occur either immediately before flower production (direct flowering) or approximately 5 to 8 months before anthesis (indirect flowering). Most species exhibit definite annual flowering periods, but a few tropical species appear to flower continuously throughout the year. The sex ratio for most species is about 50:50 (Mathiasen and others 1998, Mathiasen and Shaw 1998, Wiens and others 1996). Pollen is either dispersed by wind or insects, and because of the clustered distribution of mistletoes, pollen is seldom limiting. Although fruit maturation in some tropical species occurs in as little as 4 to 5 months, most species require about 1 year (to 19 months) from flowering to seed dispersal. The number of fruits per infection is controlled by variation in the size of the endophytic system, host–parasite physiology, activity by pathogens and insects, and weather. Strand and Roth (1976) observe that the number of seeds produced by *Arceuthobium campylopodum* is related to plant age, but the coefficient of variation usually exceeds 100 percent (even greater than 200 percent). Wicker (1967a) estimates the number of mistletoe seeds produced on trees infected by *A. campylopodum* range from 800 to 2.2 million per year. Escudero and Cibrián (1985) report that *Arceuthobium globosum* produces more than 7.3 million seeds per hectare.

As parasites, dwarf mistletoes inhabit a relatively safe and constant environment and live for many decades. Because they rely upon a host for nutrition and because reproductive success does not require annual seed production, dwarf mistletoes can persist for years without producing aerial shoots (latent infections). Although little is known of the physiological mechanisms that regulate flowering, shoot production is apparently suppressed in the low light (Shaw and Weiss 2000) and in the nutrition environment of shaded lower crowns (Kolb 2002). Opening the canopy (removing trees) commonly results in a proliferation of mistletoe shoots on the residual trees (see chapter 8).

Spread and Intensification

Because ballistic dispersal and parasitism are important attributes of life history, these features are critical factors in determining population characteristics and dynamics (Bloomberg and Smith 1982, Hawksworth and Scharpf 1984, Parmeter 1978, Smith 1977). Ballistic dispersal is effective for short- range dissemination only, and parasitism requires a living host. Consequently, mistletoe plants are clustered within trees, and infected trees occur in patches (Robinson and others 2002). The spatial dynamics of mistletoe populations operate across a range of scales—the tree, neighborhood, stand, and landscape. Because mistletoes are clustered, infestations are usually described on the bases of incidence (percent of trees infected), severity (relative abundance), area distribution (extent), and spatial patterns (contagion). Successful reproduction leads to spread (Dixon and Hawksworth 1979) and intensification (Geils and Mathiasen 1990). In this context, spread refers to an increase in number of infected trees and the extent of an infestation (including the special case of vertical spread); intensification is increase in the abundance of mistletoe in an infested population. Stand development and management often generate grouping of trees whereby mistletoe disperses readily within groups but infrequently between groups. Even in stands with random or uniform patterns of tree distribution, the abundance of dwarf mistletoe plants often displays spatial autocorrelation. Spread and intensification, of course, are limited (Trummer and others 1998). Infected trees and the dwarf mistletoes they sustain eventually die from fire, insects, disease, or cutting, leading to fragmentation or local extinction of the dwarf mistletoe population.

Rating systems—There are numerous dwarf mistletoe rating systems for describing host susceptibility, mistletoe abundance, and witches' broom abundance (Hawksworth and Wiens 1972, Hawksworth 1977, Tinnin 1998). Each rating system provides a quantitative reference scale for indicating the population status of a mistletoe infestation and its potential for spread and intensification. New systems focus on potential use by wildlife (Parker 2001), fire ecology (Maffei 2002), and adaptations for woodland trees.

The host susceptibility system developed by Hawksworth and Wiens (1972) classifies candidate host species by the percentage expected to become infected where suitably exposed to an inoculum source. The classification is based on either direct field observations or general field experience. The system is meant to reflect the potential physiological susceptibility to infection and parasite development, not the distributional commonness or rarity of the host–pathogen combination. Species with greater than 90 percent infection where exposed to a mistletoe seed source are described as principal hosts; infestations on a principal host population are self-sustaining. Secondary, occasional, and rare hosts exhibit infection levels of 90 to 50 percent, 50 to 5 percent, or less than 5 percent, respectively. Infestations in populations of occasional or rare hosts usually occur where an infected principal host is present. Some species are recognized as hosts either by artificial inoculation or by natural infection of individuals planted beyond their normal range (extralimital hosts). Incompatible hosts are those species in which the dwarf mistletoe is able to establish a parasitic, nutritional relation but not to form aerial shoots. The physiological requirements necessary for parasitism are satisfied for only a few host and mistletoe combinations; most species are immune.

Although mistletoe abundance could be quantified by number of plants, biomass, or other indicators, mistletoe severity is usually described by a relative index for the amount of host crown affected, the dwarf mistletoe rating, DMR (Hawksworth 1977). By this system (fig. 6-1), the live host crown is divided into thirds; each third is rated as 0 if no live branches are apparently infected, 1 if not more than half of the branches are infected, or 2 if more than half of the branches are infected. The system allows a description of mistletoe distribution within crown thirds, or by summing values for crown thirds, abundance for the tree as a whole (DMR), or by averaging tree ratings, severity for a group or stand of trees. If tree ratings (0 to 6) are averaged over all susceptible trees in a stand, the result is stand-DMR; if tree ratings are averaged over infected trees only (1 to 6), the result is stand-DMI (Geils and Mathiasen 1990). The distinction is useful because of the computational identity among DMR, DMI, and the fraction of trees infected (incidence):

$$\text{DMR}=\text{DMI} \times (\text{incidence}).$$

DMR is a good single index of mistletoe severity; but DMI and incidence may be preferred to illustrate separately the severity of infection upon infected trees and relative abundance of infected trees in the population.

Although the DMR system applies well to many important hosts such as spruce, larch, and yellow and white pines, it is less practical for other hosts (Dooling 1978, Shaw and others 2000). In many hemlock and fir stands, the upper crown where much of the mistletoe would be found is obscured by height and foliage. The low, round, compact form of pinyons and general distribution of mistletoe throughout the crown make division into crown thirds impractical. In Douglas-fir, individual branches are difficult to count, but systemic witches' brooms are obvious. Tinnin (1998) suggests a variation to the DMR system, BVR for broom-forming hosts; in his system broom volume substitutes (in part) for number of infected branches in rating a crown third. Other variations are possible, but to avoid confusion, these other variations should not be referred to as DMR.

Spread and intensification are both strongly influenced by the same factors and are really just alternative views of the same basic life history processes—dispersal, establishment, incubation, and reproduction. Intensification of an infected host can occur from auto-infection, allo-infection, or both. The initial infection of a previously uninfected host (both spread and intensification) can only result from allo-infection. Dispersal is primarily affected by the physical configuration of the seed's environment—tree and crown density, vertical crown distribution (structure), and stand species composition. Establishment, incubation, and reproduction are determined by weather, genetic, and other biological factors, some of which are nearly fixed such as host susceptibility. Other factors such as host height growth and predation are extremely variable and difficult to predict. In most cases, the most valuable piece of information for predicting dwarf mistletoe behavior and response to management is knowledge of the mistletoe species. Although all dwarf mistletoes share a common genus morphology, most taxon are readily identifiable when size, branching pattern, color, and brooming response are considered together. Furthermore, most species can be determined based on host and distribution.

Description of Genus

Arceuthobium
Dwarf mistletoe

Arceuthobium M. Bieb. Flora Taurico-Caucasica 3(IV) Supplement, p. 629, 1819. Nom. Cons. 2091
= *Razoumofskya* Hoffman.

Herbs or shrubs from 0.5 cm to approximately 70 cm high (see fig. 4-2 and 4-3); parasitic on Pinaceae and Cupressaceae; plants glabrous, variously colored from greenish yellow to orange, reddish, or black; dioecious; stems with variant (anomalous) patterns of secondary growth; leaves reduced to minute, opposed, connate scales; internodes angled (at least when young); flowers generally decussate or rarely whorled on young shoots, 2 to 4 mm across; staminate flowers with a central nectary, perianth segments usually three to four (rarely two and up to seven) bearing a sessile, one-chambered, circular anther on each perianth segment; pollen spherical with six alternating spiny and smooth sections; pistillate flower manifestly epigynous with one style, perianth segments persistent, adnate to ovary, two-merous; ovary one-chambered; fruit an ovoid berry, one-seeded, mucilaginous and bicolored (distal and basal portions of different shades), explosive at maturity (one exception); seeds without true integuments, usually 3 to 5 mm long, ovate-lanceolate, containing one (rarely two) distal, cylindrical embryo, with copious endosperm.

A genus of 42 species in two subgenera. Subgenus *Arceuthobium* is characterized by verticillate (whorled) branching and occurring mostly in the Old World represented in North America by three species (*A. abietis-religiosae, A. americanum*, and *A. verticilliflorum*). Subgenus *Vaginata* occurs only in the New World and characterized by flabellate (fan-like) branching. Thirty-six taxa are described for North America (table 4-1). Type species: *Arceuthobium oxycedri* (DC.) M. Bieb.

Table 4-1—Dwarf mistletoes of Canada, Mexico, and the United States.

***Arceuthobium* taxon**	**Canada**	**United States**	**Mexico**
A. abietinum f. sp. *concoloris*	-	X	X
A. abietinum f. sp. *magnificae*	-	X	-
A. abietis-religiosae	-	-	X
A. americanum	X	X	-
A. apachecum	-	X	X
A. aureum subsp. *petersonii*	-	-	X
A. blumeri	-	X	X
A. californicum	-	X	-
A. campylopodum	-	X	X
A. cyanocarpum	-	X	-
A. divaricatum	-	X	X
A. douglasii	X	X	X
A. durangense	-	-	X
A. gillii	-	X	X
A. globosum subsp. *globosum*	-	-	X
A. globosum subsp. *grandicaule*	-	-	X
A. guatemalense	-	-	X
A. hondurense	-	-	X
A. laricis	X	X	-
A. littorum	-	X	-
A. microcarpum	-	X	-
A. monticola	-	X	-
A. nigrum	-	-	X
A. oaxacanum	-	-	X
A. occidentale	-	X	-
A. pendens	-	-	X
A. pusillum	X	X	-
A. rubrum	-	-	X
A. siskiyouense	-	X	-
A. strictum	-	-	X
A. tsugense subsp. *tsugense*	X	X	-
A. tsugense subsp. *mertensianae*	X	X	-
A. vaginatum subsp. *vaginatum*	-	-	X
A. vaginatum subsp. *cryptopodum*	-	X	X
A. verticilliflorum	-	-	X
A. yecorense	-	-	X
Total number of taxa	6	21	23

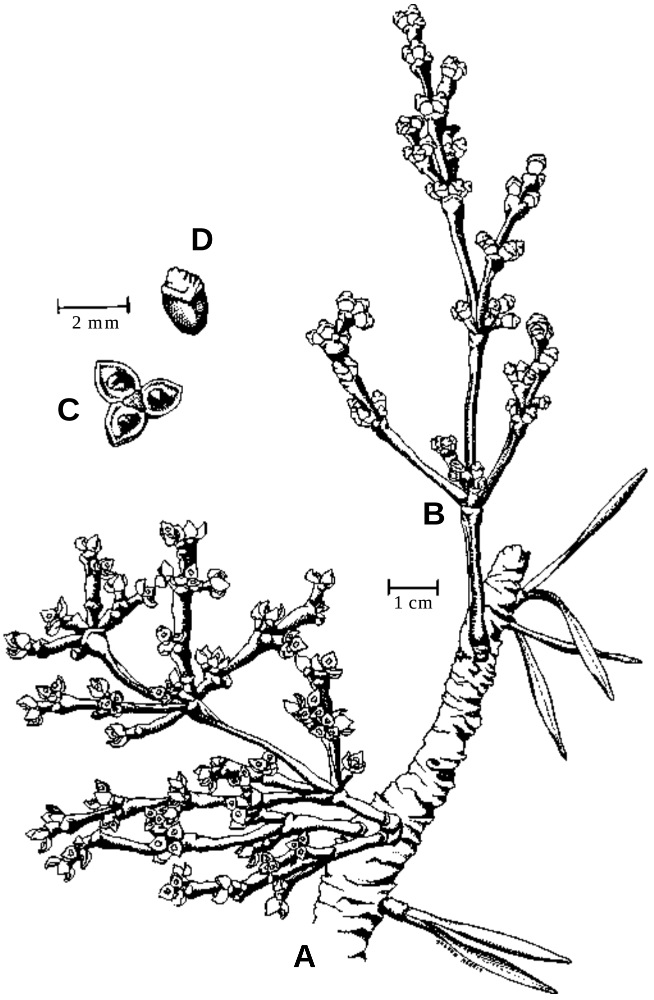


Figure 4-2—*Arceuthobium americanum* in spring, **A** staminate plant with verticillate (whorled) branching, **B** pistillate plant, **C** staminate flower, **D** pistillate flower. Illustration from Hawksworth and Wiens (1972).

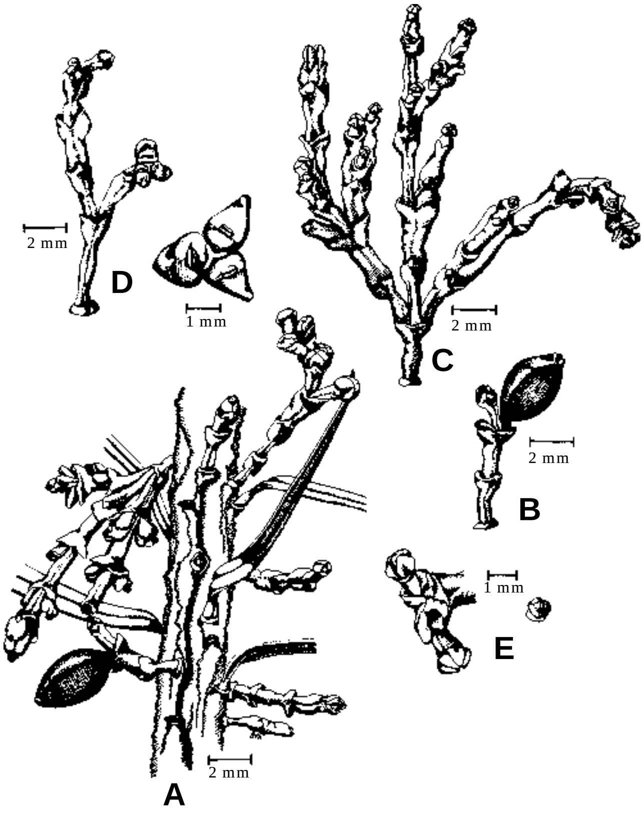


Figure 4-3—*Arceuthobium douglasii* in spring, **A** pistillate plant (left) and staminate plant (right), **B** detail of mature fruit, **C** staminate shoot, **D** staminate shoot with open mature buds (left) and detail of open flower (right), **E** staminate shoots with closed buds. Illustration from Hawksworth and Wiens (1972).

Key to North American Species of *Arceuthobium*

1. Distributed in Mexico 2
  2. Parasites of fir or Douglas-fir 3
    3. Shoots 1–3 cm high; parasites of Douglas-fir .... 11. *A. douglasii*
    3. Shoots more than 5 cm high; parasites of fir 4
      4. Shoots less than 10 cm high, not verticillate, greenish; Chihuahua .... 1. *A. abietinum*
      4. Shoots 10–20 cm high, some verticillate, yellow; Central Mexico .... 2. *A. abietis-religiosae*
  2. Parasites of pine 5
    5. Baja California 6
      6. Shoots olive–green, about 1–2 mm diameter; parasites of pinyon .... 10. *A. divaricatum*
      6. Shoots yellowish, about 2–4 mm diameter; parasites of *Pinus jeffreyi* or *P. coulteri* .... 8. *A. campylopodum*

5. Mainland Mexico 7

7. Parasites of pinyon or white pine 8

8. Parasites of pinyon .... 24. *A. pendens*

8. Parasites of white pine 9

9. Shoots greenish purple to purple; parasites of *Pinus ayacahuite* var. *ayacahuite*; southern Mexico .... 15. *A. guatemalense*

9. Shoots yellow or gray; parasites of *Pinus strobiformis* or *P. ayacahuite* var. *brachyptera*; northern Mexico 10

10. Shoots yellowish, usually less than 4 cm high; northern Coahuila .... 4. *A. apachecum*

10. Shoots gray, usually more than 6 cm high; Chihuahua, Durango, or Nuevo León .... 6. *A. blumeri*

7. Parasites of yellow pine 11

11. Shoots dark, usually some shade of black, reddish (or dull brown when dried) 12

12. Male and female plants similarly branched (little sexual dimorphism); fruits not glaucous 13

13. Shoots usually more than 10 cm high and more than 1 cm diameter at base; fruits 4–5 mm long, not shiny .... 30a. *A. vaginatum* subsp. *vaginatum*

13. Shoots usually less than 10 cm high and less than 1 cm diameter at base; fruits about 3 mm long, shiny .... 26. *A. rubrum*

12. Male and female plants dissimilarly branched (sexually dimorphic); fruits markedly glaucous .... 21. *A. nigrum*

11. Shoots yellow, brown, gray, or red 14

14. Staminate flowers verticillate on deciduous spikes; mature fruits more than 10 mm long .... 31. *A. verticilliflorum*

14. Staminate flowers not verticillate on deciduous spikes; mature fruits less than 6 mm long 15

15. Plants of northern Mexico 16

16. Male and female plants dissimilarly branched (sexually dimorphic) 17

17. Male plants essentially non-branched and female plants densely branched .... 28. *A. strictum*

17. Male plants with very open branches and female plants densely branched .... 13. *A. gillii*

16. Male and female plants similarly branched (little sexual dimorphism) 18

18. Shoots yellow or yellow–brown 19

19. Shoots bright yellow, in globose clusters, usually more than 10 cm high .... 14a. *A. globosum* subsp. *globosum*

19. Shoots yellow or brown, not in globose clusters, usually less than 10 cm high .... 32. *A. yecorense*

18. Shoots some shade of orange 20

20. Shoots dark–orange, usually more than 20 cm high; mature fruit 7 mm long; Durango or southward .... 12. *A. durangense*

20. Shoots yellow–orange, usually less than 20 cm high; mature fruit 5 mm long; Chihuahua, Sonora, or Coahuila .... 30b. *A. vaginatum* subsp. *cryptopodum*

15. Plants of southern Mexico (Chiapas and Oaxaca) 21

21. Shoots glaucous, olive-brown to gray green; parasite of *P. oocarpa* or *P. maximinoi* .... 16. *A. hondurense*

21. Shoots not glaucous; reddish, dark green, yellow, or orange 22

22. Shoots reddish; Oaxaca .... 22. *A. oaxacanum*

22. Shoots dark greenish yellow or orange; Oaxaca or Chiapas 23

23. Shoots yellow, often over 2 cm in diameter at base; elevations above 2,700 m .... 14b. *A. globosum* subsp. *grandicaule*

23. Shoots yellow–orange, usually less than 2 cm in diameter; elevations below 2,400 m .... 5. *A. aureum* subsp. *petersonii*

1. Distributed in the United States or Canada 24

24. Parasites principally of pine 25

25. Parasites of pinyon or white pine 26

26. Parasites of pinyon .... 10. *A. divaricatum*

26. Parasites of white pine 27

27. Parasites of *Pinus strobiformis* 28

28. Shoots usually less than 4 cm high, yellow; southern Arizona or southern New Mexico .... 4. *A. apachecum*

28. Shoots usually more than 6 cm high, gray; Huachuca Mountains of Arizona .... 6. *A. blumeri*

27. Parasites of white pines other than *Pinus strobiformis* 29

29. Parasites of *Pinus aristata*; Arizona .... 19. *A. microcarpum*

29. Parasites of pines other than *Pinus aristata* or if parasite of *Pinus aristata* then not Arizona 30

30. Shoots usually less than 6 cm high, densely clustered around the host branch; parasites of *Pinus flexilis*, *P. albicaulis*, *P. aristata*, or *P. longaeva* .... 9. *A. cyanocarpum*

30. Shoots usually more than 6 cm high, not densely clustered around the host branch; parasites of *Pinus monticola* or *P. lambertiana* 31

31. Shoots dark brown; parasites of *Pinus monticola*; southwestern Oregon or northeastern California .... 20. *A. monticola*

31. Shoots yellow to green; parasites of *Pinus lambertiana*; California .... 8. *A. californicum*

25. Parasites of yellow pine 32

32. Shoot branches verticillate; parasites principally of *Pinus contorta* or *P. banksiana* .... 3. *A. americanum*

32. Shoot branches flabellate; parasites principally of pines other than *Pinus contorta* and *P. banksiana* 33

33. Arizona, Utah, or eastward 34

34. Fruits glaucous; male plants much more openly branched than female plants; parasites of *Pinus leiophylla* var. *chihuahuana* .... 13. *A. gillii*

34. Fruits glabrous; male and female plants branch in similar manner; parasites of *Pinus ponderosa* var. *scopulorum*, *P. arizonica*, and *P. engelmannii*; north to Colorado .... 30b. *A. vaginatum* subsp. *cryptopodum*

33. Pacific Coast States, Nevada, Idaho, or British Columbia 35

35. Coastal areas (within 10 km of the Pacific Ocean) 36

36. Shoots usually less than 10 cm high; staminate flowers mostly 3-merous; parasites of *Pinus contorta* var. *contorta*; Orcas Island, Washington or British Columbia .... 29a. *A. tsugense* subsp. *tsugense*

36. Shoots usually more than 10 cm high; staminate flowers mostly 4-merous; parasites of *Pinus radiata* or *P. muricata*; California .... 18. *A. littorum*

35. Inland areas 37

37. Plants consistently forming witches' brooms; mature fruits about 6 mm long; shoots more than 3 mm diameter at base; parasites principally of *Pinus ponderosa* var. *ponderosa*, *P. jeffreyi*, or *P. coulteri*; California, Oregon, Washington, Idaho, or Nevada .... 8. *A. campylopodum*

37. Plants not forming witches' brooms; mature fruits about 4 mm long; shoots less than 3 mm diameter at base; parasites principally of *Pinus sabiniana* or *P. attenuata*; California or southwestern Oregon 38

38. Anthesis from late September to November; parasites principally of *Pinus sabiniana*; foothills surrounding Central Valley of California .... 23. *A. occidentale*

38. Anthesis in August; parasites of *Pinus attenuata*; southwestern Oregon or northwestern California .... 27. *A. siskiyouense*

24. Parasites principally of hemlock, larch, Douglas-fir, fir, or spruce 39

39 Parasites of hemlock, larch, or Douglas-fir 40

40. Shoots usually less than 4 cm high; parasites of Douglas-fir .... 11. *A. douglasii*

40. Shoots usually more than 5 cm high; parasites of larch or hemlock 41

41. Parasites principally of larch .... 17. *A. laricis*

41. Parasites principally of hemlock 42

42. Parasites of *Tsuga heterophylla*; California to Alaska .... 29a. *A. tsugense* subsp. *tsugense*

42. Parasites of *Tsuga mertensiana*; California to Idaho and British Columbia 43

43. Host associated with infected *Larix occidentalis*; northern Idaho .... 17. *A. laricis*

43. Host not associated with infected *Larix occidentalis*; central Sierra Nevada of California to southern British Columbia .... 29b. *A. tsugense* subsp. *mertensianae*

39. Parasites of fir or spruce 44

44. Parasites of fir 45

45. Shoots usually more than 10 cm high, yellowish; staminate buds same color as the subtending bracts; host not associated with infected hemlock; Arizona, southern Utah, Nevada, California, Oregon, or Washington east of the Cascade Crest .... 1. *A. abietinum*

45. Shoots usually less than 6 cm high, green to purplish; staminate buds conspicuously lighter than the subtending purplish bracts; host associated with infected hemlock; Oregon west of Cascade Crest to Alaska along Pacific Coast 46

46. Host associated with infected *Tsuga heterophylla* .... 29a. *A. tsugense* subsp. *tsugense*

46. Host associated with infected *Tsuga mertensianae* .... 29b. *A. tsugense* subsp. *mertensianae*

44. Parasites of spruce 47

47. Shoots less than 2 cm high; parasites of *Picea mariana*, *P. glauca*, or *P. rubens*; Saskatchewan and Great Lake region eastward to New Jersey and Newfoundland .... 25. *A. pusillum*

47. Shoots usually more than 5 cm high; parasites on *Picea engelmannii* or *P. pungens*; Arizona or southern New Mexico .... 19. *A. microcarpum*

Several other keys and floristic treatments of the dwarf mistletoes are available. Scharpf and Hawksworth (1993) provide photographs and field descriptions for the mistletoe from Washington, Oregon, and California. Unger (1992) provides a similar, general coverage for Canada. Numerous but brief and partial descriptions describe the dwarf mistletoes of Mexico (Cházaro and Olivae 1987a, Hawksworth 1987, Hawksworth and Cibrián 1985, Najera and others 1987, Rodriguez 1983). Recent taxonomic notes include Hawksworth and Wiens (1965, 1977, 1989) and Hawksworth and others (1992b). Because the taxonomy of dwarf mistletoes has changed considerably in the past few decades, especially for some regions (Mexico) and some groups (*campylopodum*, *globosum*, *vaginatum*), care is required when reading the literature to relate the information presented to the proper taxa. Host and distribution information is ultimately derived from specimen collections and field observations. When the name applied to a specimen changes, the information also refers to a different taxa; published information goes out of date and may be associated with the wrong mistletoe.

Description of Species

1. *Arceuthobium abietinum*
Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz, Manual Southern California Botany: 114, 1935.
=*A. campylopodum* f. *abietinum*.

Description. Mean shoot height 8 (maximum 22) cm. Shoots yellow green to yellow, branches flabellate. Basal diameter of dominant shoots 1.5 to 6.0 (mean 2) mm. Third internode 4 to 23 (mean 14) mm long, 1.5 to 4.0 mm (mean 2) mm wide; length/width ratio is 7:1 to 9:1. Staminate flowers 2.5 mm across; perianth three-merous, sometimes four-merous, apex acute; same color as shoots; segments 1.2 mm long, 1.0 mm wide. Mature fruit 4 by 2 mm; proximal portion 2.5 mm long. Seeds 2.8 by 1.2 mm.

Key to the Formae Speciales

1. Parasitic principally on *Abies concolor* or *A. grandis*; known in two areas in Chihuahua on *A. durangensis*. The primary distribution is from southern Washington southward through the Cascade and southern Coast Ranges in Oregon, and the North Coast and Cascade Ranges, Sierra Nevada to southern California. Isolated populations occur in southern Utah, northern and southern Arizona, and Chihuahua .... 1a. *A. abietinum* f. sp. *concoloris*.
1. Parasitic principally on *Abies magnifica* from southwestern Oregon (Josephine) to the southern Sierra Nevada, California .... 1b. *A. abietinum* f. sp. *magnificae*.

Phenology. Meiosis in July. Anthesis usually August and September. Fruits mature in September or October of the year following pollination; maturation period averages 13 to 14 months. Seeds germinate from February through June.

Hosts. Fir.

Discussion. Parmeter and Scharpf (1963) first report that the dwarf mistletoe on *Abies concolor* does not infect associated *A. magnifica,* and conversely, the parasite of *A. magnifica* does not parasitize associated *A. concolor*. We are unable, however, to find any morphological, phenological, or chemical differences useful to distinguish between the two mistletoes. Because the host affinities of these two dwarf mistletoes are distinct and they are of considerable importance in forestry, we treat them as *formae speciales*. Branch death or "flagging" by the fungus *Cytospora abietis* is one of the most conspicuous field symptoms for infection by this dwarf mistletoe (Scharpf 1969a). The biology, pathology, and management of fir dwarf mistletoe are discussed by Filip and others (2000), Scharpf (1969b), and Scharpf and Parmeter (1967, 1982).

Hunt (1993) reorganizes the taxonomy of *Abies* and recognizes several combinations not previously used in the dwarf mistletoe literature. In his treatment, *Abies lasiocarpa* refers to west-side populations in the Pacific Northwest and British Columbia and *A. bifolia* to east-side and Rocky Mountain populations. Status of the corkbark fir (=*Abies lasiocarpa* var. *arizonica*) in the Southwest is left as uncertain. *Abies lowiana* is recognized as species rather than subspecies.

1a. *Arceuthobium abietinum*
White Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens, Brittonia 22:267, 1970.

Hosts. The principal hosts of this dwarf mistletoe are *Abies concolor*, *A. grandis*, *A. durangensis*, and *A. lowiana*. *Abies concolor* (Nevada, Utah, and Arizona) and *A. lowiana* (California) are about equally susceptible, although the dwarf mistletoe is more widely distributed on the latter. The rare *Picea breweriana* in Oregon is associated with infected *Abies concolor* and is heavy infected by *Arceuthobium abietinum*. On the North Rim of Grand Canyon, Arizona, *Abies bifolia* (usually referred to *Abies lasiocarpa* var. *arizonica*) is occasionally parasitized where this tree grows in association with infected *A. concolor*. *Abies amabilis* is a rare host of this dwarf mistletoe at Crater Lake, Oregon. *Pinus ayacahuite* var. *brachyptera*, *P. contorta* var. *murrayana*, *P. lambertiana*, and *P. monticola* are rare hosts.

Distribution. United States (Washington, Oregon, California, Nevada, Utah, and Arizona), and Mexico (Chihuahua). *Arceuthobium abietinum* f. sp. *concoloris* is widely distributed from southern Washington (Skamania, Wenatchee, and Klickitat) south through the Cascade Range and Sierra Nevada to the San Bernardino Mountains, California. A single, relict population is known in the Willamette Valley, Oregon. It also occurs along the coast ranges from Mendocino, California, to Curry, Oregon. Isolated populations are known in Nevada (Spring, Sheep, and Groom Mountains) and Utah (Kane). The parasite is known in Arizona from the Grand Canyon, the Chiricahua Mountains (Cochise), and the Santa Catalina Mountains (Pima). This dwarf mistletoe is reported on *Abies durangensis* from in two localities in Chihuahua 1,000 km south of Arizona. *Arceuthobium abietinum* f. sp. *concoloris* occurs from near sea level along the coast of northern California and southern Oregon to over 2,650 m in the Spring Mountains of southern Nevada.

Discussion. In the Northwest, two other species of *Arceuthobium* occur on fir: (1) *Arceuthobium tsugense* on *Abies amabilis*, *A. grandis*, and *A. lasiocarpa* and (2) *Arceuthobium laricis* on *Abies grandis* and *A. lasiocarpa*. However, insofar as we are aware, neither of these dwarf mistletoes is sympatric with *Arceuthobium abietinum*. *Arceuthobium tsugense* and *A. laricis* rarely infect pure stands of fir, but they may parasitize fir secondarily in stands where the principal hosts of these dwarf mistletoes are parasitized (for example, hemlock by *A. tsugense* and larch by *A. laricis*). *Arceuthobium tsugense* differs from *A. abietinum* by shorter (7 cm), green to purple shoots compared with the longer (10 cm), yellowish shoots of *A. abietinum*. *Arceuthobium* *laricis* is readily distinguished from *A. abietinum* by shorter, darker shoots (4 cm versus 10 cm) and shorter (in summer) staminate spikes (2 to 3 mm versus 5 to 7 mm). 1b.

Arceuthobium abietinum
Red Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz f. sp. *magnificae* Hawksw. & Wiens, Brittonia 22:268, 1970.

Hosts. *Abies magnifica.*

Distribution. United States (Oregon and California). *Arceuthobium abietinum* f. sp. *magnificae* is distributed from Josephine, Oregon, to Kern, California, in the southern Sierra Nevada. Guyon and Munson (1991) record it within 3 km of the Nevada border. Elevational range is 1,500 to 2,400 m.

Discussion. *Arceuthobium abietinum* f. sp. *magnificae* is a common and serious disease agent of the *Abies magnifica* forests of the Sierra Nevada (Scharpf 1969b).

2. *Arceuthobium abietis-religiosae*
Mexican Fir Dwarf Mistletoe

Arceuthobium abietis-religiosae Heil, Zentralblatt f¸r Bakteriologie Abteilung 2:28, 1923 [and see Hawksworth and Wiens, Brittonia 17:231, 1965].

Description. Mean shoot height 10 (maximum 16) cm. Shoots olive green, older shoots typically with black variegations, occasionally with verticillate branching. Basal diameter of dominant shoots 2 to 10 (mean 4) mm. Third internode 8 to 24 (mean 15.4 ±5.3) mm long, 1 to 4 (mean 2.8) mm wide, length/width ratio 5.5:1. Staminate buds two to four per node. Staminate flowers 2 mm long, 2.4 mm across; perianth mostly three-merous, sometimes four-merous; apex obtuse-acute; same color as shoots on outer surface, reddish on inner surface distal to anther; segments 1.2 mm long, 0.9 mm wide. Pistillate flowers 1.0 mm long, 0.5 mm across. Mature fruit 3.5 by 2 mm; proximal portion 2.5 mm long. Seeds 2.2 by 1.0 mm.

Phenology. Meiosis in September. Anthesis poorly known but apparently flowering in March to April and September to October. Fruits probably mature in October or November.

Hosts. Known only on fir. *Abies religiosa* (including var. *emarginata*) is by far the most common host, but also this dwarf mistletoe also parasitizes *A. vejarii* and probably other Mexican firs.

Distribution. Mexico (Distrito Federal, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Puebla, Tamaulipas, Tlaxcala). This dwarf mistletoe is common in the *Abies religiosa* forests of Central Mexico and Sierra Madre Oriental (Hernandez and others 1992, Madrigal 1967). Elevational range is 2,500 to 3,350 m.

Discussion. This distinctive Mexican dwarf mistletoe is characterized by its large shoots, occasional verticillate branching, and exclusive parasitism of fir. With the exception of the rare occurrence of *Arceuthobium abietinum* in Chihuahua, this is the only dwarf mistletoe that parasitizes fir in Mexico.

3. *Arceuthobium americanum*
Lodgepole Pine Dwarf Mistletoe

Arceuthobium americanum Nutt. ex Engelm. in Gray, Boston Journal Natural History 6:214, 1850.

Description. Mean shoot height 5 to 9 (maximum 30) cm. Shoots yellowish to olive green, with verticillate branching (fig. 4-2). Basal diameter of dominant shoots 1 to 3 (mean 1.5) mm. Third internode 6 to 23 (mean 12 ±3.0) mm long, 1 to 2 (mean 1.2) mm wide (20 collections), length/width ratio 10.1:1. Staminate flowers borne on pedicel-like segments, 2 mm long, 2.2 mm across; perianth mostly three-merous, sometimes four-merous; same color as the shoots; segments 1.1 mm long, 1.0 mm wide. Pistillate flowers verticillate; 1.5 mm long, 1.0 mm across; two-merous. Mature fruit 3.5 to 4.5 (mean 4) mm long, 1.5 to 2.5 (mean 2) mm wide; proximal portion about 2.5 mm long. Seeds 2.4 by 1.1 mm.

Phenology. Meiosis in August. Anthesis usually from early April to early June, with extremes from late March to late June. Fruits mature in late August or September of the year following pollination; maturation period averages 16 months. Germination begins in May in Colorado.

Hosts. The principal hosts are *Pinus contorta* var. *latifolia*, var. *murrayana*, and *P. banksiana*; all are about equally susceptible. *Pinus contorta* var. *contorta* is infected in southern coastal British Columbia (Smith and Wass 1979). *Pinus ponderosa* var. *scopulorum* is frequently parasitized in Colorado, Utah, and Wyoming, usually where this tree is associated with infected *P. contorta* but also in pure stands of *Pinus ponderosa*. *Pinus ponderosa* var. *ponderosa*, however, is less susceptible and only occasionally infected. Other occasional hosts include *P. albicaulis*, *P. flexilis*, and *P. jeffreyi*. Rare, artificially inoculated, or extra-limital hosts are *Abies lasiocarpa* (Mathiasen and others 1996a), *Picea engelmannii*, *P. glauca* (incompatible), *P. pungens*, *P. mariana* (incompatible), *Pinus aristata*, *P. mugo*, *P. sylvestris*, and *Pseudotsuga menziesii* (incompatible).

Distribution. Canada (British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario) and the United States (Washington, Idaho, Montana, Oregon, California, Utah, Wyoming, Colorado, and possibly Nevada). *Arceuthobium americanum* has the most extensive distribution of any North American dwarf mistletoe. The distribution of *Arceuthobium americanum* is centered on the range of its principal host, *Pinus contorta*, and rarely occurs within the distribution of *Pinus contorta* var. *contorta* (shore pine). *Arceuthobium americanum* occurs in outlying populations of *Pinus* *contorta* var. *latifolia* in Southeastern Alberta and in north central Montana (Phillips, Hill, and Liberty). *Arceuthobium americanum* distribution maps include Alberta, British Columbia, Manitoba, Saskatchewan, Montana, Utah, Colorado, and California (see Brandt and others 1998, Hawksworth and Wiens 1996, Muir 2002). This dwarf mistletoe varies in elevation from 200 m near Lake Athabasca in northern Alberta and Saskatchewan to 3,350 m in central Colorado.

Discussion. *Arceuthobium americanum* induces characteristic systemic witches' brooms on *Pinus contorta* and produces the same type of broom on *P. ponderosa*. The witches' brooms formed on *Picea engelmannii*, however, are nonsystemic (Hawksworth and Graham 1963a). Kuijt (1960a) notes that *A. americanum* cannot perpetuate itself over time on *Pinus jeffreyi* or *P. ponderosa* var. *ponderosa* in California. In northern Colorado and southern Wyoming, however, the parasite is aggressive in pure stands of *P. ponderosa* var. *scopulorum* outside the range of *A. vaginatum* subsp. *cryptopodum*, which is the typical parasite on *P. ponderosa* in the Rocky Mountains. Hawksworth and Johnson (1989a) provide a synopsis of the biology and management of this mistletoe in the Rocky Mountains. Other general and silvicultural information is given by Baranyay (1970), Hawksworth and Dooling (1984), van der Kamp and Hawksworth (1985), and Van Sickle and Wegwitz (1978).

4. *Arceuthobium apachecum*

Apache Dwarf Mistletoe

Arceuthobium apachecum Hawksw. & Wiens, Brittonia 22:266, 1970.

=*A. campylopodum* f. *blumeri*

Description. Mean shoot height 3 to 4 (maximum 9) cm. Shoots yellow, green, or reddish, branches flabellate and densely clustered. Basal diameter of dominant shoots 1 to 2 (mean 1.8) mm. Third internode 5 to 10 (mean 7.2 ± 2.0) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 4.8:1. Flowers axillary. Staminate flowers 2.7 mm across; perianth three- to four-merous; same color as shoots; segments 1.3 mm long, 0.9 mm wide. Mature fruit 4 by 2.5 mm; proximal portion 2.5 mm long. Seeds 2.8 by 1.2 mm.

Phenology. Meiosis in July. Anthesis from late July to mid-September, peak in mid-August. Fruits mature from mid-August to mid-October, peak in September; maturation period averages about 13 months.

Host. Known only naturally on *Pinus strobiformis*, but successfully inoculated by Mathiasen (1978) on *Pinus flexilis*.

Distribution. United States (Arizona, New Mexico) and Mexico (Coahuila). This dwarf mistletoe has a limited distribution in southern Arizona and central New Mexico, with an outlier in the Sierra del Carmen in northern Coahuila. In Arizona, it occurs in the White, Pinaleno, Santa Catalina, Santa Rita, and Chiricahua Mountains and in New Mexico in the Mangas, San Mateo, Magdalena, and Capitan Mountains. Elevational range is 2,000 to 3,000 m.

Discussion. The exclusive occurrence of two dwarf mistletoes species, *Arceuthobium apachecum* and *A. blumeri*, on a single host species, *Pinus strobiformis*, is unique in *Arceuthobium*. Geographically consistent morphological and broom differences indicate that separate taxonomic status is warranted (Mathiasen 1982). Although they are not sympatric, they approach 60 km of each other in southern Arizona. *Arceuthobium apachecum*, but not *A. blumeri*, frequently induces witches' broom formation.

5. *Arceuthobium aureum* subsp. *petersonii*

Peterson's Dwarf Mistletoe

Arceuthobium aureum Hawksw. & Wiens subsp. *petersonii* Hawksw. & Wiens, Brittonia 29:415, 1977.

=*A. globosum*

Description. Shoots 14 to 40 (mean 24) cm tall, golden to yellow-brown, branches flabellate. Basal diameter of dominant shoots 14 to 35 (mean 23) mm. Third internode 14 to 35 (mean 23) mm long and 2.5 to 8 (mean 5) mm wide.

Phenology. Anthesis in September. Fruits mature June and July; maturation period of 9 to 10 months, which is several months less than is common for many dwarf mistletoes.

Hosts. *Pinus michoacana*, *P. montezumae*, *P. oaxacana*, *P. oocarpa*, *P. patula*, and *P. pseudostrobus* are the principal and only hosts. *Pinus michoacana* is somewhat less susceptible and is infected only when it grows in association with the other principal hosts.

Distribution. Mexico (Oaxaca, Chiapas). This dwarf mistletoe is common between San Cristóbal de las Casas and Teopisabout (Chiapas). Its distribution in Oaxaca is poorly known by a few collections from Miahuátlan to Suchixtepec. Elevational range is 2,200 to 2,450 m.

Discussion. The taxon recognized here as *Arceuthobium aureum* had been in the *Arceuthobium globosum* complex (Hawksworth and Wiens 1972, 1977). *Arceuthobium aureum* includes two subspecies, but only subspecies *petersonii* is found in Mexico. This subspecies is characterized by tall, slender, brown to golden shoots, long fruits (5 mm), long pedicels (4 mm), and tendency to form witches' brooms.

6. *Arceuthobium blumeri*

Blumer's Dwarf Mistletoe

Arceuthobium blumeri A. Nels., Botanical Gazette 56:65, 1913.

=*A. campylopodum* var. *cryptopodum*

=*A. campylopodum* f. *blumeri*.

Description. Mean shoot height 6 to 7 (maximum 18) cm, gray to straw or light green, branches flabellate.

Basal diameter of dominant shoots 1 to 3 (mean 2.1) mm. Third internode 5 to 14 (mean 9.1 ±2.5) mm long, 1 to 2 (mean 1.6) mm wide, length/width ratio 5.5:1. Staminate flowers 2.5 mm long, 2.5 to 3.0 mm across; perianth three- to six-merous (mostly three- or four-merous), segments 1.3 mm long, 1.0 mm wide, apex acute. Mature fruit 4 by 2.5 mm, proximal portion 2.5 mm long. Seeds 2.7 by 1.0 mm.

Phenology. Meiosis in July. Anthesis from mid-July to late-August, with a peak in early August (Mathiasen 1982). Fruits mature from late August to early October, with a peak in mid-September; maturation period averages 13 to 14 months.

Hosts. *Pinus strobiformis* and *P. ayacahuite* var. *brachyptera*. The host affinities of *Arceuthobium blumeri* are not clear because of the taxonomic confusion surrounding the white pine complex of *Pinus flexilis-strobiformis-ayacahuite* (Equiluz 1991, Hawksworth 1991, Perry 1991). Most host populations of this dwarf mistletoe are best referred to *P. ayacahuite* var. *brachyptera* in the Sierra Madre Occidental and *P. strobiformis* var. *potosiensis* on Cerro Potosí (Nuevo León). *Pinus flexilis* can be infected by inoculation (Mathiasen 1978).

Distribution. United States (Arizona) and Mexico (Sonora, Chihuahua, Durango, Nuevo León, and Coahuila). This dwarf mistletoe extends southward from the Huachuca Mountains in southern Arizona through the Sierra Madre Occidental in Chihuahua and Sonora to southern Durango. In the Sierra Madre Oriental, it is known only from Cerro Potosi (Nuevo León) and San Antonio de las Alazanas (Coahuila), but it probably occurs elsewhere over this extensive distribution (Cibrián and others 1980). Elevational range is 2,150 to 3,250 m.

Discussion. The parasitism of *Arceuthobium blumeri* and *A. apachecum* on *Pinus strobiformis* is discussed under *A. apachecum*. Distinctive features of *Arceuthobium blumeri* include its gray-colored shoots, four- to six-merous staminate flowers, and rare formation of witches' brooms.

7. *Arceuthobium californicum*

Sugar Pine Dwarf Mistletoe

Arceuthobium californicum Hawksw. & Wiens, Brittonia 22:266, 1970.
=*A. campylopodum* f. *cryptopodum*
=*A. campylopodum* f. *blumeri*.

Description. Mean shoot height 8 cm (maximum 12) cm, greenish to bright yellow, turning brown at base of older shoots, branches flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2) mm. Third internode 6 to 16 (mean 10.5 ±2.9) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 7.0:1. Flowers axillary. Staminate flowers 3.3 mm across; perianth three- or four-merous, segments 1.5 mm long, 1.1 mm wide. Mature fruit 4 by 2.5 mm; proximal portion 2.0 mm long. Seeds 3.2 by 1.2 mm.

Phenology. Meiosis in July. Anthesis usually in mid-July to mid-August, with extremes from early July to late August. Fruits mature from mid-September to mid-October, with extremes from late August to early November; maturation period averages 13 to 14 months.

Hosts. The only principal host is *Pinus lambertiana*. In association with infected *P. lambertiana*, *P. monticola* is secondarily parasitized (Mathiasen and Hawksworth 1988). Infected *P. lambertiana* produce large, compact witches' brooms.

Distribution. United States (California). This species is distributed from Mount Shasta southward through the North Coast Range, and through the Cascade Range south to Lake County and the west side of the Sierra Nevada to the Cuayamaca Mountains (San Diego). Elevational range is 600 to 2,000 m.

Discussion. *Arceuthobium californicum* is common in many areas and a serious pathogen of *Pinus lambertiana* (Scharpf and Hawksworth 1968).

8. *Arceuthobium campylopodum*

Western Dwarf Mistletoe

Arceuthobium campylopodum Engelm. in Gray, Boston Journal Natural History 6:214, 1850.
=*A. campylopodum* f. *typicum*.

Description. Mean shoot height 8 (maximum 13) cm, olive green to yellow, branches flabellate. Staminate plants brownish, and pistillate plants greenish. Basal diameter of dominant shoots 1.5 to 5.0 (mean 3) mm. Third internode 7 to 22 (mean 11.3 ±3.8) mm long, 1.5 to 2.5 (mean 2.0) mm wide, length/width ratio 5.6:1. Staminate flowers 3.0 mm across; perianth three-merous (occasionally four-merous), segments 1.4 mm long, 1.0 mm wide. Mature fruit 5.0 by 3.0 mm.

Phenology. Meiosis in July. Peak anthesis usually from mid-August to early October, with extremes from early August to late October. Fruits usually mature from early September to mid-November, with extremes from late August to late November; maturation period averages 13 months.

Hosts. The principal and most commonly infected hosts are *Pinus ponderosa* var. *ponderosa* and *P. jeffreyi*. *Pinus jeffreyi* is somewhat more susceptible than *P. ponderosa*, but both species incur considerable damage. Other trees frequently infected, particularly when associated with the above hosts, are *Pinus attenuata* and *P. coulteri*. In the Spring Mountains, Nevada, *P. ponderosa* var. *scopulorum* is a common and seriously damaged host, but this is the only known area where *Arceuthobium campylopodum* occurs naturally within the range of *scopulorum*. Occasional hosts for *A. campylopodum* are *P. contorta* var. *latifolia*, var. *murrayana*, and *P. sabiniana*. *Pinus lambertiana* is a rare host. Hosts by artificial inoculation are *Abies concolor*, *A. grandis*, *Picea abies*, *Pinus sylvestris*, *P. mugo*, *P. resinosa*, and *Larix occidentalis*. Although *Abies concolor*, *A. grandis*, and *Larix occidentalis* are commonly associated with *Pinus ponderosa* infected by *A. campylopodum*, they are not known to be naturally infected. *Pinus washoensis* is expected to be susceptible, but we know of no collections or reports on this species.

Distribution. United States (Washington, Idaho, Oregon, California, and Nevada) and Mexico (Baja California Norte). *Arceuthobium campylopodum* occurs from northern Washington and eastern Idaho, south through Oregon and California (but not the southern Coast Range) to the Sierra Juárez and Sierra de San Pedro Mártir (Baja California Norte). The distribution of this and other taxa in California is discussed by Kuijt (1960a). In Nevada, it occurs near Lake Tahoe and in the Spring Mountains (Clark). *Arceuthobium campylopodum* is distributed by elevation from 30 m along the Columbia River, near Hood River, Oregon, to 2,500 m in the Spring Mountains, Nevada.

Discussion. *Arceuthobium campylopodum* is a serious pathogen of *Pinus jeffreyi* and *P. ponderosa*. Our observations suggest that host damage is more severe in the southern or drier parts of the distribution. The most severely infested stands are in the California Laguna Mountains and on the east-side of the Sierra–Cascade forests. The biology, ecology, and management of this mistletoe are discussed by Kimmey and Mielke (1959), Schmitt (1996), and Stand and Roth (1976). The serious mortality caused by this mistletoe to pine in Oregon is described by Roth (2001).

9. *Arceuthobium cyanocarpum*
Limber Pine Dwarf Mistletoe

Arceuthobium cyanocarpum (A. Nels. ex Rydb.) A. Nels., New Manual of Botany of the Central Rocky Mountains, p. 146, 1909.

=*A. campylopodum* f. *cyanocarpum*.

Description. Mean shoot height 3 (maximum 7) cm, yellow–green, branches flabellate, densely clustered. Basal diameter of dominant shoots 1 to 2 (mean 1.4) mm. Third internode 2 to 14 (mean 5.2 ±2.0) mm long, 1.0 to 1.5 (mean 1.1) mm wide; length/width ratio 4.7:1. Staminate flowers 3.0 mm across; perianth three-merous (rarely four-merous), same color as shoots; segments 1.4 mm long, 1.0 mm wide, apex acute. Mature fruit 3.5 by 2.0 mm; proximal portion 2.0 mm long. Seeds 2.0 b 0.9 mm.

Phenology. Meiosis in July. Peak anthesis from mid-July to early September, with extremes from early July to mid-September. Fruits mature from mid-August to late September; maturation averages 12 months. Seed germination mostly in June.

Hosts. *Pinus flexilis* is the most common host of this dwarf mistletoe throughout its extensive geographical range. *Pinus albicaulis*, *P. aristata*, and *P. longaeva* are also principal hosts even though they are not common within the range of *Arceuthobium cyanocarpum*. *Pinus albicaulis* is infected in western Wyoming, northern Nevada, central Oregon, and northern California. Infection of *P. aristata* is known from La Veta Pass, Colorado, in association with infected *P. flexilis*. *Pinus longaeva* is parasitized in many areas of Utah and Nevada. In northern California, *Pinus monticola* is a secondary host; and *Pinus balfouriana* is an occasional host (Mathiasen and Daughtery 2001). *Tsuga mertensiana* in central Oregon is another secondary host; and other occasional or rare hosts include *Picea engelmannii* (doubtful), *P. contorta* var. *latifolia*, and *P. ponderosa* var. *scopulorum*. *Pinus strobus* and *P. strobiformis* are susceptible to infection by artificial inoculation (Hawksworth and Wiens 1972).

Distribution. United States (Idaho, Montana, Oregon, California, Nevada, Utah, Wyoming, and Colorado). This dwarf mistletoe occurs from southern Montana and northern Wyoming south to southern Colorado and west to Oregon and California where it occurs on the east side of the Sierra Nevada, in the Panamint Mountains (Death Valley National Monument), and in the San Bernardino to San Jacinto Mountains (southern California). Distribution maps for *Arceuthobium cyanocarpum* are available for Colorado and Nevada (see Hawksworth and Wiens 1996). Elevational range is 1,600 m in southern Montana to nearly 3,050 m in central Colorado.

Discussion. This dwarf mistletoe, which characteristically infects *Pinus flexilis* and associated high-altitude white pines, is easily recognized by small, densely clustered shoots and common branch flagging. Witches' brooms are typically small and compact, and infection is usually throughout the entire crown. *Arceuthobium cyanocarpum* causes heavy mortality in *Pinus flexilis* in the Rocky Mountains and in *P. albicaulis* on Mount Shasta, California (Mathiasen and Hawksworth 1988).

10. *Arceuthobium divaricatum*
Pinyon Dwarf Mistletoe

Arceuthobium divaricatum Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:253, 1878.

=*A. campylopodum* f. *divaricatum*.

Description. Mean shoot height 8 (maximum 3) cm, olive green to brown, branches flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2) mm. Third internode 6 to 15 (mean 9.8 ±2.4) mm long, 1 to 2 (mean 1.6) mm wide, length/width ratio 6.1:1. Staminate flowers 2.5 mm across; perianth three-merous; segments 1.1 mm long, 0.9 mm wide. Mature fruit 3.5 by 2.0 mm; proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Meiosis in July. Peak anthesis usually from early August to late September. Fruits usually mature from early September to late October in the year following pollination; maturation period averages 13 months.

Hosts. *Arceuthobium divaricatum* is restricted to pinyon. The most common principal hosts are *Pinus edulis* (Arizona, Colorado, New Mexico, Texas, and Utah) and *P. monophylla* (California, Nevada). A second set of pinyons including *P. californiarum*, *P. cembroides*, *P. discolor*, and *P. quadrifolia* are also classed as principal hosts even though the mistletoe is not common in their distributions. Infestations occur locally on *P. californiarum* in the Mojave Desert Ranges of New York Mountains, Providence Mountains, Joshua Tree National Monument (subsp. *californiarum*), and Southwest mountains of Zion National Park, Black Hole, and central Arizona (subsp. *fallax*). *Pinus cembroides* is parasitized only in the Davis Mountains, Texas. *Pinus discolor* is parasitized only at Fort Bayard and the Mule Mountains, New Mexico. *Pinus quadrifolia* is parasitized in the Sierra Juárez and Sierra San Pedro Mártir of Baja California and Laguna Mountains, California.

Distribution. United States (California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Baja California Norte). *Arceuthobium divaricatum* occurs in eastern and southern California (the White and Inyo Mountains, the Mount Pinos area, the San Bernardino Mountains, and the Mojave Desert Ranges), the southern three-fourths of Nevada and Utah, western Colorado, Arizona (except far southwest), New Mexico (except far northeast), and south to the Davis Mountains (western Texas). In Mexico, it is known only in northern Baja California. The northernmost population of which we are aware is in the Pilot Range (Box Elder, Utah). Kuijt (1960a) identifies several the scattered populations of this parasite in California; its distribution is probably more common than indicated by collections. *Arceuthobium divaricatum* and *Phoradendron juniperinum* commonly infest the two dominant species respectively of pinyon–juniper woodlands of the Southwestern United States, especially at the Grand Canyon (Hreha and Weber 1979). Distribution maps are published for Colorado, Utah, and New Mexico (see Hawksworth and Wiens 1996). Elevational range is from 1,200 m near Sedona, Arizona to 3,000 m in the San Mateo Mountains of New Mexico.

Discussion. The witches' brooms induced by this dwarf mistletoe are often poorly developed and not conspicuous because of the stunted habit of even healthy trees. Our observations suggest that witches' brooms are more consistent in *Pinus edulis* than in *P. monophylla*. Shoots of the mistletoe are often long, slender, and spreading, especially the staminate plants that also tend to have relatively few flowers per shoot. *Arceuthobium divaricatum* is the only dwarf mistletoe of pinyon in the United States. Mathiasen and others (2002a) summarize information on this mistletoe.

11. *Arceuthobium douglasii*
Douglas-fir Dwarf Mistletoe

Arceuthobium douglasii Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:253, 1878.

Description. Mean shoot height 2 (maximum 8) cm, olive green, branches flabellate (fig. 4-3). Basal diameter of dominant shoots 1.0 to 1.5 (mean 1) mm. Third internode 2 to 6 (mean 3.6 ±1.2) mm long, 1.0 mm wide, length/width ratio 3.6:1. Flowers usually axillary in pairs, occasionally borne on pedicel-like segments. Staminate flowers 2.0 mm long, 2.3 mm across; perianth mostly three-merous (occasionally four- or two-merous); segments rounded at the apex, without a keel, inner surface reddish to purple, lower surface same color as shoots, about 1.0 mm long, 1.0 mm wide. Pistillate flowers 1.5 mm long, 1.5 mm across. Mature fruit olive–green 3.5 to 4.5 (mean 4) mm long, 1.5 to 2.0 mm wide, obovate; proximal portion 2.5 mm long. Seeds 2.4 by 1.1 mm.

Phenology. Staminate meiosis in September, pistillate meiosis in April. Peak anthesis is usually in April or May, but with marked latitudinal variation—March in Mexico, late April to early May in Arizona and New Mexico, late May in Colorado, Utah, and Oregon, and early to mid-June in Washington, northern Idaho, and Montana. Fruit maturity is more uniform throughout the distribution, however, usually from late August to late September; maturation period averages 17 to 18 months. The seeds germinate in March.

Hosts. The principal and only commonly infected host is *Pseudotsuga menziesii*. Both var. *menziesii* (Washington, Oregon, and California) and var. *glauca* (from British Columbia through the Rocky Mountains to Central Mexico) are parasitized, although it is much more common on var. *glauca*. Where associated with infected *Pseudotsuga menziesii*, *Abies amabilis* is occasionally infected. Rare hosts are *Abies concolor*, *A. grandis*, *Picea pungens*, and *P. engelmannii*. Mathiasen (1999) reports that the two taxa *Abies lasiocarpa*, a secondary host (66 percent infected), and *Abies bifolia*, an occasional host (15 percent infected) differed significantly in susceptibility to *Arceuthobium douglasii* on plots where the principal host was over 90 percent infected.

Distribution. Canada (British Columbia), United States (Washington, Idaho, Montana, Oregon, California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Chihuahua, Durango, Coahuila, and Nuevo León). *Arceuthobium douglasii* has the greatest latitudinal range (3,000 km) of any species in the genus. This dwarf mistletoe is common in eastern Washington, eastern Oregon, Idaho, western Montana, Idaho, Utah, Colorado, and New Mexico. It is rare in Nevada (Wheeler Peak), Wyoming (Teton), and Texas (Guadalupe Mountains). Marshall and Filip (1999) relate the occurrence of this mistletoe to stand and ecological relations in Oregon. The distribution of the dwarf mistletoe in Mexico is poorly known, and it is probably more widespread than suggested by a few available records from Chihuahua, Coahuila, Durango, and Nuevo León. Distribution maps of *Arceuthobium douglasii* are published for British Columbia, Montana, Utah, Colorado, New Mexico, and California (see Hawksworth and Wiens 1996). The altitudinal range of this dwarf mistletoe is correlated with latitude; it occurs as low as 300 m near Lytton (British Columbia) and as high as 3,250 m on Cerro Potosí (Nuevo León).

Discussion. This dwarf mistletoe is the smallest in Western North America, but its typically systemic mode of infection produces large witches' brooms and causes severe growth loss and mortality in *Pseudotsuga menziesii* (Tinnin and others 1999). Brooms provide special wildlife habitat for foraging, resting, and nesting (see chapter 5). Hadfield and others (2000) and Schmitt (1997) discuss the biology, ecology, and management of this mistletoe.

12. *Arceuthobium durangense*
Durangan Dwarf Mistletoe

Arceuthobium durangense (Hawksw. & Wiens) Hawksw. & Wiens, Phytologia 66:7, 1989.

=*A. vaginatum* subsp. *durangense*.

Description. Mean shoot height 20 to 30 (50) cm, bright orange; older shoots becoming pendulous. Basal diameter of dominant shoots 4 to 8 (mean 6) mm. Third internode 9 to 22 (mean 17.9 ±4.1) mm long, 3.5 to 6.0 (mean 4.5) mm wide, length/width ratio 3.3:1. Internodes often slightly swollen at base. Staminate flowers 2.5 mm long, 2.5 mm across, segments 1 mm long, 1 mm wide. Mature fruit 7 by 3.5 mm; bluish; proximal portion 4 mm long. Seeds 4 by 1.5 mm.

Phenology. Time of meiosis unknown (probably February). Anthesis usually in April. Fruits mature from mid-July to September of the year following pollination; maturation period averages 15 to 18 months.

Hosts. *Pinus douglasiana*, *P. durangensis*, *P. michoacana*, *P. montezumae*, and *P. pseudostrobus* are the principal hosts. *Pinus herrerai* is occasionally parasitized when it occurs near infected principal hosts. The host status of *Pinus oocarpa* needs confirmation.

Distribution. Mexico (Durango, Sinaloa, and Jalisco). This rather local dwarf mistletoe occurs on the western escarpment of the Sierra Madre Occidental (Durango, Sinaloa, and perhaps Nayarit) and in the Sierra de Quilla (Jalisco). Elevational range is 1,450 to 2,750 m.

Discussion. Although previously referred to as a subspecies of *Arceuthobium vaginatum*, we now recognize this dwarf mistletoe as a distinct species. *Arceuthobium durangense* is not sympatric with *A. vaginatum* and differs by its larger, bright orange shoots, distinct branching pattern, and larger fruit.

13. *Arceuthobium gillii*
Chihuahua Pine Dwarf Mistletoe

Arceuthobium gillii Hawksw, & Wiens, Brittonia 16:22, 1964.

=*A. vaginatum* subsp. *cryptopodum*.

Description. Mean shoot height 8 to 15 (maximum 25) cm, greenish–brown, branches flabellate. Basal diameter of dominant shoots 2.5 to 8.0 (mean 4) mm. Third internode 5 to 18 (mean 10.7 ±3.4) mm long, 2.0 to 4.5 (mean 2.8) mm wide, length/width ratio 3.8:1. Staminate flowers 3.5 mm long, 2.5 to 4.0 (mean 3.2) mm across. Pistillate flowers 1.5 mm long, 1 mm across. Mature fruit 4 to 5 mm long, 2 to 3 mm wide, the proximal portion of fruit conspicuously glaucous. Seeds 3.1 by 1.4 mm.

Phenology. Meiosis in September. Anthesis usually in March and April. Fruits mature in October of the year following pollination; maturation period averages 19 months, the longest in the genus. Seed germination begins in April.

Hosts. The principal and only commonly infected hosts are *Pinus leiophylla* var. *chihuahuana*, *P. lumholtzii*, and *P. herrerai*. Although *Pinus. leiophylla* var. *leiophylla* is a principal host, it is not common within the range of *Arceuthobium gillii*. In western Chihuahua, this dwarf mistletoe rarely parasitizes *Pinus arizonica* var. *arizonica* and *P. cooperi*.

Distribution. United States (Arizona and New Mexico) and Mexico (Chihuahua, Durango, Sinaloa, and Sonora). This dwarf mistletoe occurs in southeastern Arizona (Santa Catalina, Rincon, Santa Rita, Huachuca, and Chiricahua Mountains) and the Animas Mountains in southwestern New Mexico. It is most common in western Chihuahua, but it is also distributed in adjacent northern and eastern Sonora, northern Durango, and northeastern Sinaloa. Elevational range is from 1,700 m in southern Arizona to 2,650 m in southern Chihuahua.

Discussion. This dwarf mistletoe has long been confused with *Arceuthobium vaginatum* subsp. *cryptopodum*, but it differs in host preference, phenology, and its conspicuously glaucous fruits. These two dwarf mistletoes are usually separated by at least 300 m of elevation in Arizona and New Mexico. Where they co-occur in central Chihuahua, there is no evidence of hybridization. A characteristic feature of *Arceuthobium gillii* is its strong sexual dimorphism—staminate plants tall and openly branched and pistillate plants small and densely branched. This dwarf mistletoe causes open, nonsystemic witches' brooms and serious mortality in *Pinus leiophylla* var. *chihuahuana* and *P. lumholtzii*.

14. *Arceuthobium globosum*

Arceuthobium globosum Hawksw. & Wiens, Brittonia 17:223, 1965.

Description. Shoot height 20 to 50 (maximum 70) cm, yellow to greenish, branches flabellate. Basal diameter of dominant shoots 3 to 48 mm. Third internode 4 to 37 mm long, 2 to 24 mm wide. Staminate flowers about 3.5 to 5.0 mm long, 3.0 to 3.5 mm across; perianth three- or four-merous; same color as shoots; segments 1.3 mm long, 1.0 mm wide. Pistillate flowers 1.5 mm long, 1.5 mm across. Mature fruit 5 to 7 mm long, 3 to 4 mm wide; proximal portion 3.5 mm long, with pedicels 4.0 to 5.0 mm long. Seeds 5 by 2 mm.

Hosts. Common on yellow pine.

Discussion. Hawksworth and Wiens (1972) note considerable variation within collections determined as *Arceuthobium globosum*. Subsequent studies by Hawksworth and Wiens (1977) and Wiens and Shaw (1994) have resulted in the segregation of *Arceuthobium globosum* (*sensu lato*) into five taxa:

- *Arceuthobium aureum* subsp. *aureum* (Guatemala)
- *Arceuthobium aureum* subsp. *petersonii* (Southern Mexico)
- *Arceuthobium globosum* subsp. *globosum* (Northwestern Mexico)
- *Arceuthobium globosum* subsp. *grandicaule* (Central Mexico and Central America)
- *Arceuthobium hawksworthii* (Central America)

14a. *Arceuthobium globosum* subsp. *globosum*
Rounded Dwarf Mistletoe

Description. Shoots 15 to 20 (maximum 50) cm high, bright yellow, branches flabellate. Basal diameter of dominant shoots 3 to 10 (mean 7) mm. Third internode 19 mm long, 4 mm wide. Staminate flowers 4 mm wide. Mature fruit 5 by 2.5 mm. Seeds 4 by 2 mm.

Phenology. Anthesis usually March and April. Fruits mature June and July; maturation period averages 15 to 16 months.

Hosts. The principal hosts are *Pinus cooperi*, *P. durangensis*, and *P. engelmannii*. *Pinus arizonica* is occasionally parasitized; *Pinus teocote* is a rare host.

Distribution. Mexico (Sonora, Chihuahua, Durango, and Jalisco). This subspecies is widely distributed in the pine forests of the Sierra Madre Occidental from northwestern Chihuahua and adjacent Sonora, through Durango to northern Jalisco. Elevational range is 2,300 to 2,800 m.

Discussion. This dwarf mistletoe is characterized by its bright yellow, globose clusters, and absence of witches' broom formation.

14b. *Arceuthobium globosum* subsp. *grandicaule*
Large-Stemmed Dwarf Mistletoe

Arceuthobium globosum Hawksw. & Wiens subsp. grandicaule Hawksw. & Wiens, Brittonia 29:413, 1977.

Description. Shoots 18 to 50 (maximum 70, mean 25) cm tall, yellow green, typically dark at the base of older shoots, branches flabellate. Basal diameter of dominant shoots 10 to 48 (mean 17) mm. Third internode 14 to 37 (mean 27) mm long, 3 to 20 (mean 7) mm wide. Staminate flowers 5 mm wide, four-merous. Mature fruits 6 to 7 mm long, 3.5 mm wide. Seeds 5 by 3 mm.

Phenology. Meiosis in December. Anthesis from January through May, with peak March and April. Fruits maturing July through October; maturation period averages 16 to 18 months. Seed dispersal from early July to early November, with a peak from mid-August to mid-September (Escudero and Cibrián 1985).

Hosts. This subspecies has one of the broadest host ranges of any dwarf mistletoe. It infects at least 12 species of Mexican pines, all of which appear to be about equally susceptible (but see Valdivia 1964): *Pinus douglasiana*, *P. durangensis*, *P. hartwegii*, *P.*

Key to the Subspecies of *Arceuthobium globosum*

1. Plants yellowish; shoots usually 15 to 20 (maximum 50) cm tall, less than 1 cm diameter at the base; witches' brooms not formed; shoots usually only on the host branches; northern Mexico .... 14a. *A. globosum* subsp. *globosum*

1. Plants greenish to yellow–green, typically dark at the base of older shoots; shoots usually 25 to 40 (maximum 70) cm tall, greater than 1 cm diameter at the base; witches' brooms usually induced; shoots on branches, but also frequently on the lower main trunks; central and southern Mexico to the highlands of western Guatemala .... 14b. *A. globosum* subsp. *grandicaule*.

lawsonii, P. maximinoi, P. michoacana, P. montezumae, P. patula, P. pringlei, P. pseudostrobus, P. rudis, and *P. teocote*.

Distribution. Mexico (Jalisco, Michoacán, Mexico, Hidalgo, Distrito Federal, Guerrero, Puebla, Tlaxcala, Veracruz, and Oaxaca), Guatemala, and Honduras. *Arceuthobium globosum* subsp. *grandicaule* is the most abundant dwarf mistletoe in Central Mexico, common in western Guatemala, and recently reported in Honduras (Melgar and others 2001). Elevational range is 2,450 to 4,000 m (Hernandez and others 1992).

Discussion. This subspecies has large shoots reaching a height of 70 cm and with a basal diameter of 5 cm. Valdivia (1964) reports *Arceuthobium globosum* is present on nearly 40 percent of 400,000 ha of pine forest in northeastern Michoacán. Vázquez (1994a) discusses the importance and sampling method for this mistletoe.

15. *Arceuthobium guatemalense*
Guatemalan Dwarf Mistletoe

Arceuthobium guatemalense Hawksw. & Wiens, Brittonia 22:267, 1970.

Description. Mean shoot height 1 to 3 cm on systemic witches' brooms, but shoots on nonsystemic infections up to 7 cm high; living shoots greenish to purple, yellow to brown when dried, branches flabellate. Basal diameter of dominant shoots 2.0 to 2.5 mm. Third internode 8 to 15 (mean 11.4 ±2.8) mm long, 1.5 to 2.0 (mean 1.7) mm wide; length/width ratio 6.7:1. Staminate flowers 2 mm across; perianth two- or three-merous, segments 0.9 mm long, 0.7 mm wide. Mature fruit 3.5 to 4.0 mm long, 1.5 to 2.0 mm wide; distal portion 1.2 mm long; dark green, glabrous, with a slightly swollen ring at the base of the fruit where it joins the pedicel. Seeds 2.0 by 0.8 mm.

Phenology. Time of meiosis unknown. Anthesis apparently in August and early September. Fruits mature in September; maturation period about 12 to 13 months. Seed germination in September.

Hosts. Known only on *Pinus ayacahuite* var. *ayacahuite*.

Distribution. Mexico (Oaxaca and Chiapas) and Guatemala. This distinctive species is known only from the high mountains of Western Guatemala and Southern Mexico. Elevational range is poorly known; our collections are from 2,450 to 3,100 m.

Discussion. The consistent formation of systemic witches' brooms is a distinctive characteristic of this species; brooms sometimes measure 3 to 5 m across. An unusual feature of these witches' brooms is that the shoots of the dwarf mistletoe are consistently formed on 1-year-old host shoots and, in some cases, on the current year's growth. This species causes extensive damage and considerable mortality to *Pinus ayacahuite*.

16. *Arceuthobium hondurense*
Honduran Dwarf Mistletoe

Arceuthobium hondurense Hawksworth & Wiens, Brittonia 22: 267, 1970.
=*Arceuthobium nigrum*

Description. Mean shoot height ca. 14 (max. 21) cm, olive brown to grayish green, markedly glaucous; branches flabellate. Basal diameter of dominant shoots 3 to 9 (mean 5) mm; nodes of older shoots swollen; lateral branches of staminate plants at nearly right angles to the axis of the main shoot; third internode 7 to 12 (mean 9.1 ± 1.5) mm long, 2.5 to 4.0 (mean 3.2) mm wide; length/width ratio 6.1:1. Staminate flowers approximately 2.5 mm across; inner surface reddish, lower surface the same color as the shoots; perianth usually three-merous (sometimes two- or four-merous), segments approximately 1.2 mm long, 0.8 mm wide; nectary with two large and one small lobe. Pistillate flowers with stigmas exserted approximately 0.5 mm, with copious stigmatic exudate at anthesis. Mature fruit 5.5 by 3.0 mm, greenish glaucous; proximal portion approximately 4.0 mm long. Seeds approximately 3.1 by 1.5 mm. n = 14.

Phenology. Meiosis in August or early September. Anthesis and fruit maturity in September; maturation period averages ca. 12 months.

Hosts. The only known hosts are *Pinus oocarpa* var. *oocarpa*, var. *ochoterenia*, and *P. tecunumanii* (Mathiasen and others 1998, 2000a).

Distribution. Honduras, Mexico (Chiapas, Oaxaca), and possibly El Salvador. The distribution of this species is poorly known; only four collections are known from Honduras and three from Mexico (Mathiasen and others 2001, 2002b). Elevational range is poorly known, probably between 1,200 and 1,650 m.

Discussion. Collections from Mexico had been previously confused with *Arceuthobium nigrum* (Mathiasen and others 2001, 2002b). *Arceuthobium hondurense* and *A. bicarinatum*, a species endemic to Hispaniola, are both rare species threatened by deforestation and are distributed at the southern limits of dwarf mistletoes and pines in the New World.

17. *Arceuthobium laricis*
Larch Dwarf Mistletoe

Arceuthobium laricis (Piper) St. John, Flora of Southeast Washington and Adjacent Idaho: 115, 1937.
=*A. campylopodum* f. *laricis*.

Description. Mean shoot height 4 (maximum 6) cm, mostly dark purple, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.0 (mean 2) mm. Third internode 5 to 14 (mean 8.0 to 2.0) mm long, 1.0 to 2.5 (mean 1.3) mm wide, length/width ratio 6.1:1.

Staminate flowers 2.7 mm across; perianth mostly three-merous (sometimes four-merous); segments 1.4 mm long, 1.1 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 4.5 by 2.5 mm; proximal portion 2.5 mm long.

Phenology. Meiosis in June. Peak anthesis from mid-July to late August, with extremes from early July to early September. Fruits usually mature in September, with extremes from early August to early October; maturation period averages 13 to 14 months.

Hosts. Mathiasen (1998a) revises the host relations of *Arceuthobium laricis* based on field studies and previous reports (Mathiasen and others 1995a). The principal and commonly infected host is *Larix occidentalis. Tsuga mertensiana* and *Pinus contorta* var. *latifolia* are secondary hosts. Occasional hosts are *Abies lasiocarpa* and *P. ponderosa* var. *ponderosa*; but *Abies amabilis* and *Pinus albicaulis* are tentatively classified occasional as well. *Abies grandis, Picea engelmannii, Pinus monticola,* and *Tsuga heterophylla* are rare hosts. Extra-limital hosts and artificially inoculated hosts include *Larix decidua, L. leptolepis, Picea abies, P. glauca, Pinus banksiana, P. resinosa,* and *P. sylvestris.* (Hawksworth and Wiens 1996). Although natural population of the high-elevation *Larix lyallii* appear not to be infested, this species may become infected if planted in a suitable environment (Mathiasen and others 1995b).

Distribution. Canada (British Columbia) and the United States (Washington, Oregon, Idaho, and Montana). *Arceuthobium laricis* occurs generally throughout the range of its principal host, *Larix occidentalis,* in southern British Columbia, east of the Cascade Mountains in Washington and northern Oregon, northern and central Idaho, and western Montana. Distribution maps of *Arceuthobium laricis* are published for British Columbia and Montana (see Hawksworth and Wiens 1996). Elevational range is 650 to 2,250 m.

Discussion. *Arceuthobium laricis* has long been recognized as a serious pathogen of *Larix occidentalis* (Weir 1916a). Infection usually results in the formation of heavy but compact brooms. Because larch branches are brittle, larger brooms are readily broken off. Surveys in the Inland Empire (eastern Washington, northern Idaho, and western Montana) show that most larch stands are infested and infection rates are commonly high (Hawksworth and Wiens 1996). Mathiasen (1998b) reports that initial infection of *Larix occidentalis* can be when the plants are quite young; Mathiasen recommends that, to avoid spread, removal of the infected overstory should be done before regeneration is 7 years old or 1 m tall. Other publications of interest to managers include those by Beatty and others (1997), Taylor (1995), Wicker and Hawksworth (1991), and Weir (1961a).

18. *Arceuthobium littorum*
Coastal Dwarf Mistletoe

Arceuthobium littorum Hawksw., Wiens & Nickrent, Novon 2:206, 1992.
=*A. campylopodum* f. *typicum*
=*A. occidentale*

Description. Shoots 8 to 20 (mean 12) cm, brown to yellow-brown, branches flabellate. Basal diameter of dominant shoots 2 to 5 (mean 3.5) mm. Third internode 10 to 20 (mean 15) mm long, 2 to 2.5 (mean 2.2) mm wide, mature fruits 4 to 5 mm long; staminate flowers mostly four-merous.

Phenology. Meiosis occurs in July, flowering begins in August, with peak anthesis probably occurring in September. Seed dispersal probably peaks in September or October.

Hosts. *Pinus radiata* and *P. muricata* are the primary hosts. It occasionally infects Bolander pine (*Pinus contorta*) where this tree is associated with infected *P. muricata.*

Distribution. United States (California: Mendocino, Sonoma, Marin, Monterey, and San Luis Obispo). *Arceuthobium littorum* is restricted to a region within 10 km of the Pacific Ocean from Fort Bragg south to Point Reyes on *Pinus muricata* and along the central coast at Monterey and Cambria on *P. radiata*. It also parasitizes the small population of *P. muricata* associated with infected *P. radiata* at Huckleberry Hill, Monterey, and is established at three locations by transplanting infected *Pinus radiata*—Stanford Arboretum, North Berkeley, and Hillsborough. Elevational range is from sea level to 250 m.

Discussion. Previously, Hawksworth and Wiens (1972) include *Arceuthobium littorum* in *A. occidentale.* A primary feature for distinguishing *A. littorum* from *A. occidentale* is the production of large, nonsystemic witches' brooms.

19. *Arceuthobium microcarpum*
Western Spruce Dwarf Mistletoe

Arceuthobium microcarpum (Engelm.) Hawksw. & Wiens, Brittonia 22:268, 1970.
=*A. campylopodum* f. *microcarpum*.

Description. Mean shoot height 5 (maximum 11) cm, green to purple, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.0 (mean 2) mm. Third internode 5 to 16 (mean 9.3 ±2.2) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 6.2:1. Staminate flowers 2.3 mm across; perianth mostly three-merous (rarely four-merous); segments 1.2 mm long, 1.0 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 3.5 by 2.0 mm; proximal portion 2.5 mm long. Seeds 2.4 by 1.0 mm.

Phenology. Meiosis in July. Anthesis in mid-August to early September, with extremes from late July to late September. Fruits mature in September, with extremes from late August to early October; maturation period averages 12 to 13 months.

Hosts. This dwarf mistletoe is a common and serious pathogen only on *Picea engelmannii* and *P. pungens*. On the San Francisco Peaks of northern Arizona, however, it also parasitizes *Pinus aristata*. *Pinus strobiformis* and *Abies lasiocarpa* var. *arizonica* are rarely infected even where they are associated with infected principal hosts. If populations of a spruce in southern Arizona were determined to be *Picea mexicana* rather than *P. engelmannii* (Taylor and others 1994), this species would be an additional host.

Distribution. United States (Arizona and New Mexico). *Arceuthobium microcarpum* has one of the more restricted distributions in the genus. In Arizona, the parasite occurs on the North Rim of the Grand Canyon, the San Francisco Peaks and nearby Kendrick Peak, White Mountains, and Pinaleno Mountains. In New Mexico, this dwarf mistletoe is present at several locations in the Mogollon Mountains and in the Sacramento Mountains. Elevational range is 2,400 to 3,150 m.

Discussion. This localized species in Arizona and New Mexico is characterized by its near exclusive occurrence on spruce (Hawksworth and Graham 1963a). This species induces small, dense witches' brooms. Heavily infected trees bear hundreds of such witches' brooms. This dwarf mistletoe causes heavy mortality in stands of *Picea pungens* and, to a lesser extent, of *P. engelmannii*.

20. *Arceuthobium monticola*
Western White Pine Dwarf Mistletoe

Arceuthobium monticola Hawksw., Wiens & Nickrent, Novon 2:205, 1992.
=*A. campylopodum* f. *blumeri*
=*A. californicum*

Description. Shoots 5 to 10 (mean 7) cm tall, dark brown, branches flabellate. Basal diameter of dominant shoots 2 to 4 (mean 3) mm; third internode 8 to 15 (mean 12) mm long, 1.5 to 2.0 mm wide. Staminate flowers mostly three-merous. Mature fruits 4.0 to 4.5 mm long, 2.0 to 2.5 mm wide.

Phenology. The period of anthesis is poorly known but apparently occurs late July through August. Fruits mature October and November; maturation period averages 15 months.

Hosts. The principal and only commonly infected host is *Pinus monticola*. *Pinus lambertiana* is a secondary host; *Picea breweriana* an occasional host; and *Pinus jeffreyi* a rare host.

Distribution. United States (Oregon, California). *Arceuthobium monticola* is a local endemic in the Klamath Mountains of southwestern Oregon (Coos, Curry, and Josephine) and the Siskiyou Mountains of adjacent northwestern California (Del Norte and possibly Siskiyou). Elevational range is 700 to 1,900 m.

Discussion. Hawksworth and Wiens (1972) include this taxon under *Arceuthobium californicum*; but subsequent field and laboratory studies demonstrate that it is a distinct species and not apparently sympatric with *A. californicum*. *Arceuthobium monticola* differs from *A. californicum* in its much darker shoot color, later flowering and seed dispersal periods, and host preference for *Pinus monticola* rather than *P. lambertiana*.

21. *Arceuthobium nigrum*
Black Dwarf Mistletoe

Arceuthobium nigrum (Hawksw & Wiens) Hawksw. & Wiens, Phytologia 66:9, 1989.
=*A. gillii* subsp. *nigrum*.

Description. Mean shoot height 15 to 35 (45) cm, dark brown to black. Basal diameter of dominant shoots 3 to 8 (mean 5) mm. Third internode 5 to 19 (mean 10.8 ±3.8) mm long, 2.5 to 6.0 (mean 3.7) mm wide (six collections), length/width ratio 2.9:1. Staminate flowers 3 mm long, 3.5 mm across. Mature fruit 6 to 9 (mean 7) mm long, 3.5 mm wide, proximal portion 2 to 3 mm. Seeds 3.5 by 1.3 mm.

Phenology. This dwarf mistletoe is unusual in *Arceuthobium* by having flowering periods in March and April and September and October. Seed dispersal occurs in September, presumably from flowers pollinated the previous year; when the seeds from the March through April pollinations mature is unknown.

Hosts. This dwarf mistletoe is most common on the principal hosts *Pinus leiophylla* vars. *leiophylla*, var. *chihuahuana*, and *P. lumholtzii*. *Pinus lawsonii*, *P. oaxacana*, *P. patula*, *P. teocote* are also highly susceptible and rated as principal hosts. *Pinus montezumae* and *P. pseudostrobus* are occasional hosts. *Pinus arizonica* var. *arizonica* and *P. cooperi* are rare hosts.

Distribution. Mexico (Durango, Zacatecas, Guanajuato, Querétaro, Hidalgo, Michoacán, Mexico, Tlaxcala, Puebla, Veracruz, Oaxaca, Chiapas) and possibly Western Guatemala. This mistletoe is reported from the northeastern slope of Volcán la Malintzi (Malinche), Tlaxcala (Hernandez and others 1992), and is common on pines in Central and Eastern Mexico. Elevational range is 1,800 to 2,800 m.

Discussion. *Arceuthobium nigrum* resembles *A. gillii*. Both species possess markedly glaucous fruits, strong sexual dimorphism (open, divaricate branching in staminate plants versus densely branched in pistillate plants), and parasitize similar hosts. Although *A. nigrum* was previously classed as a subspecies of *A. gillii*, specific status is warranted (Hawksworth and Wiens 1989). *Arceuthobium nigrum* is a larger plant than *A. gillii* and has dark green to black shoots 15 to 35 (maximum 45) cm high, whereas those of *A. gillii* are only 8 to 15 (maximum 25) cm tall, and colored greenish brown. *Arceuthobium nigrum* also has the two flowering periods (March and April, and September and October) compared to only one for

A. gillii (March and April). To our knowledge, these species are not sympatric.

22. *Arceuthobium oaxacanum*
Oaxacan Dwarf Mistletoe

Arceuthobium oaxacanum Hawksw. & Wiens, Phytologia 66:7, 1989.
=*A. rubrum*

Description. Shoots 8 to 20 (mean 12) cm tall, pale brown to reddish, branches flabellate. Basal diameter of dominant shoots 2 to 4 (mean 3) mm. Third internode 10 to 17 (mean 12) mm long and 2 to 3 mm wide.

Phenology. Anthesis in July. Fruits mature in August of the following year; maturation period averages 13 months.

Hosts. *Pinus lawsonii*, *P. michoacana*, and *P. pseudostrobus* are principal hosts; all are about equally susceptible. *Pinus oaxacana* is an occasional host.

Distribution. Mexico (Oaxaca). This species is known from only three localities (two south of Miahuatlán and one near Ixtlán). Elevational range is 2,000 to 2,200 m.

Discussion. Hawksworth and Wiens (1989) recognize *Arceuthobium oaxacanum* as a distinct species previously considered an extreme disjunct (about 1,200 km) of *A. rubrum*. In general, *A. oaxacanum* is a larger, lighter colored, more openly branched plant and causes larger witches' brooms than *A. rubrum*. Furthermore, *Arceuthobium oaxacanum* principally parasitizes *Pinus lawsonii*, *P. michoacana*, *P. pseudostrobus*, and occasionally *P. oaxacana*; none of these pines occurs within the range of *A. rubrum*.

23. *Arceuthobium occidentale*
Digger Pine Dwarf Mistletoe

Arceuthobium occidentale Engelm., U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:375, 1878.
=*A. campylopodum* f. *typicum*.

Description. Mean shoot height 8 (maximum 17) cm, yellowish, glaucous, branches flabellate. Basal diameter of dominant shoots 1.5 to 5.0 (mean 2) mm. Third internode 7 to 18 (mean 12.7 ±2.0) mm long, 1.5 to 3.5 (mean 1.8) mm wide, length/width ratio 7.1:1. Staminate flowers 3.0 mm across; perianth three- or four-merous; segments 1.5 mm long, 1.0 mm wide. Mature fruit 4.5 by 3.0 mm; proximal portion 3.0 mm long. Seeds 2.6 by 1.0 mm.

Phenology. Meiosis in August. Peak anthesis from late September to late November, extremes from early September to early December. Most fruits mature from mid-October to mid-January, with extremes from late September to early February; maturation period averages 13 months.

Hosts. *Pinus sabiniana* is the most common and only principal host. *Pinus coulteri* and *P. attenuata* are secondary hosts where they occur with infected *P. sabiniana*. Whether the occasional hosts *Pinus ponderosa* and *P. jeffreyi* are infected, however, varies by location and association with their principal dwarf mistletoe, *A. campylopodum*. In the California Coast Range (outside the distribution of *Arceuthobium campylopodum*), these pines are commonly infected where they are occur with infected *P. sabiniana*. In the Sierra Nevada (where *A. campylopodum* occurs), they are seldom infected even under infected *P. sabiniana*. Extralimital and hosts by artificial inoculation are *Pinus banksiana*, *P. bungeana*, *P. caribaea*, *P. halepensis*, *P. palustris*, *P. pinea*, *P. radiata*, *P. sylvestris*, *P. thunbergii*, *P. torreyana*, and *P. virginiana*.

Distribution. United States (California). This dwarf mistletoe is a California endemic and commonly occurs on *Pinus sabiniana* throughout the foothills and low mountains surrounding the Central Valley of California and along the Coast Ranges from Mount Pinos (Ventura) north to Mendocino. Elevational range is about 30 to 1,200 m in the southern Sierra Nevada.

Discussion. Even though *Pinus sabiniana* typically occurs in open, savanna-like forests, *Arceuthobium occidentale* is widely distributed in these stands. Isolated, infected trees more than 100 m away from the closest infected trees are sometimes found, which suggests that bird vectors (possibly phainopepla) are involved in long-distance seed transport of this dwarf mistletoe.

24. *Arceuthobium pendens*
Pendent Dwarf Mistletoe

Arceuthobium pendens Hawksw. & Wiens, Brittonia 32:348, 1980.

Description. Mean shoot height 15 (maximum 22) cm, light green, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.5 (mean 2) mm. Third internode 12 to 20 (mean 16) mm long, 1 to 2 (mean 1.5) mm wide. Staminate flowers 2.5 mm across, three-merous.

Phenology. Peak anthesis possibly in September. Fruit maturity from June to September (Cházaro and Oliva 1987a).

Hosts. Known only on *Pinus discolor* (San Luis Potosí) and *P. cembroides* subsp. *orizabensis* (Veracruz and Puebla).

Distribution. Mexico (San Luis Potosí, Veracruz, and Puebla). The distribution of this dwarf mistletoe is poorly known (Cházaro and Oliva 1987a) from only Sierra San Miguelito (San Luis Potosí) and Frijol Colorado (Veracruz), and on the nearby Cerro Pizzaro (Puebla). Elevational range is 2,250 to 2,700 m.

Discussion. The species exhibits striking sexual dimorphism—pistillate plants are densely branched and typically less than 8 cm tall, and mature staminate plants are openly branched and pendant, 15 to 20 cm long. A unique feature of this species, at least in one population, is that only the staminate plants appear to induce systemic witches' brooms. This dwarf mistletoe likely occurs in other areas and on other pinyons.

25. *Arceuthobium pusillum*

Eastern Dwarf Mistletoe

Arceuthobium pusillum Peck, Transactions Albany Institute 7:191, 1872.

=*A. minutum*

=*A. abigenium*.

Description. Mean shoot height 1 (maximum 3) cm, green to brown, usually without secondary branching, but flabellate when occurs. Basal diameter of dominant shoots 1.0 mm. Third internode 1 to 4 (mean 1.9 ±0.8) mm long, 0.5 to 1.5 (mean 1.0) mm wide, length/width ratio 1.9:1, often markedly wider at top than at base. Pistillate shoots often longer than the staminate. Staminate flowers 1.7 to 2.2 (mean 1.8 mm) across; perianth mostly three-merous (sometimes two- or four-merous); segments 0.8 mm long, 0.7 mm wide. Mature fruit 3.0 mm long, 1.25 to 1.75 mm wide (mean 1.5 mm); proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Staminate meiosis in September, pistillate meiosis in May. Anthesis usually in April or May, with extremes from late March to June. Fruits mature in September or early October of the same year as pollination; maturation period averages 5 months, perhaps the shortest in the genus. Seed germination mostly in May and June.

Hosts. *Arceuthobium pusillum* is most common and widely distributed on *Picea mariana*. *Picea glauca* and *P. rubens* appear to be about as susceptible as *P. mariana*, so are also principal hosts, although the dwarf mistletoe is not as common (except in some old-growth stands). *Larix laricina* is an occasional host. *Abies balsamea*, *Pinus banksiana*, *P resinosa*, and *P. strobus* are rare hosts. *Picea pungens* is an extralimital host.

Distribution. Canada (Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland) and the United States (Minnesota, Wisconsin, Michigan, New York, Pennsylvania, New Jersey, Connecticut, Massachusetts, Vermont, New Hampshire, Rhode Island, and Maine). *Arceuthobium pusillum* occurs in Canada from Hudson Bay, the Cumberland areas in eastern Saskatchewan to southern Manitoba, southern Ontario, Québec, and the Maritime Provinces including Newfoundland. Its northern limits in Ontario and Québec are poorly known. In the United States, it occurs in the northern parts of Minnesota, Wisconsin, and Michigan, northeastern Pennsylvania, extreme northwestern New Jersey, and all of New England. It is rare near the limits of its southern distribution. *Arceuthobium pusillum* occurs on several islands isolated 30 km or more from the nearest known populations of the dwarf mistletoe—Mantinicus and Monhegan Islands off the Maine Coast and Beaver Island in Lake Michigan. The numerous distribution maps published for *Arceuthobium pusillum* are identified by Hawksworth and Wiens (1996). Elevational ranges from sea level in Maine and the Maritime Provinces to 800 m on Mount Katahdin, Maine.

Discussion. In spite of having the smallest shoots of any North American mistletoe, *Arceuthobium pusillum* is a damaging pathogen of spruce in many parts of its distribution (Singh and Carew 1989). Mortality is severe in *Picea glauca* along the Maine Coast, and the parasite is considered the most serious disease agent of *P. mariana* in the Great Lakes region. Its biology and management are discussed by Ostry and Nicholls (1979). Witches' brooms appear to be mostly of the systemic type. Shoots usually first appear in late summer or autumn as small eruptions in the bark of host branches 2 years old and mature during the third season. They flower the following spring; fruits mature by autumn. Shoots usually fall after flowering (staminate) or fruiting (pistillate), and only rarely do shoots produce a second crop of flowers. This pattern of reproduction is unique among northern temperate species of the genus. Large swellings on the main trunk are commonly induced by *Arceuthobium pusillum* in old-growth *P. rubens* in New England and New York, but such swellings have not been reported on other spruces. *Arceuthobium pusillum* has an interesting literary and historic past in Thoreau's (1858) description of the witches' broom in spruce at Walden Pond and Lucy Millington's later discovery of the mistletoe itself (Smith 1992). *Arceuthobium pusillum* is common in spruce bogs and generally absent from drier upland sites. In Québec, *A. pusillum* is apparently restricted to within 2 km of lakes or rivers. In Maine, it occurs on *P. glauca* only within 300 to 400 m of the coast. *A. pusillum* may require an uninterrupted period of high atmospheric humidity in the spring for normal growth.

26. *Arceuthobium rubrum*

Ruby Dwarf Mistletoe

Arceuthobium rubrum Hawksw. & Wiens, Brittonia 17:233, 1965.

Description. Mean shoot height 10 (maximum 18) cm, dark red, brown to blackish, branches flabellate. Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2 to 3 (mean 2.4) mm. Third internode 4 to 12 (mean 6.9 ±2.7) mm long, 2 to 3 (mean 2.3) mm wide, length/width ratio 3.4:1. Staminate flowers 1.0 to 1.5 mm across; mostly three-merous; segments 0.6 mm long, 0.6 mm wide. Mature fruit 3.5 by 2.0 mm. Seeds 2.0 by 1.0 mm.

Phenology. Meiosis probably in June. Anthesis usually in July. Fruits mature from mid-July to August of the year following pollination; maturation period averages 12 to 13 months.

Hosts. Principal hosts are *P. cooperi*, *P. durangensis*, *P. engelmannii*, *P. herrerai*, and *Pinus teocote*, all of which appear to be highly susceptible.

Distribution. Mexico (Durango and Sinaloa). This species has a localized distribution in the Sierra Madre Occidental of Western Mexico. Elevational range is 2,250 to 2,900 m.

Discussion. This distinctive, slender, reddish dwarf mistletoe is apparently widespread in the mountains of Durango. As the plants dry, the red color turns to dull brown, and the apical portion of each segment becomes golden yellow. This gives dried specimens a characteristic banded appearance. The shiny fruits, a character shared only with *Arceuthobium oaxacanum*, readily distinguish this species. Another distinctive characteristic of *A. rubrum* is the exceptionally small, scarcely opened staminate flowers. The populations in the Pueblo Altares area in northern Durango, about 150 km north of the populations around El Salto, have taller, darker, and stouter shoots that superficially resemble *Arceuthobium vaginatum* subsp. *vaginatum*.

27. *Arceuthobium siskiyouense*
Knobcone Pine Dwarf Mistletoe

Arceuthobium siskiyouense Hawksw., Wiens & Nickrent, Novon 2:204, 1992.
=*A. campylopodum*

Description. Mean shoot height 8 (maximum 10) cm, dark brown, branches flabellate. Basal diameter of dominant shoots 2.0 to 2.5 mm across. Third internode 8 to 15 (mean 9) mm long, 2 mm wide. Mature fruits 3.6 by 2.1 mm.

Phenology. Peak anthesis in August. Fruits at maturation not observed.

Hosts. *Pinus attenuata* is the principal and only common host of *Arceuthobium siskiyouense*. This dwarf mistletoe rarely parasitizes *P. contorta*, *P. jeffreyi*, and *P. ponderosa* where these trees grow in association with infected *P. attenuata*.

Distribution. United States (California and Oregon). The distribution of *Arceuthobium siskiyouense* is restricted to the Klamath Mountains of southwestern Oregon (Curry and Josephine) and the Siskiyou Mountains in adjacent northwestern California (Del Norte and Siskiyou). Elevational range is 400 to 1,200 m.

Discussion. Hawksworth and Wiens (1972) include this taxon in *Arceuthobium campylopodum*, but subsequent studies demonstrate it a distinct species related to *A. campylopodum*. The two species are sympatric in several areas, and their flowering periods partially overlap; but each maintains its own host preferences and distinctive morphologies (for example, *A. siskiyouense* does not induce witches' brooms).

28. *Arceuthobium strictum*
Unbranched Dwarf Mistletoe

Arceuthobium strictum Hawksw. & Wiens, Brittonia 17:234, 1965.

Description. Mean shoot height 7 (maximum 13) cm, pistillate shoots generally greenish yellow brown, branches flabellate. Staminate plants brownish, rarely branching. Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2.5 to 4.0 (mean 3.1) mm. Third internode 1 to 8 (mean 3.6 ±2.0) mm long, 1.5 to 3.5 (mean 2.3) mm wide; length/width ratio 1.6:1. Staminate flowers 3 mm across, perianth three-, four-, or five-merous (rarely six or seven-merous), segments 1.5 mm long, 1 mm wide. Mature fruit 4 by 2.5 mm. Seeds 2.5 by 1.0 mm.

Phenology. Meiosis in July. Anthesis late July through October, with peak in September. Fruits mature from mid-September to October of the year following pollination; maturation period averages 13 months.

Hosts. *Pinus leiophylla* var. *chihuahuana* is the principal host. *Pinus teocote* is an occasional host, and *P. engelmannii* is a rare host.

Distribution. Mexico (Durango). This species is known only in the Sierra Madre Occidental south and west of the city of Durango. Elevational range is 2,200 to 2,500 m.

Discussion. The most distinctive feature of this dwarf mistletoe is the lack of branching by staminate plants. The staminate shoots at anthesis become single spikes 6 to 13 cm long with numerous perianth segments (up to seven, more than any other dwarf mistletoe). The pistillate plants, in contrast, exhibit abundant secondary branching. This dwarf mistletoe causes heavy mortality in its principal host, *Pinus leiophylla* var. *chihuahuana*.

29. *Arceuthobium tsugense*
Hemlock Dwarf Mistletoe

Arceuthobium tsugense (Rosendahl) G.N. Jones, University of Washington Publications in Biology 5:139, 1936 (as *A. tsugensis*).
=*A. campylopodum* f. *tsugensis*.

Description. Mean shoot height 5 to 7 (13) (cm), greenish to reddish, darker in winter, branches

Key to the Subspecies

1. Parasitic primarily on *Tsuga heterophylla* or *Pinus contorta* var. *contorta*; shoots 3–13 (mean 7) cm high .... 29a. *A. tsugense* subsp. *tsugense*

1. Parasitic primarily on *Tsuga mertensiana*; shoots 3–9 (mean 5) cm high .... 29b. *A. tsugense* subsp. *mertensianae*

flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2.0) mm. Third internode 4 to 16 (mean 9.2 ±2.5) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 6.1:1. Staminate flowers 2.8 mm across; perianth three- or four-merous, segments 1.2 mm long, 1.0 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 3 by 2 mm; proximal portion 2.0 mm long.

Hosts. Mathiasen (1994) reviews the host range of the several taxa included here under *Arceuthobium tsugense* based on natural infection and artificial inoculation. His report provides the basis for hosts and susceptibility used here.

Discussion. Hawksworth and Wiens (1972) comment on the unusually broad host range of *Arceuthobium tsugense,* which encompasses not only both western species of hemlock but also several species of fir, spruce, and pine. *Arceuthobium tsugense* is segregated into subspecies *tsugense* and *mertensianae* and subspecies *tsugense* into two physiologically differentiated host races as western hemlock and shore pine (Hawksworth and others 1992b). Additional field studies on distribution, host preference, and phenology are being conducted to resolve continuing taxonomic uncertainty (see Mathiasen 1994). At this time, however, we retain the taxonomy and host relations presented by Hawksworth and Wiens (1996). Hennon and others (2001) provide a general review and management guide for hemlock dwarf mistletoe. The subspecies are similar morphologically, but the shoots are about 30 percent taller in subsp. *tsugense* than in subsp. *mertensianae* (differences statistically significant at *P*<0.01).

Phenology. Meiosis in July for both subspecies, but the subsequent phenologies of flowering for the subspecies differ. Flowering averages about 1 to 2 weeks earlier in subsp. *tsugense* (peak anthesis in August, extremes from late July to late September) than for subsp. *mertensianae* (peak anthesis from mid-August to mid-September). In contrast to flowering, the seed dispersal for subsp. *tsugense* averages about 2 to 4 weeks later (late September to early November) than for subsp. *mertensianae* (mid-August, rarely to late October).

29a. *Arceuthobium tsugense* subsp. *tsugense* Western Hemlock Dwarf Mistletoe

Description. As the species, but shoots vary from 3 to 13 cm high, mean 7 cm.

Hosts. *Tsuga heterophylla* is the principal and common host; but *A. lasiocarpa* var. *lasiocarpa* is also considered a principal host, as are (tentatively) *Abies amabilis* and *A. procera*. *Abies grandis* and *Pinus contorta* var. *latifolia* are occasional hosts. Rare hosts are *Picea engelmannii*, *P. sitchensis, Pinus monticola, Pseudotsuga menziesii*, and *Tsuga mertensiana*. The status of *Pinus contorta* var. *contorta* (shore pine) as a host is discussed below. Extra-limital and hosts by inoculation (for the western hemlock race) are *Larix decidua* (incompatible), *L. occidentalis* (incompatible), *Picea abies, P. glauca, Pinus contorta* var. *latifolia, Pinus ponderosa, P. radiata, P. sylvestris, Pseudotsuga menziesii*, and *Tsuga canadensis*.

Distribution. Canada (British Columbia) and the United States (Alaska, Washington, Oregon, and California). *Arceuthobium tsugense* subsp. *tsugense* is distributed from Haines, Alaska, to Mendocino, California. *Arceuthobium tsugense* subsp. *tsugense* is common in the *Tsuga heterophylla* forests of coastal Alaska, British Columbia, Washington, and Oregon; but rare in northwestern California; and unlikely in northern Idaho. Elevational range is from sea level in Alaska, British Columbia, and Washington to about 1,250 m in Oregon.

Discussion. Many of the lower infections in *Tsuga heterophylla* produce few shoots of the dwarf mistletoe (Shaw and Weiss 2000). Because dwarf mistletoes are sensitive to light, the absence of dwarf mistletoe shoots from the lower infections may be explained by the dense shade in the lower portions of coastal hemlock forests (Smith 1969). In such situations, vigorous shoots are often found only along margins of stands, on young trees in openings, or in higher branches of older trees. Information on the epidemiology of this mistletoe and management of hemlock is available for Alaska (Shaw and Hennon 1991, Trummer and others 1998, and Wittwer 2002) and Canada (Bloomberg and Smith 1982, Edwards 2001, Muir 1993, Smith 1977).

Discussion on Western Hemlock Compared to Shore Pine. The taxonomic status of the dwarf mistletoe populations on *Pinus contorta* var. *contorta* is the subject of continued debate (Hawksworth and Wiens 1972, 1996, Hunt and Smith 1978, Smith and Wass 1976, 1979). Dwarf mistletoe population on western hemlock (*Tsuga heterophylla*) and shore pine (*P. contorta* var. *contorta*) are similar morphologically, phenologically, and chemically but appear to have consistent differences in host compatibility. Comparing dwarf mistletoe populations on western hemlock to those on shore pine, respectively, maximum shoot height is about 30 percent greater; fruits are slightly but statistically smaller; anthesis and peak dispersal are later. Flavonoid composition and isozyme patterns are similar. Inoculation of shore pine with dwarf mistletoe seeds from western hemlock produce few infections, but those infections that are successful produce abundant aerial shoots. In contrast, inoculations of western hemlock with dwarf mistletoe seeds from shore pine result in more infections but few produce any shoots. *Tsuga heterophylla* and *Pinus monticola* are considered rare hosts. Other species infected by the shore pine race by artificial inoculation include *Abies amabilis, A. grandis*, *Larix occidentalis*, *Picea glauca*, *P. engelmannii*, *Pinus contorta* var. *latifolia*, *P. ponderosa*, and *Pseudotsuga menziesii*.

Arceuthobium tsugense subsp. *tsugense* parasitizes *Pinus contorta* var. *contorta* in southwestern British Columbia and the San Juan Islands, Washington. Populations of this dwarf mistletoe are distributed on isolated rocky outcrops along the east coast of Vancouver Island, on the Channel Islands, and the mainland of British Columbia north of Vancouver. Two outlying populations occur 250 km north at Port Clements (Queen Charlotte Islands) and at Terrace (British Columbia mainland). In the United States, populations are known from Orcas and San Juan Islands (Washington). The elevational range is from sea level to 800 m.

29b. *Arceuthobium tsugense* subsp. *mertensianae*
Mountain Hemlock Dwarf Mistletoe

Arceuthobium tsugense (Rosendahl) G.N. Jones subsp. *mertensianae* Hawksw & Nickrent, Novon 2:209, 1992.

Description. Shoots are typically shorter (5 cm) than in subsp. *tsugense* (7 cm).

Hosts. The common principal host of *Arceuthobium tsugense* subsp. *mertensianae* is *Tsuga mertensiana*; *T. heterophylla* is only rarely infected, even where this species is closely associated with infected *T. mertensiana*. Other principal hosts are *A. amabilis and Abies lasiocarpa*. *Pinus albicaulis* is a secondary host, and *Pinus monticola* is an occasional host. *Picea breweriana* and *Pinus contorta* var. *latifolia,* are rarely infected.

Distribution. Western Canada (southern British Columbia) and Western United States (Washington, Oregon, and California). The distribution of *Arceuthobium tsugense* subsp. *mertensianae* is still poorly known, but it extends from near Vancouver (British Columbia), in the Olympic Mountains, through the Cascade Mountains (Washington and Oregon), and to the central Sierra Nevada (Alpine, California). Hildebrand and others (1997) report on a distribution survey in Washington. Elevational range is 1,200 to 2,500 m.

Discussion. Some populations of *Tsuga mertensiana* such as on Mount Baker and in the Olympic Mountains are exceptionally heavily infected by this dwarf mistletoe.

30. *Arceuthobium vaginatum*

Arceuthobium vaginatum (Willd.) Presl in Berchtold, O PUirozenosti Rostlin aneb Rostinár 2:28, 1825.

Description. Mean shoot height from 20 to 30 (maximum 55 or greater) cm, orange to dark brown, reddish, or black, usually densely branched and erect, but large older plants sometimes become pendulous; branches flabellate; basal diameter of dominant shoots 1 to 3 cm long, 0.2 to 0.4 cm wide. Staminate flower up to 3.5 mm long and up to 3.5 mm across, mostly thremerous (sometimes four-merous), segments up to 2.0 mm long and up to 1.5 mm wide, apex acute to obtuse. Pistillate flower up to 2.5 mm long, up to 1.5 mm across. Fruit 4 to 6 mm long, 2 to 3 mm wide, elliptical to obovate.

Phenology. Anthesis from approximately late March through May.

Hosts. Parasitic on yellow pine.

Discussion. The distributions of the two subspecies overlap in the mountains of central Chihuahua (between latitudes 28° 00' and 28° 30' N) where intermediate characteristics are shown in some populations. Even here, however, there is a tendency to segregate by elevation with subsp. *vaginatum* at lower elevations and subsp. *cryptopodum* at higher elevations. Although the characteristics distinguishing subspecies are greater than those in other species (such as *Arceuthobium tsugense*), this is the only case where we find intermediate populations, therefore we use subspecific rank rather than species rank for this taxon.

30a. *A. vaginatum* subsp. *vaginatum*
Mexican Dwarf Mistletoe

Description. Mean shoot height 20 (maximum 55) cm, dark brown to black, rarely reddish. Basal diameter of dominant shoots 4 to 20 (mean 7) mm. Third internode 5 to 30 (mean 17.4 ±6.0) mm long, 2.5 to 8.5 (mean 5.0) mm wide, length/width ratio 2.9: 1. Staminate flower segments 1.6 mm long, 1.1 mm wide. Mature fruit 5.5 by 3.5 mm.

Phenology. Meiosis in February. Anthesis usually March and April. Fruits mature in August of the year following pollination; maturation period averages 16 to 17 months.

Key to the Subspecies

1. Plants dark brown to black, usually over 20 cm tall; staminate flowers usually greater than 3 mm long and wide; anthesis March–April; Sierra Madre Occidental from central Chihuahua southward to the Central Cordillera, and in the Sierra Madre Oriental .... 30a. *A. vaginatum* subsp. *vaginatum*

1. Plants orange, usually less than 20 cm tall; staminate flowers usually less than 3 mm long and wide; anthesis May–June; Sierra Madre Occidental of central Chihuahua and Sonora and mountains of central Coahuila northward to central Utah and northern Colorado .... 30b. *A. vaginatum* subsp. *cryptopodum*

Hosts. *Arceuthobium vaginatum* subsp. *vaginatum* has the broadest known host range of any species in the genus. It is collected on 13 species of Mexican pines and undoubtedly occurs on others. It is common on the principal hosts *Pinus arizonica* vars. *arizonica*, var. *stormiae, P. cooperi*, *P. durangensis*, *P. engelmannii*, *P. hartwegii*, *P. herrerai*, *P. lawsonii*, *P. montezumae*, *P. patula*, and *P. rudis*. *Pinus teocote* is a secondary host because it was parasitized only when it was associated with an infected principal hosts. It rarely infects *Pinus culminicola* under infested *P. rudis* on Cerro Potosí (Nuevo León).

Distribution. Mexico (Chihuahua, Coahuila, Distrito Federal, Durango, Hidalgo, Jalisco, Mexico, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Sinaloa, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas). This is the most widely distributed dwarf mistletoe in Mexico, extending from the Sierra Madre Occidental in western Chihuahua south through Durango, Jalisco; into the Central Cordillera of Mexico and Puebla; and occurring in the Sierra Madre Oriental from Coahuila and Nuevo León to Oaxaca. Elevational range is from 2,100 m in Nuevo León to 3,900 m on Nevado de Toluca near Mexico City.

Discussion. The shoots of *Arceuthobium vaginatum* subsp. *vaginatum* exceed 55 cm in height in Central Mexico. The plants exhibit considerable sexual dimorphism and variation. The staminate plants tend to be taller than the pistillate plants, but Vázquez (1991) reports on a population near Texcoco, Mexico, where the pistillate plants were short, erect, and dark, and staminate plants were long, pendulous, and reddish. Plants in some areas of the northern Sierra Madre Oriental are often reddish, but plants just 40 km to the south are again typically black (Hawksworth and Cibrián 1985). The hosts and ecological requirements of *Arceuthobium vaginatum* subsp. *vaginatum* and *A. globosum* are similar; and they frequently sympatric and even occur on the same tree.

30b. *Arceuthobium vaginatum* subsp. *cryptopodum* Southwestern Dwarf Mistletoe

Arceuthobium vaginatum (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens, Brittonia 17:230, 1965.
=*A. vaginatum* f. *cryptopodum*.

Description. Mean shoot height 10 cm (maximum 27) cm, usually orange to reddish brown, sometimes dark to near black. Basal diameter of dominant shoots 2 to 10 (mean 4) mm. Third internode 4 to 16 (mean 7.8 ±3.2) mm long, 2.0 to 4.5 (mean 3.1) mm wide, length/width ratio 2.5:1. Staminate flowers 2.5 to 3.0 (mean 2.7) mm across; perianth segments 1.3 mm long, 1.0 mm wide. Mature fruit 4.5 to 5.5 (mean 5.0) mm long, 2.0 to 3.0 (mean 2.5) mm wide; proximal portion 3.5 mm long. Seeds 2.7 by 1.1 mm.

Phenology. Meiosis in March or April. Anthesis usually in May and June, with extremes from late April to early July. Fruits mature in late July or early August, with extremes from early July to early September. Both anthesis and seed dispersal in Colorado occur 1 to 2 weeks later than in Arizona and New Mexico; maturation period averages 14 to 15 months. Seed germination from August to September, immediately following dispersal.

Hosts. *Pinus ponderosa* var. *scopulorum* is the most common host in Arizona, New Mexico, Colorado, Utah, and Texas. The two races of var. *scopulorum* recognized by Conkle and Critchfield (1988) (Rocky Mountain and Southwestern) appear to be about equally susceptible, but most of the distribution of the Rocky Mountain race is primarily north of that of *Arceuthobium vaginatum* subsp. *cryptopodum*. Other principal hosts include *P. arizonica* var. *arizonica* (Arizona, New Mexico, Chihuahua, and Sonora) and var. *stormiae* (Coahuila), *P. engelmannii* (Arizona, Chihuahua, and Sonora), and *P. durangensis* (Chihuahua and Jalisco). *Pinus cooperi* is a secondary host. Occasional hosts are *Pinus aristata* and *P. contorta* var. *latifolia*. Rare hosts are *Pinus flexilis* and *P. strobiformis*. *Pinus sylvestris* is an extra-limital host.

Distribution. Northern Mexico (Sonora, Chihuahua, and Coahuila) and United States (Utah, Arizona, Colorado, New Mexico, and Texas). *Arceuthobium vaginatum* subsp. *cryptopodum* is widely distributed on *Pinus ponderosa* var. *scopulorum* from central Utah (Sevier and Emery) and northern Colorado (Larimer) to Arizona, New Mexico, western Texas (Guadalupe and Davis Mountains), at least as far south as the Sierra de la Madera (Coahuila) and the Sierra Madre Occidental (Sonora and Chihuahua). *Arceuthobium vaginatum* subsp. *cryptopodum* occurs in nearly every mountain range where *P. ponderosa* var. *scopulorum* grows, including isolated ranges such as the Virgin, Trumbull, and Hualapai Mountains (Arizona), the Ladron, Organ, Guadalupe, and San Andreas Mountains (New Mexico), Navajo Mountain (Utah), and Mesa de Maya (Colorado). *Arceuthobium vaginatum* subsp. *cryptopodum* distribution maps have been published for Colorado, Utah, and New Mexico (see Hawksworth and Wiens 1996). Elevational range is 1,700 to 3,000 m, although it is found primarily between 2,000 and 2,600 m in Arizona and New Mexico.

Discussion. *Arceuthobium vaginatum* subsp. *cryptopodum* is characterized by thick, orange-colored shoots. Populations, however, show various color gradations commonly from yellow to red, greenish in deep shade or on *Pinus contorta* var. *latifolia* or rarely from dark purple such as in the Black Forest of Colorado. This dwarf mistletoe is particularly damaging to *Pinus ponderosa* in the Sacramento Mountains in south-central New Mexico (Lincoln National Forest and adjacent Mescalero Apache Indian Reservation; Hawksworth and Lusher 1956), central Arizona, and along the Front Range in Colorado. For reasons yet to be explained, the parasite is common but less damaging in southwestern Colorado and southeastern Utah. The witches' brooms induced by *Arceuthobium vaginatum* subsp. *cryptopodum* are similar on all hosts except for *Pinus contorta* var. *latifolia* with small witches' brooms and large branch swellings. Because of the severe damage caused by this mistletoe and the importance of its principal host, there are numerous reports on its biology and management; the most comprehensive study is by Hawksworth (1961) and a general leaflet by Lightle and Weiss (1974).

31. *Arceuthobium verticilliflorum*

Big-Fruited Dwarf Mistletoe

Arceuthobium verticilliflorum Engelm., Botany of California 2:107, 1880.

Description. Mean shoot height 7 (maximum 11) cm, mostly yellow to yellow-green to purplish, without secondary branching, lightly glaucous when young. Basal diameter of dominant shoots 2.5 to 5.0 (mean 3.6) mm. Third internode 2 to 7 (mean 3.0 ±1.2) mm long, 2.5 to 4.5 (mean 3.2) mm wide, length/width ratio 0.9:1. Staminate flowers 3.5 to 4.5 (mean 4.0) mm across; perianth mostly four-merous (sometimes three-merous); verticillate, with five to 10 flowers per whorl; segments 1.8 mm long, 1.2 mm wide. Mature fruit 15 by 10 mm. Seeds about 11 by 6 mm; embryos 4 by 1 mm.

Phenology. Meiosis September to October. Anthesis usually March and April. Fruits mature in September and October of the year following pollination; maturation period averages 18 to 19 months.

Hosts. This dwarf mistletoe principally parasitizes *Pinus arizonica*, *P. cooperi*, *P. durangensis*, and *P. engelmannii*.

Distribution. Mexico (Durango). Populations occur east of El Salto on the Durango–Mazatlán Highway, in the Sierra Candella, Sierra Huacol, Sierra Guanacevi, and along the road from Santiago Papasquiaro to Altares (Cibrián Tovar and others 1980). Elevational range is 2,000 to 2,750 m.

Discussion. Hawksworth and Wiens (1965) report the rediscovery of this unusual species, first described by Engelmann in 1880, from El Salto, Durango. The species is perhaps the most distinctive and primitive in the genus. The staminate shoots are characterized by thick spikes (4 to 6 mm) with verticillate, four-merous flowers; the entire spikes are deciduous after flowering. This is the only dwarf mistletoe in which the pedicels do not elongate and curve downward when the fruits mature. Typically, the pericarp oozes off the top of the seed, and seeds are released but not explosively discharged. Compared to other dwarf mistletoes, mature fruits are more than twice as large and seeds weight 100 times more (200 to 270 mg). In further contrast, most dwarf mistletoes are found in closed canopy stands as pockets of infested trees with severe infections in the lower crowns; but *Arceuthobium verticilliflorum* is found in open stands with random distributions in trees and crowns. Fruit and seed morphology, ecological distribution, and observation of birds feeding in infected crowns suggest this dwarf mistletoe is dispersed by birds. This dwarf mistletoe causes massive witches' brooms, and the diameter of infected branches is sometimes greater than that of the trunk where the infected branch emerges. Infections on the main trunks of pines sometimes extend up to 3 m in length.

32. *Arceuthobium yecorense*

Yecoran Dwarf Mistletoe

Arceuthobium yecorense Hawksw. & Wiens, Phytologia 66:6, 1989.

Description. Mean shoot height 12 (maximum 17) cm, yellow-green to brown, branches flabellate. Basal diameter of dominant shoots 2 to 5 (mean 3) mm. Third internode 10 to 21 (mean 15) mm long, 2 to 4 (mean 2.4) mm wide.

Phenology. Time of anthesis is unknown but suspected to be June. Time of fruit maturity is unknown, but presumed to be September and October.

Hosts. The principal hosts in the Yecora region are *Pinus leiophylla* var. *chihuahuana* and *P. herrerai*. In the Sierra Madre Occidental, it occurs principally on *Pinus durangensis*, *P. herrerai*, *P. lumholtzii*, and *P. leiophylla* var. *chihuahuana*. *Pinus engelmannii* is a secondary host.

Distribution. Mexico (Sonora, Chihuahua, and Durango). The distribution of this dwarf mistletoe is poorly known and only collected from the Yecora region (Sonora and Chihuahua) and about 100 km west of Santiago Papasquiaro (Durango). Because it is abundant at two locations separated by more than 400 km, the dwarf mistletoe should be expected in the intervening forest areas as well. Elevational range is 1,600 to 2,500 m.

Discussion. *Arceuthobium yecorense* is characterized by its slender, greenish–yellow to brownish shoots and early summer flowering period. The plants are morphologically most similar to *A. aureum* subsp. *aureum* of the lowlands of Guatemala. The two populations are similar except that shoots from western Durango have more yellowish and slightly taller shoots. Yecora is the primary pine-producing area of Sonora; the dwarf mistletoe there is both common and damaging.

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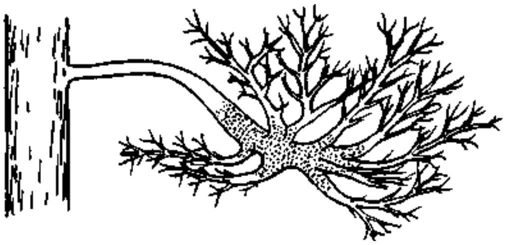
Chapter 5

Damage, Effects, and Importance of Dwarf Mistletoes



All dwarf mistletoes are parasites that extract water, nutrients, and carbohydrates from the infected host; they are also pathogens that alter host physiology and morphology (Gill and Hawksworth 1961, Hawksworth and Wiens 1996). Disease or direct effects are reductions in diameter and height increment, survival, reproduction, and quality; witches' brooms are formed in many pathosystems (Knutson and Tinnin 1980). Where dwarf mistletoe populations develop significant, long-term infestations, cumulative tree damages have various ecological and evolutionary effects. Depending on management objectives and priorities, these effects are interpreted as positive, negative, or usually of mixed consequences. In chapter 4, we discuss in general how the mistletoe's environment affects its growth and development and relate how mistletoe abundance is described by a relative severity index, DMR. In following chapters, the authors present information for quantifying host and mistletoe populations;

they also indicate numerous ways in which managers can influence mistletoe through manipulation of biotic agents, host genetics, and forest stands. In this chapter, we review the physiology of mistletoe parasitism, describe disease effects on infected host trees, identify some of the complex ecological and evolutionary interactions of which mistletoes play a role, and relate these effects and interactions to their consequences for resource management.

Physiology of Dwarf Mistletoe Parasitism

Dwarf mistletoes cause tree disease by affecting host water relations and growth (Knutson 1983, Kolb 2002). The shoot and leaf surface of dwarf mistletoes is small compared to other mistletoes, but they have significant effects on host water relations (Fisher 1983, Sala and others 2001, Wilson and Calvin 1996). Although dwarf mistletoe shoots do transpire, significant transpiration loss is by host foliage, especially those with large witches' brooms. Dwarf mistletoes affect host growth through the interaction of the host with the mistletoe endophytic system (Alosi and Calvin 1985, Calvin and Wilson 1996). The physiological processes involved include: (1) production of growth regulating compounds and (2) expropriation and reallocation of water, minerals, and carbohydrates (Livingston and others 1984, Rey and others 1991, 1992, Snyder and others 1996). The pathological symptoms are retention of infected branches, abnormal growth of infected branches (witches' brooms), crown dieback, and death (Anderson and Kaufert 1959, Broshot and Tinnin 1986, Hawksworth 1961).

Dwarf mistletoe infection affects host foliage, phenology, and respiration. Numerous authors report that needles of severely infected trees are smaller, fewer, and yellowish (Andrade and Cibrián 1981, Hawksworth 1961, Hawksworth and Johnson 1989a, Korstian and Long 1922, Weir 1916b). *Pseudotsuga menziesii* with *Arceuthobium douglasii* initiate bud break earlier and form longer shoots on brooms (Briede and others 1991). Dwarf mistletoe infected trees have lower respiration rates (Ryan 1990, Wanner and Tinnin 1986), perhaps the result of carbohydrate deficiency. Tree vigor as a single "health" index is evaluated in numerous ways; Schaffer and others (1983a) relate mistletoe infection with vigor and electrical resistance of bark tissues. Srivastava and Esau (1961) and Cibrián and others (1980) examine the effects of infection for distorting the host wood anatomy. One difficulty in researching dwarf mistletoe–host physiology is detecting and quantifying the endophytic system especially during incubation and latency. Marler and others (1999) demonstrate a polymerase chain reaction (PCR) method for identifying infected branches based on presence of mistletoe DNA.

Direct Effects to Host Trees

The pathological results of dwarf mistletoe infection are seen as reductions in reproduction, growth, longevity, and quality. The nature and magnitude of these effects are determined by the mistletoe and host species involved, infestation severity (usually measured as DMR, see chapter 4), and vigor of the host. These factors are in turn affected by age, history, and the influences of insects, other disease agents, competition, site quality, and climate (Hawksworth and Scharpf 1978, Hawksworth and Shaw 1984, Hawksworth and others 1992a). From a management perspective of mitigating these effects, the important considerations are time and opportunity. Both mistletoe intensification and damage are progressive and cumulative; they begin at a slow rate, with little effect, but increase exponentially, accumulating to a large effect. Damage first becomes evident when the crown of the host tree is about half infected (moderately infected, DMR class 3) and becomes increasingly severe as the infection intensifies to its culmination when the entire crown is infected and the tree dies. Mistletoe intensification and damage are also interactive with each other and responsive to numerous external factors. Models such as documented by Hawksworth and others (1995) integrate these numerous interactions and factors and portray the development of an infestation with useful management indicators such as numbers of trees, basal area, volume, and ingrowth.

Reproduction

Dwarf mistletoe affects host reproduction through cone production, seed quantity and quality, and seedling survival. Mature trees are large and usually have numerous reserves; a severe mistletoe infection, however, can reduce cone and seed production. Seedlings are especially vulnerable; a single mistletoe infection on the seedling is either lethal or so damaging the host sapling appears more like a bush than a tree.

Cones and seeds—Few studies are available on cone and seed production of dwarf mistletoe-infected trees. Cone production on witches' brooms as measured by numbers and size is usually reduced, but some viable seed may still be produced (Bonga 1964, Kuijt 1960b, Sproule 1996b, Weir 1916b). The reproductive output of infected trees appears to vary by species and severity of infection. Seed germination from parent *Pinus ponderosa* trees infected by mistletoe is reduced (Pearson 1912); germination is only 60 percent for seeds from moderately infected trees and

75 percent for severely infected trees (Korstian and Long 1922). Seed from infected *P. jeffreyi* are smaller, germinate less (80 percent), and produce poor seedlings (Munns 1919). For *P. contorta*, Schaffer and others (1983b) report cone size, seed size, and seed germination are negatively correlated with infection severity. Although Wanner (1986) has similar results for cones and seeds, he observes an initial increase in seedling stocking (at age 1 year) for some in heavily infested stands and attributes this increase to better seedbed conditions, which in these cases offset reduced numbers of seeds produced. Infected *Picea mariana* produce fewer cones, fewer seeds, lighter seeds, and lower germination rates than uninfected trees (Singh 1981, Singh and Carew 1989). In contrast to these reports, Reid and others (1987) did not observe an effect on cone production for infected *Pinus rudis*.

Seedlings—Disease incidence in young stands can be high (see for example Roth 1971, Scharpf and Vogler 1986, Weir 1916b). This is especially serious because seedlings and saplings are severely damaged by infection with even a few mistletoe plants. Reduced height of infected seedlings compared to uninfected seedlings is reported by Knutson and Toevs (1972) and Roth (1971). Seedlings are usually infected on the main stem and quickly killed by the mistletoe. Because of high turnover rates and rapid deterioration after death, mortality rates among seedlings are difficult to determine. Studies such as Roth (1971) in which he observed 50 percent loss of infected seedlings after 12 years, however, support the claim that early mistletoe infection is usually lethal. Those that survive for a few years at least, often develop into little more than a single broom and resemble a bush or bonsai.

Growth

An obvious and important fact about conifer trees is that they grow; they accumulate stem wood on a bole that increases in width, length, and volume. The annual increment for accretion in width varies along the bole and is measured for convenience at a given reference height. The variation in width along the bole is described as form; measures of width, length, and form are used to compute volume. By diverting the tree's resources to other outputs, a mistletoe infestation in a tree affects diameter growth and height growth, and so consequently affects form and volume. Fundamental to forest management is the ability to project expected tree growth under various treatment options. These projections are now often made with simulation models such as the Forest Vegetation Simulator (FVS, Forest Management Service Center 2001) and PrognosisBC (British Columbia Ministry of Forests 2000). Numerous intrinsic and extrinsic factors determine tree growth; these can be categorized as species, site, history, competition, and for infected trees, mistletoe severity. Site covers those long-term, generally fixed factors related to the potential productivity of the area such as soil fertility, water holding capacity, and climatic suitability. History reflects past events (droughts) and conditions (stagnation) that affect a tree's crown, its photosynthetic engine. Competition encompasses factors measured by stand density as basal area. Mistletoe severity is usually quantified as DMR (Hawksworth 1977, chapter 4). Quantitative studies reveal that these factors are usually confounded; that is, they interact so the effect of one factor varies as the level of another factor is changed.

Several techniques exist for study of tree growth. Stem analysis (for example, Baranyay and Safranyik 1970) is the most intensive but provides detailed information on diameter and height increment as well as form and volume. Individual trees can be identified and reexamined after a period of time to obtain information on each tree's change in diameter and height (for example, Hawksworth 1961). Alternatively, trees can be examined once and past diameter growth determined from an increment core (for example, Tinnin and others 1999). Some studies compare the diameters (or heights) for trees of different mistletoe classes; but unless all the trees were the same size and infected at the same time, this method introduces several complications and does not really measure growth response to infection.

Although numerous studies relate mistletoe severity to tree growth, few generalities can be made (Hawksworth and Wiens 1996). Some recent studies use a stem analysis technique (Andrade and Cibrián 1980, Baranyay and Safranyik 1970, Pousette 1991, and Smith 1969). Other studies that examined trees and increment cores include those by Barrett and Roth (1985), Filip and others (1993), Knutson and Tinnin (1986), Mathiasen and others (1990), Tinnin (2001), Tinnin and others (1999), and Vera (1984). Reduction in diameter increment is related to infection severity in nonlinear fashion: with little or no significant reduction for the DMR classes 1 to 3, some reduction for DMR class 4, more for DMR class 5, and much for DMR class 6. The magnitude of these reductions depends on numerous factors (Hawksworth and others 1995, Hawksworth and Shaw 1984, Thomson and others 1997, Wicker and Hawksworth 1988). Reduction in height increment is also related to infection severity; height effects usually appear at a lower severity and are proportionally greater with increase by DMR class. The combined effects of diameter reduction and height reduction on form and volume can vary by species and age (Pousette 1991, Tinnin 2001). Volume reductions, either accounting for stem form or not, are proportionately greater than reductions for diameter or height alone. Because mistletoe infection often occurs earliest on some of the larger trees of a stand, size comparisons of trees in different severity classes do not well reflect effects on growth increment.

Longevity

Mistletoe not only kills small trees but in time, a severe infection can even kill a mature, large tree (Roth 2001). A severe infestation (for example, Wood and others 1979) with many seriously infected trees can generate a high mortality rate. Mortality rates (see Hawksworth and Wiens 1996) are determined from either reexamining a plot after a known period of time (dependable) or estimating which trees had died within the reference period (undependable). The effect of mistletoe on tree survival can also be expressed in terms of tree longevity, the period of time over which a fraction (usually 50 percent) of trees are expected die. Because tree mortality is infrequent and then occasionally synchronous with events such as droughts (Childs 1960, Page 1981, Smith 1983), longevity studies over a long period with frequent observations (Hawksworth and Geils 1990) are especially useful. Like growth effects, mortality is related to a number of interacting factors; the most important are species, size, infection severity, and other mortality agents.

Hawksworth and Wiens (1996) identify 17 mistletoe species that are especially lethal for certain hosts and locations (table 5-1). These hosts include many important forest species such as *Abies magnifica* (Parmeter and Scharpf 1982), *Larix occidentalis* (Weir 1916a), *Picea mariana* (Baker and French 1991), *Pinus contorta* (Baranyay and Safranyik 1970, Hawksworth and Johnson 1989a), *P. ponderosa* (Hawksworth 1961, Roth 2001), and *Pseudotsuga menziesii* (Filip and others 1993, Mathiasen and others 1990). A study reported by Hawksworth and Geils (1990) and Geils and others (1991) demonstrates the interacting (and nonlinear) effects of tree size (diameter) and infection severity (DMR) on the longevity of mistletoe-infected pine. The expected longevity for 50 percent of trees with a severe infection (DMR 6) is less than 10 years for smaller trees (less than 9 inches diameter) and more than 10 years for larger trees. Over 40 years, however, many of the larger, severely infected trees died. During this time, some of the originally moderately infected trees became severely infected and died at a rate greater than that for uninfected trees. Elevated mortality rates due to mistletoe infection are built into the Dwarf Mistletoe Model Impact Model (Forest Health Technology Enterprise Team 2002).

Extremes in temperature and moisture can affect mortality rates of dwarf mistletoe-infected trees. Mortality rates are often highest following periods of drought, but there are few quantitative data. The most comprehensive studies of the interaction of drought and mistletoe are by Page (1981) and Smith (1983) for the California drought of 1975 through 1977. Drought may increase mortality of mistletoe-infected trees more than four times that of uninfected trees. Smith and McMahan (2002) describe an eco-physiology extension for the Forest Vegetation Simulator (Forest Management Service Center 2001). The method they present could be modified and developed for adjusting mistletoe-caused mortality rates to account for climatic variation.

Table 5-1—Combinations of North American taxa of *Arceuthobium* and their hosts in which host mortality rates are particularly high.

Arceuthobium	Host	Location
A. abietinum f. sp. *magnificae*	*Abies magnifica*	CA
A. americanum	*Pinus contorta*; *Pinus banksiana*	Western US and Canada; MB, SK, and AB, Canada
A. blumeri	*Pinus* spp.	Chihuahua and Durango, Mexico
A. campylopodum	*Pinus ponderosa*	Southern CA
A. cyanocarpum	*Pinus flexilis*; *Pinus albicaulis*	ID, UT, WY, CO; northern CA
A. douglasii	*Pseudotsuga menziesii*	Western North America
A. durangense	*Pinus* spp.	Jalisco, Mexico
A. gillii	*Pinus* spp.	Chihuahua and Durango, Mexico
A. guatemalense	*Pinus ayacahuite*	Southern Mexico and Guatemala
A. laricis	*Larix occidentalis*	Northwestern US and BC, Canada
A. microcarpum	*Picea pungens*	AZ, NM
A. nigrum	*Pinus* spp.	Durango and Puebla, Mexico
A. occidentale	*Pinus sabiniana*	CA
A. pusillum	*Picea mariana; Picea glauca*	Eastern North America
A. strictum	*Pinus leiophylla*	Durango, Mexico

Wood Quality, Decay, and Breakage

Although mistletoe infections usually occur on branches, the endophytic system can invade the bole and potentially affect wood quality. Infections and broken branches caused by heavy witches' brooms provide an entry court for decay fungi. Infected branches and brooms are resinous and dense with other flammable materials. These effects of mistletoe infection are important in some situations.

Wood quality of mistletoe-infected trees is affected by production of larger knots, development of abnormal grain, reduced strength, and other altered physical and chemical properties. Infected wood such as found in mistletoe-burls is characterized by shorter, distorted tracheids, increased ray volume, included pitch, frass, and decay (Cibrián and others 1980, Piirto and others 1974, Weir 1916a). The effects on sapwood moisture content and specific gravity are variable: higher, lower, or not different from uninfected wood (Hawksworth 1961, Knutson 1970, Wellwood 1956). Piirto and others (1974) report, however, that infected wood and wood from other parts of infected trees is weaker in strength for modulus of elasticity, modulus of rupture, and work to proportional limit. The effects on pulp quality, however, are negligible (Dobie and Britneff 1975, Hunt 1971, Wilcox and others 1973).

The association of decay and mistletoe varies by species and tree age. In fir, larch, or hemlock trees, mistletoe infections often provide an infection court for decay fungi, especially if the wood is exposed (Aho 1982). Englerth (1942) reports that nearly a third of the decay in hemlock entered through dwarf mistletoe stem infections and adjacent swollen limbs. Several decay fungi are associated; the most frequent is the common brown cubical slash decay fungus *Fomitopsis pinicola* (Etheridge 1973). Decay is usually limited to the area of the swollen bole canker (Aho 1982). Decay is rarely associated with mistletoe infection in the more resinous pines, spruce, and Douglas-fir. Well-managed, young-growth stands of true fir in California should also have little loss from mistletoe-associated decay (Parmeter and Scharpf 1982).

Witches' Brooms

Most dwarf mistletoes and several other disease agents induce abnormal development of host branches into witches' brooms. Mistletoe brooms are infected host branches with excessive branching and shortened (or lengthened) internodes that develop in response to elevated levels of plant growth compounds (Schaffer and others 1983c). Broom form is determined by the mistletoe and may even be a useful taxonomic character. There are a variety of broom forms and classification schemes based on the distribution of the endophytic system, on the host branching pattern, and on the boom position relative to the bole. Systemic or isophasic brooms are those in which the endophytic system of the mistletoe grows with the apical and cambial tissues of the host and produces mistletoe shoots either along the branch or at branch girdles (Hawksworth 1961, Kuijt 1960b). Nonsystemic or anisophasic brooms are those in which the endophytic system remains localized near the original site of infection and only grows with the host cambium (fig. 5-1). *Arceuthobium globosum* subsp. *globosum* and *A. occidentale* do not induce typical broom formation. Most North American mistletoes usually develop nonsystemic brooms and rarely systemic brooms. *Arceuthobium americanum*, *A. douglasii*, *A. guatemalense*, and *A. pusillum* consistently produce systemic brooms (Hawksworth and Wiens 1996). Hawksworth (1961) classifies brooms of *Arceuthobium vaginatum* as typical for nonsystemic brooms where the localized infection is far from the bole, and although branching is prolific, segments are short (fig. 5-1A). He describes the uncommon, volunteer leader

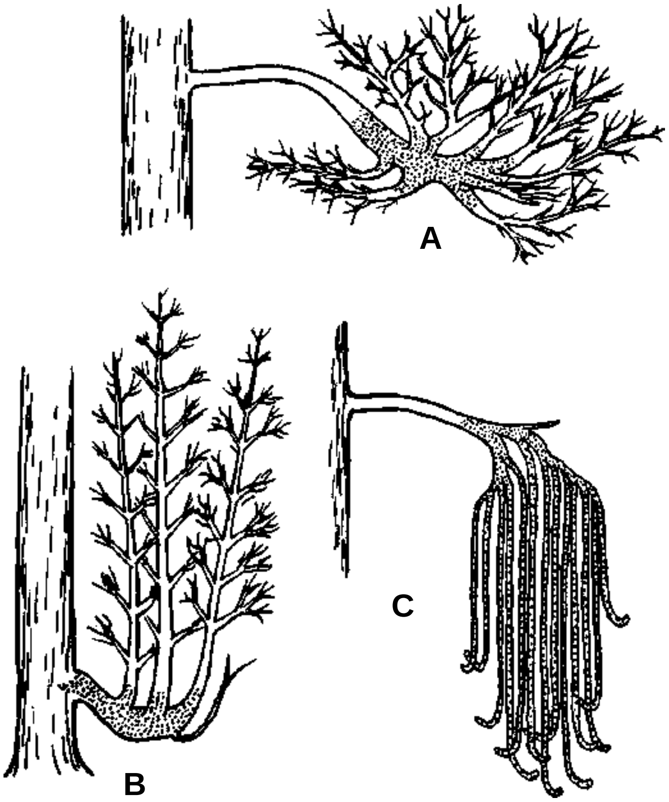


Figure 5-1—Witches' brooms on *Pinus ponderosa* induced by *Arceuthobium vaginatum*; stipple areas indicate region invaded by the mistletoe. **A**, typical broom; **B**, volunteer leader broom; **C**, weeping broom. Adapted from Hawksworth (1961), figure 45.

brooms (fig. 5-1B) as localized infections, near the base of the bole in which one or several leaders develop as long, erect, normally branched forks. Weeping brooms are very rare systemic brooms of numerous, long, pendulous infected branches (fig 5-1C). Tinnin and Knutson (1985) classify the systemic brooms of *A. douglasii* by position. Type I brooms originate away from the bole on long branches and thereby form large brooms on drooping branches. Type II brooms form on branches but near the bole and with a sturdy, upright supporting branch; the supporting branch makes a horizontal platform between the bole and mass of the broom. Type III brooms form at or close to the bole and lack the dominant, platform branch. Witches' brooms can also be produced by rust fungi (broom rusts and gall rusts), other fungi (*Elytroderma deformens*), chromosomal condition (trisomatic cells), and physiological reaction to canopy opening or age (stimulation brooms). Mistletoe brooms can be distinguished by the presence of aerial shoots or their remnant basal cups.

Witches' broom formation by dwarf mistletoes can have a major impact on host growth and crown form. Brooms become quite large on Douglas-fir or numerous on pine and larch. Brooms are a preferred growth-sink; host resources that would have gone to the bole and roots are diverted into broom growth. The importance of this effect is evident from the improved vigor, growth, and survival of broom pruned trees (Lightle and Hawksworth 1973, Scharpf and others 1988). Large brooms, especially on trees with brittle wood, may break off (Hadfield 1999). Brooms differ from normal crown branches for numerous features: needles, twigs, and accumulated detritus (Bonga 1964, Broshot and others 1986, Tinnin and Knutson 1980). These differences are important for their consequences on canopy structure, wildlife habitat, and fuel loading.

Ecological and Evolutionary Effects

The effects of mistletoe infection on trees have numerous consequences for associated species and various natural processes. Mistletoes, especially in significant infestations, act as both keystone species (Watson 2001) and controlling disturbance agents (Holling 1992). From this perspective, we view how dwarf mistletoes affect community dynamics by their interactions with fungi, insects, and fire, effects on vegetation, and use by wildlife. Hawksworth and Wiens (1996) also discuss these topics and providing examples of pathogenic and biotic associates.

Interactions

The forest communities to which dwarf mistletoes belong include large numbers of species of various taxonomic groups and ecological roles. For consideration of the most obvious ecological effects, we focus here on the interactions of mistletoes with other disease, injury, or disturbance agents.

Fungi—Forest fungi are important in nutrient recycling (decay and mycorrhiza) and as pathogens of mistletoes and their hosts. The relation of mistletoes and decay fungi is discussed above, and the pathogens of mistletoes are described in chapter 7 as biological control agents. In many forests, mistletoes are only one of many tree pathogens; the most important are canker fungi (Filip 1984), root disease fungi (Marsden and others 1993), and stem rusts (Hawksworth and others 1983).

Insects and Spiders—Insects and spiders that react to mistletoe infestations can be categorized as those associated with shoots, with brooms and infected branches, and with infested trees (Stevens and Hawksworth 1970, 1984). Insects associated with shoots include pollinators, herbivores, and their predators, parasites, and associates. Some of the important shoot insects are potential biocontrol agents (see chapter 7), others include lepidopterians such as *Mitoura spinetorum* (Grimble and Beckworth 1993) and aphids with their attending ants. Numerous insects and spiders use mistletoe brooms with their accumulation of needles and other detritus as a special habitat for foraging and hunting. The significant insects associated with infected trees are tree defoliators and bark beetles. Defoliators may feed upon mistletoe-infected trees and contribute to tree damage and mortality (Filip and others 1993, Wagner and Mathiasen 1985). Mistletoe may affect tree phenology and shoot development, which has a consequence to defoliator development (Briede and others 1991). The attraction of bark beetles to mistletoe-infected trees depends on the species combination (mistletoe-tree-insect) and severity of infection. Hawksworth and Wiens (1996) review the combinations for which mistletoe infection appears to increase, decrease, or be unrelated to bark beetle attack. For example, Johnson and others (1976), McCambridge and others (1982), and McGregor (1978) discuss mistletoe as a predisposing factor for mountain pine beetle; Wilson and Tkacz (1992) for an outbreak of *Ips* in pinyon. Nebeker and others (1995) and Linhart and others (1994) consider the possible chemical bases for insect attraction to infected trees. An intermediate hypothesis to explain aggressive bark beetle (for example, mountain pine beetle) attraction to infected trees suggests that there would be no difference in beetle attack between similar sized trees that are uninfected or lightly infected (DMR 1 or 2), greater attack for moderately infected trees (DMR 3 or 4), and reduced attack for severely infected trees (DMR5 or 6). This hypothesis requires testing in various situations.

Fire and Fuels—The fire ecology of dwarf mistletoes is reviewed by Alexander and Hawksworth (1975) and updated by Zimmerman and Laven (1984). Several features of mistletoe infection increase the tree's flammability. Infection induces excess resin deposition and increases litter accumulation (including detached brooms). Retained brooms and infected branches form a fuel ladder from the ground into the canopy. Mistletoe severity (DMR) is related to scorching, mortality, and sanitation (Conklin and Armstrong 2001). Although an extreme, stand-replacing fire kills most trees, a few isolated mistletoe-infected trees can escape to not only reseed the stand but also reinfest it. Disturbance regimes and stand structure resulting from mistletoe and fire interactions are discussed by Bradley and others (1992) and Kipfmueller and Baker (1998).

Forest Structure and Composition

Forest insects and pathogens are increasingly being recognized as important agents in shaping the structure and composition of forests (Hessburg and others 1994, Holling 1992, Monning and Byler 1992). Besides their interaction with fire described above, mistletoes affect the forest canopy, landscape pattern, and tree species mix (Baker and French 1991, Mathiasen 1996, Parker and Parker 1994, Reich and others 1991, Wanner and Tinnin 1989). The ecological importance of witches' brooms on community dynamics is examined by Tinnin and others (1982); and the role of mistletoes in forest canopies is reviewed by Mathiasen (1996). The paper on canopy light and mistletoe distribution by Shaw and Weiss (2000) is an example of detailed, canopy ecology studies at the Wind River Canopy Crane. Mistletoe and forest vegetation studies include examinations of plant association (Marshall and Filip 1999) and biotic diversity (Mathiasen and Marshall 1999). Two additional topics that have received special attention are effects and dynamics of mistletoe in old-growth stands and on wildlife habitat.

Old-Growth Forests—Numerous studies have examined mistletoe effects on immature and mature trees in managed stands, but there are few studies for old trees (over 200 years) and old-growth stands. Hawksworth and others (1992a) described a 300-year-old *Pinus contorta* stand infested with *Arceuthobium americanum*. Although infected trees occurred on over half the area, there were no isolated infection centers as were found in nearby 70-year-old stands. Tree mortality was higher among infected trees, but diameter growth was significantly reduced only among the most severely infected trees (DMR 6). These older trees grew slower, and on a percentage basis mistletoe had less effect than seen in younger, faster growing trees. Parker and Parker (1994) examined the spatial pattern of tree density in seven *P. contorta* stands about 120 to 140 years old. They observed dense, closed-canopy stands that appeared to have developed and closed rapidly after initiation (fire) and low density, open-canopy stands with recruitment that is more continuous. They speculated that the open stand might have resulted from low initial stocking and high mortality from mistletoe. Kipfmueller and Baker (1998) describe another set of 43 *P. contorta* stands also in the Central Rocky Mountains and also representative of unmanaged, older stands (some to 500 years). They found that half of the stands were infested, and the average disease severity (DMR) increased with time since stand establishment. At the landscape scale, mistletoe often occurred as severe infestation patches but was absent from other areas of similar age. They concluded that a healthy forest would include a mosaic of infection centers and uninfested stands with periodic stand-replacing fires that vary in intensity.

Wildlife Habitat—Although dwarf mistletoes do not provide large incentives for birds or mammals to visit for pollination or seed dispersal as do other mistletoes, dwarf mistletoes provide forage, foraging sites, protected and special sites, and desirable stand structures for numerous wildlife species. (Bird dispersal is important for *Arceuthobium verticilliflorum* and possibly *A. occidentale*.) Hawksworth and Geils (1996) review the use of mistletoe by birds and mammals for food, nesting, and cover. Numerous studies have since been reported. Allred and Gaud (1994) describe tree selection and bark grazing by Abert squirrels and their high use of mistletoe-infected trees. Brooms in Douglas-fir are frequently used for cover and nesting (Hedwall 2000, Parks and others 1999a, Parks and Bull 1997, Tinnin and Forbes 1999). Brooms in ponderosa pine are also used (Garnett 2002). Brooms and associated mistletoe-infested sites are important for nesting by the northern spotted owl (Everett and others 1997, Marshall and others 2000). Steeger and Hitchcock (1998) describe the effects of several tree diseases, including mistletoe, on stand structure preference for nuthatches. Reich and others (2000) examine the relationship of canopy opening in a mistletoe-infested strand on bird usage. Although Bennetts and others (1996) found a positive association between the stand severity of mistletoe and bird usage in Colorado, Parker (2001) for a similar study in Arizona found a mixture of responses depending on bird species. Mistletoe presence, incidence, and severity may not be good indicators themselves of wildlife habitat value. Wildlife species are probably responding in a complex way to special features such as brooms and snags, to vertical crown structure, to canopy gap pattern, and other factors affected by mistletoes (Reynolds and others 1992).

Consequences to Resources and Other Values

Dwarf mistletoes are important because they are serious pathogens of valuable conifers in many forests of North America. These conifers are valuable economically, primarily for their timber yields and ecologically for their role in forest ecosystems (Hawksworth and Shaw 1984). Importance and worth, however, are only meaningful and relevant within a given value system that is selected by the forest manager, owner, policymaker, stakeholder, or society.

Importance

Species Affected—Conifers that are hosts to dwarf mistletoes can be divided between major species that occur in great numbers over large areas, and rare species with few, sparse populations. In Canada, the major host species are *Larix occidentalis, Picea mariana, Pinus contorta, P. banksiana*, and *Tsuga heterophylla*. In the Eastern United States, the major species are *Picea mariana, P. glauca,* and *P. rubens*; and in the Western United States, they are *Abies magnificae, A. concolor, Larix occidentalis, Pinus ponderosa, P. contorta, Pseudotsuga menziesii,* and *Tsuga heterophylla*. Mexico has a great abundance and diversity of conifers (over 30 taxa) that are mistletoe hosts (Hawksworth 1980, Hawksworth and Cibrián 1985). *Abies religiosa* and *Pseudotsuga menziesii* are infected; but the most common hosts are pines, including yellow pines, white pines, and pinyon pines. One of the more rare conifers that are hosts for *Arceuthobium abietinum* is *Picea breweriana* in Oregon; it is severely infected (Hawksworth and Wiens 1996).

Area Affected—In Canada, Magasi (1984) reports *Arceuthobium pusillum* is common in the Maritime Provinces. Overall, 20 percent of sites are infested and 6 percent of trees infected, but nearly all of the infested sites, infected trees, and mistletoe-caused mortality are in wet areas. Brandt and others (1998) map and summarize the distribution of severe mistletoe infestation (by *A. americanum*) in Manitoba, Saskatchewan, and Alberta. About 5 percent of the forest area or 500,000 ha are specifically identified as severely infested sites, where mistletoe-caused mortality and brooming are visually obvious (also see Baker and others 1992). Moody and Amirault (1992) estimate mistletoe incidence in individual, severely infested stands ranges from 73 to 100 percent. In British Columbia, *A. americanum* and *A. tsugense* are widespread, common, and damaging at many sites (Moody 1992, Thomson and others 1997). Hodge and others (1994) report only 2 percent of managed stands infested and only 3 percent of trees infected (except in a few stands, however, infection reaches 34 percent).

In the United States, *Arceuthobium pusillum* ranges widely across the Northeastern and Lake States; but its occurrence varies from locally common to rare in some States (Hawksworth and Wiens 1996). Drummond (1982) estimates 14 percent of the spruce area in the Lake States is infested. Numbers for dwarf mistletoe-infested area for each of the Western United States, however, are available (Forest Health Protection 2002). Westwide, about 25 percent (Drummond 1982, Bolsinger 1978) or 28.7 million acres of Western forests are infested (Forest Health Protection 2002). In contrast to the report (and accompanying compact disk) by Brandt and others, the United States' summaries (Drummond 1982, Forest Health Protection 2002) and the data on which they are based provide only statistical estimates of area infested and cannot map the specific, infested sites. A number of regional summaries are available. Andrews and Daniels (1960) report on the distribution of dwarf mistletoe in Arizona and Mexico in terms of administrative area (forest), harvest status, and various ecological factors. The most important forest types are ponderosa pine and Douglas-fir; Andrews and Daniels classify 36 percent of the ponderosa pine type as infested and 47 percent of the Douglas-fir type as infested. Maffei and Beatty (1988) report on a resurvey of the ponderosa pine area examined 30 years previously by Andrews and Daniels (1960). Maffei and Beatty (1988) attribute the apparent increase of infested area (8 percent more of the type) to ineffective mistletoe control. Other regional summaries are prepared by Bolsinger (1978) for the Pacific Northwest, Byler (1978) for California, DeNitto (2002) and Stipe and others (1992) for the Northern Region (Montana), and Johnson and others (1981) for the Rocky Mountain Region (Colorado and Wyoming).

Dwarf mistletoe occurs throughout the conifer forests of Mexico. Vázquez (1994a) states that an estimated 1.8 million ha in Mexico are infested. Most the information related to mistletoe damage in Mexico occurs as reports of infested area and infection incidence at various localities (see Hawksworth 1980). Caballero (1968, 1970) indicates the percentage of inventoried forest sites infested for several States: Zacatecas 24 percent, Durango 15 percent, Jalisco 12 percent, Nayarit 10 percent, Sinaloa 10 percent, Sonora 9 percent, Chihuahua 8.5 percent, and Baja California 7 percent. Within stands, the extent of the area infested and the percent of infected trees can be as high as 85 percent (Acosta and Rodriguez 1989, Gutierrez and Salinas 1989).

Growth Loss—Information on reduction of volume increment, mortality, and area infested can be used to estimate mistletoe impact to stand yield on an area basis. The difference between realized volume in an infested stand (reduced by loss of increment and mortality) and potential yield for the site (if mistletoe were not present) is described as *growth loss*. The growth loss concept can be applied nationally, regionally, forestwide, and to individual stands (Baker and Durham 1997 describe a method for computing growth loss). Drummond (1982) estimates a total annual growth loss from mistletoe in the United States at 418 million cubic feet per year; Vázquez (1994a) for Mexico reports a loss of 2 million cubic m per year. Estimates for Canada are available for Newfoundland at 1 cubic m per year per ha (Singh and Carew (1989); for Manitoba, Saskatchewan, and Alberta at 2.4 cubic m per year (Brandt and others 1998); and for British Columbia at 1.8 million cubic m per year (Forest Insect and Disease Survey 1994). DeNitto (2002) provides a growth loss estimate of 33 million cubic feet per for Montana (broken down by host species). Johnson and others (1981) describe growth loss for forests of Colorado and Wyoming. Marsden and others (1993) illustrate use of a forest growth and yield program to compare expected yield for a mistletoe-infested stand to what might be had were the stand not infested. Growth loss can be so significant in severely infested stands (especially immature and infected at an early age) that commercial yield cannot be obtained (Hawksworth and Hinds 1964).

Amenity Values

Dwarf mistletoes are sufficiently unusual and influential that they are important to a number of resource and amenity values besides commercial timber yield. Other forest products have traditionally included watershed protection, recreation opportunity, and wildlife habitat. Over a half century ago, concern over the effects of dwarf mistletoe to old-growth ponderosa pine at the Grand Canyon National Park lead managers to an intensive control project (Lightle and Hawksworth 1973). The effects of dwarf mistletoe on fuel loading and fire behavior are still a serious interest to managers (Zimmerman and Leven 1984). We have already discussed how witches' brooms and forest structure affect wildlife abundance and diversity (Bennetts and others 1996, Parker 2001, Reich and others 2000). Mistletoes are also valuable as mistletoes themselves and as members of a biotic community.

Mistletoes possess aesthetic, scientific, and intrinsic values. Although the mistletoe plant and diseased trees are not usually considered attractive (exceptive by some forest pathologists), a distinctively broomed, dead tree against the backdrop of the Grand Canyon does make a strong and interesting picture. Mistletoes can provide chemical analogs that may be developed into useful drugs. They serve as models for understanding the evolution of parasitism (Atsatt 1983a) and phylogeny of their hosts (Hawksworth 1991). Rolston (1994) describes the value of living entities beyond their worth to humans as achievement and part of the system of life.

Forests are not only managed for the resources they produce but also to sustain and protect forest health (Monning and Byler 1992) and ecosystem values (Taylor 1995). Dwarf mistletoes are important disturbance agents (Holling 1992) with distinct ecological functions (Hessburg and others 1994). They contribute to natural diversity structurally (Mathiasen 1996) and biologically (Mathiasen and Marshall 1999). Some mistletoes are considered species of special concern (Hildebrand 1995), and truly rare species such as *Arceuthobium hondurense* probably deserve protection. A balanced view of mistletoes as the cause of losses of valuable resources, but also as natural agents that shape forests, is emerging (Wittwer 2002).

Coevolution

Information from biogeography, paleobotany, host relations, and molecular systematics indicates the dwarf mistletoes have a long evolutionary history of parasitism with their conifer hosts (Hawksworth and Wiens 1996). Mistletoes are physiologically dependent on their hosts but cause symptoms that eventually result in death for both. What really matters, however, from an evolutionary perspective is their success at leaving descendents. To the present, host and parasite have lived, reproduced, and died in natural ecosystems. These natural ecosystems, even wildlands, are increasingly controlled and affected by managers and human society. We have a fair understanding of the physiology of mistletoe–host parasitism and a good ability to predict the effects of infection on tree growth and survival. We are beginning to appreciate the complex ecological interactions in which mistletoes participate. By management with biological agents, chemicals, genetic manipulation, and silviculture, we attempt to influence how mistletoe affects resources and our environment. For that management to have a beneficial outcome, which is sustaining to the biotic system on which we depend, it is advisable to consider not only immediate results but also ecological and eventually evolutionary consequences.

J.A. Muir
B. Moody

Chapter 6

Dwarf Mistletoe Surveys

Dwarf mistletoe surveys are conducted for a variety of vegetation management objectives. Various survey and sampling techniques are used either at a broad, landscape scale in forest planning or program review, or at an individual, stand, site level for specific project implementation. Standard and special surveys provide data to map mistletoe distributions and quantify disease severity. At a landscape scale, extensive surveys assess regional impacts, estimate mistletoe occurrence, intensity, and effects, and estimate future growth and yield. Intensive surveys evaluate stands, campgrounds, and other sites to design projects and monitor treatments.

Numerous variations and combinations of techniques such as aerial survey and photography, forest inventory, road and plot survey, transects and grid survey, and permanent plots are used to obtain dwarf mistletoe information for program and project management (table 6-1). Only a few studies compare alternative survey and sampling methods (Drummond 1978, Hildebrand and others 1997, Mathiasen

Table 6-1—Surveys for mapping the distribution and quantifying the effects of dwarf mistletoes.

Technique	Objective(s)	Reference Example
Aerial survey	Landscape assessments	Brandt and others 1998
Aerial photography	Landscape assessments	Baker and French 1991
Forest inventory plots	Landscape assessments	Hildebrand and others 1997
Road and plot surveys	Landscape assessments	Thomson and others 1997
Transects and grids	Landscape assessments	Maffei and Arena 1993
Permanent plots	Detailed assessments Project monitoring	Hawksworth and Marsden 1990 Lightle and Hawksworth 1973
Project area assessment	Management prescription Stand or Land Unit examination Recreation management Wildlife habitat	Tkacz 1989 Vásquez 1994 Scharpf and others 1988 Parks and others 1999

and others 1996b, Vázquez 1993b, 1994a). Effective and efficient sampling benefits from use of explicit objectives recognizing the resources of interest (such as timber, recreation, wildlife), specification of statistical standards, and consideration of cost and safety issues (Tkacz 1989, and see assistance provided at Forest Service 2002). In this chapter, we identify the major types of dwarf mistletoe surveys, uses of that data, and subjects for research and development.

General Requirements and Procedures

Before selecting or adapting one or more methods, a user should carefully consider and articulate the purpose and scope of the proposed survey. Almost all the available methods for estimating mistletoe occurrence and effects can be adapted to a variety of purposes including timber management, vegetation inventory, recreation, and wildlife management. Many techniques can be adapted to a range of scales from regional or forest landscapes to individual stands or sites. For any management decision, a wide variety of information from numerous sources on various subjects is needed. In areas with significant dwarf mistletoe infestations, data on mistletoe extent, severity, and potential make an important contribution to the decision process (Stage and others 1986, Tkacz 1989). Given the variety of objectives and constraints encountered by managers, only general guidelines can be stated here. The benefits of proposed treatment in each particular case should be evaluated for expected costs and benefits, impacts to other resources, and conflicts with other objectives. Assessments for landscape-scale management usually require only extensive, relatively broad information on dwarf mistletoe occurrence and effects. A general strategy for dwarf mistletoe management in areas of significant occurrence may be sufficient. At the level of particular stands and sites, however, management prescription may require detailed information on resource and ecological conditions and specific data for mistletoe distribution and abundance. Site prescriptions also require consideration of the general principles for managing infested stands (see chapters 7 and 8) as well as local issues and forest-level management objectives.

Several Provinces and States require a professionally certified evaluation of young forests to ensure that damages from insects and diseases are less than specified levels. This is especially important where the previous stand had been infested by dwarf mistletoe because the regeneration process may have left an infected, residual overstory that allowed spread to the seedlings (Alfaro 1985). In British Columbia, evaluations assess whether the young stand is free-growing and contractor obligations satisfied (British Columbia Ministry of Forests 1995); in other regions, this standard is described as producing adequate stocking of healthy seedlings.

Several existing data sources are available for general information on regional occurrence and potential impacts of dwarf mistletoes. These include Forest Inventory and Analysis (2002), Forest Health Monitoring Program (1994), Current Vegetation Survey (2002, Gregg and Michaels Goheen 1997), and the Canadian Forest Insect and Disease Survey (Cerezke and Emond 1989, Moody 1992, Myren and Gross 1977, Wood 1986). Use of these kinds of data is reviewed by Bolsinger (1978), Drummond (1982); limitations are described by Drummond (1978), Hildebrand and others (1997), and Marsden and others (1990).

If archive, large-scale data are either lacking or not sufficient, other established forest management plots are available from standard resource inventories. Data for dwarf mistletoes are relatively easily determined, as described below (see Forest Inventory Plots). For landscape-level surveys, several techniques such as road surveys or aerial photography can be used separately or in conjunction with inventory plots.

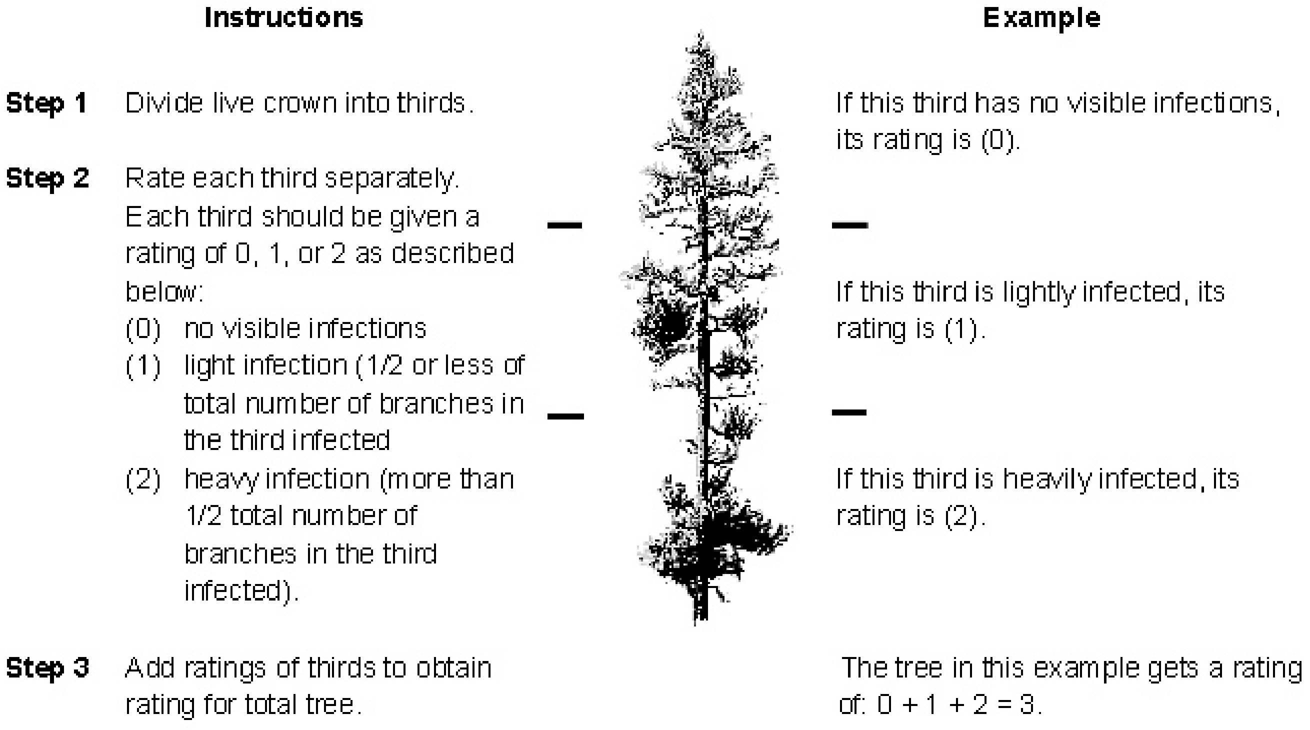
Surveys of dwarf mistletoes on a landscape or large geographic area are undertaken to determine the overall returns from a national or regional program or to compare returns from standard operational treatments applied to a large forest area. More frequently, landscape surveys are used to substantiate the general extent and effects of mistletoes and rank areas for treatment priority. Exercises range from botanical surveys for detection and identification of dwarf mistletoe species (for example, Hernandez 1991) to large-scale, annual programs for tracking broad forest health conditions and trends (Forest Health Monitoring Program 1994). Large-scale surveys have been conducted for Canada (Moody 1992, Myren and Gross 1977), the Southwestern States (Andrews and Daniels 1960, Maffei and Beatty 1988), and California (Byler 1978).

Occasionally, there is a need for a detailed dwarf mistletoe survey on a land unit for a specific purpose such as determining disease impacts to forest ecology, stand structure, productivity, or treatment effectiveness. Generally, detailed analyses are feasible only if foresters or specialists have access to agency-endorsed methods or models for analysis of forest growth and dwarf mistletoe effects (for example, British Columbia Ministry of Forests 2000, Forest Management Service Center 2001). These models are useful in developing detailed prescriptions for harvesting, silvicultural treatment, and other management objectives such as visual quality, wildlife, and recreation management. Use of models to predict the effects of dwarf mistletoe damage and analyze benefits from silvicultural treatments is described in chapter 8.

For intensive surveys such as silvicultural inspections and timber cruising, several tree stand attributes related to dwarf mistletoe status are useful. These include dwarf mistletoe species (see chapter 4), extent of infested area, mistletoe incidence as percent of host trees that are infected, and a measure or rating of disease severity such as DMR (fig. 6-1) or other rating for intensity of infection within trees.

Dwarf Mistletoe Surveys

Dooling (1978) summarizes several methods suitable for dwarf mistletoe surveys. The most commonly used methods and recent examples (table 6-1) are briefly described in the following sections.



Step 1 Divide live crown into thirds.

Step 2 Rate each third separately. Each third should be given a rating of 0, 1, or 2 as described below:

(0) no visible infections
(1) light infection (1/2 or less of total number of branches in the third infected
(2) heavy infection (more than 1/2 total number of branches in the third infected).

Step 3 Add ratings of thirds to obtain rating for total tree.

If this third has no visible infections, its rating is (0).

If this third is lightly infected, its rating is (1).

If this third is heavily infected, its rating is (2).

The tree in this example gets a rating of: 0 + 1 + 2 = 3.

Figure 6-1—Dwarf mistletoe rating system (DMR).

Aerial Surveys

A major technique or approach used for extensive examinations is aerial survey. This technique is described for dwarf mistletoe (*A. americanum*) on jack pine (Robins 1972) and lodgepole pine (Brandt and others 1998), and Eastern spruce dwarf mistletoe (*A. pusillum*) on black spruce (Baker and others 1992). Aerial survey observers can best detect severe infestations by the distinct infection centers associated with heavy mortality and brooming. Total extent and incidence are under estimated. Aerial survey is most practical over low-relief terrain, but rotary-wing aircraft have been used successfully over mountainous areas (Brandt and others 1998, Schwandt and Page 1978). Flight lines are run parallel at intervals of 5 to 10 km (or wider) through areas of susceptible forest types. Fixed, overhead-wing aircraft can be used on clear, bright days at ground speeds of 150 km per hour. One observer alone or one observer on each side of the aircraft draws or sketches the extent of each mistletoe-infested area on an appropriate map (which may be a topographic, forest type, or inventory base map). In some surveys, a lap-top computer with a digital map display of topographic and forest-type features is used with a global positioning system (GPS) to sketch-map directly on the computer screen; this method is in development (L. Rankin, 1999 personal communication). Geographic positions of infested stands can also be located with a GPS-receiver (Brandt and others 1998, Zavala and Zavala 1993). Information is eventually incorporated into a GIS-database. Brandt and others (1998) demonstrate the capability of this technique for mapping the severe damage caused by dwarf mistletoe to jack pine and lodgepole pine for an area of over 28 million ha in Central Canada (Alberta, Saskatchewan, Manitoba).

Aerial Photography

Aerial photography is routinely used for vegetation and forest inventory typing, classification, and sampling. Aerial photography is feasible, however, for landscape dwarf mistletoe surveys only where there are highly distinctive features such as mortality or infection centers. These occur in Central to Eastern, North American forests of black spruce (Baker and French 1991) and jack pine (Muir and Robins 1973). Especially in young infestations, mistletoe infections are often most common in the lower crown and obscure to aerial view. Large-scale aerial photography can be used for individual stands to detect infected trees with large witches' brooms or to identify susceptible tree species and suspect individuals based on various crown attributes.

Forest Inventory Plots

Vegetation or forest inventory sampling is the commonly accepted means of describing and quantifying the forest resource, and it is often the only acceptable data source for projecting dwarf mistletoe impacts on forest growth. Established inventory plots ensure an acceptable sampling scheme and avoid the expense of recollecting associated tree data. Dwarf mistletoe data from routine inventories, however, may have low or uncertain reliability because inventory crews may lack the experience to recognize mistletoe presence and damage (Drummond 1978, Marsden and others 1990). Where inventory plots are reexamined to obtain mistletoe specific data, trained personnel and check cruises are appropriate (Hildebrand and others 1997). Forest inventory plots are often situated by a stratification scheme that if not properly accounted may lead to biased estimates. Nonetheless, this is described and used by several authors including Caballero (1970), Filip and others (1993), DeMars (1980), Gregg and Michaels Goheen (1997), Hildebrand and others (1997).

Surveys for dwarf mistletoes using an existing inventory plot system can be relatively simple and easy to conduct. Each sample tree on the inventory plot is examined and a rating (such as DMR) is recorded. Wide-field, high-quality binoculars (for example, 8x40) are useful; yellow-tinted eyeglasses are not used because they obscure dwarf mistletoe shoots (B. Geils 1999, personal communication). Training and quality checks are appropriate to maintain quality and consistency (Shaw and others 2000).

Growth impacts are calculated from tree data and information for mistletoe severity using the sample design of the inventory (Marsden and others 1990). In many situations, covariate factors are useful. For example, Thomson and others (1997) point out that for lodgepole pine, stand density (number of stems per hectare) has a major effect on tree volume and should be used to adjust estimates. Supplemental data can determine the correlations between radial growth, DMR, tree age, and stand density.

Road and Plot Surveys

Roadside surveys for dwarf mistletoes are popular and suitable for many forests in Western North America with reasonably extensive road access (Andrews and Daniels 1960, Johnson and others 1981, Maffei and Beatty 1988, Merrill and others 1985, Mathiasen and others 1996b, Thomson and others 1997). Good results are obtained in forests of almost pure, even-aged stands of trees at least 20 years old. A vehicle driver and an observer traverse roads through susceptible forest stands at a low speed (say, 30 to 40 km per hour) and rate levels of infestation in segments or fixed intervals (such as 100 to 200 m) along the roads. Data are recorded on inventory maps with cover type information.

Tree infection along roads is usually rated using percentage incidence categories: nil or 0, no infection visible; low, 1 to 33 percent of trees infected; medium, 34 to 66 percent infected; and severe, 67 to 100 percent infected. These data are converted to DMR by correlating roadside incidence ratings with plot DMR. A more direct and probably more efficient method is to directly estimate average DMR along roadsides rather than estimating percentage incidence.

To obtain inventory tree data, fixed-radius or prism plots are established at intervals of 5 to 10 km along roads at a distance 50 m back from the road. On each plot the usual inventory tree measurements are taken for each tree, including DMR (fig. 6-1). Although it is suspected that road development or some forest practices might have increased incidence of dwarf mistletoe at roadside units, Merrill and others (1985) found that incidence at roadsides was similar to that in the adjacent stand (also see Maffei and Beatty 1988).

Although a roadside survey is relatively easy to conduct and produces estimates of growth impacts, it is often difficult to reconcile these results with forest inventory data. Locating plots along roads introduces a sampling bias that may result in substantial discrepancies of tree species volumes and growth estimates between roadside plots and standard inventory plots. Data from a roadside survey as area infested or percent of trees infected cannot be readily incorporated into forest inventory record systems. A potentially more accurate and cost-effective alternative is to move directly to resampling already established forest inventory plots that also have a history of tree growth and mortality.

Transects and Grids

Sample plots systematically distributed as either strip transects or on a gird are another approach for surveying dwarf mistletoe. Transects and grid sampling have been used for landscape-scale surveys (Hawksworth and Lusher 1956, Maffei and Arena 1993), but they are more frequently applied to individual stands. Their use has been largely superseded by vegetation or inventory plots (for example, Current Vegetation Survey 2002).

Permanent Plots

Another type of dwarf mistletoe survey technique is the permanent sample plot system. Hawksworth and Marsden (1990) catalogue a number of these installations. Permanent sample plots are also established to monitor efficacy of management projects (Lightle and Hawksworth 1973). These plots typically are much larger than routine forest inventory plots, have fixed boundaries, and include a map of the position of all plot trees. Given the relatively high costs of establishment and remeasurements, relatively few permanent sample plots have been established recently or are currently being maintained. They are, however, extremely valuable for measuring spatial aspects of dwarf mistletoe spread and intensification and as benchmark stands used to validate simulation models (Taylor and Marsden 1997).

Project Area Assessments

Several methods or techniques for dwarf mistletoe surveys are used primarily to assess stands or sites for a variety of objectives including developing management prescriptions and management of recreation areas and wildlife habitat.

Developing Management Prescriptions—Detailed surveys of stands are used to develop management prescriptions (Tkacz 1989) and for general stand examinations (Mathiasen 1984, Vázquez 1994a).

For dwarf mistletoe infested sites, distribution and severity data are used to assess management options (Hawksworth 1978a, Parmeter 1978, van der Kamp and Hawksworth 1985). The expected effects of a treatment, for example, such as leaving dwarf mistletoe-infected trees on partially or selectively cutover areas, can be evaluated in the specific context in which it is to be applied. These effects can be projected with data representing the actual stand of interest and using the agency-supported growth model or simulation program (for example, PrognosisBC or Forest Vegetation Simulator). The data required from the survey are determined by the requirements of the selected model. Generally these include tree data, DMR (see fig. 6-1), and some ecological classification describing site productivity. Data are usually collected using a grid or series of prism plots or fixed-radius plots according to prescribe methods of the agency (DeMars 1980). Baker and Durham (1997) describe a transect survey for mistletoe in young jack pine and a model to simulate expansion of infection or mortality centers. Marsden and others (1993) evaluate management options for Southwestern ponderosa pine stands with Armillaria root disease and dwarf mistletoe with data from a systematic grid of inventory plots and the Forest Vegetation Simulator. Chapter 8 provides further information on use of models to evaluate silvicultural treatments.

When dwarf mistletoe sanitation practices are planned or have been undertaken, an important consideration is to determine both the potential and realized benefits. In many regions of Western North America, sanitation treatments after harvesting have been a common practice for several years or even decades. Postcontrol or postsuppression surveys and evaluations have been undertaken in several regions (Hawksworth and Johnson 1989b, Knutson and Tinnin 1986, Van Sickle and Wegwitz 1978).

The spatial pattern of infected trees and spatial autocorrelation of mistletoe are important in some situations (Robinson and others 2002). Infected young trees may be clustered around residual infected trees left as blocks, strips, or groups trees. Patterns that deviate greatly from random or uniform toward clusters have significant consequences for sampling design and model projections. The spatial pattern of infected trees and the spatial autocorrelation of mistletoe can be computed from a stem map of the stand of interest or selected from another stand with a similar appearance.

Assessing complex stands—that is, those consisting of two or more tree species, age classes, and height classes — often involves making a compromise between number of locations visited and the detail recorded at each location. Because the dynamics and effects of dwarf mistletoes vary by tree size, it is important that surveys provide data on incidence and severity by tree size class. This can be accomplished by recording DMR and either tree diameter or height for each sample tree and later computing class averages. Alternatively, trees can be grouped into classes and assigned average incidence and severity ratings while the observer is at the plot. With training and experience, observers are able to retain data quality and increase productivity. Vegetation structural stages such as described in table 6-2 or other classification schemes can be used to group trees into size classes. The criteria for determining classes vary by situation but represent canopy structure classes meaningful to the manager. Where there are several mistletoe species with different host tree species, mistletoe incidence and severity should be estimated by structure class for each susceptible tree species.

Assessments of Recreation Areas and Wildlife Habitat—Dwarf mistletoe effects on trees (chapter 5)—including suppression of tree growth, formation of large witches' brooms, and increased mortality—can be important considerations for management of recreation sites and for wildlife habitat. Occasionally, dwarf mistletoe surveys are required for evaluating the need for, or efficacy of, silvicultural treatments (see chapter 8) for these types of management.

Trees in recreation sites are regularly inspected for defects and evaluated for potential hazard to users and facilities (Hadfield 1999, Lightle and Hawksworth 1973, Scharpf and others 1988). Dwarf mistletoe infection is usually included in the inspections. In some areas, as described in chapter 8, infected trees are replaced with other less susceptible tree species. Severely infected trees are pruned to maintain tree vigor. Tree data generally recorded are DMR and an estimate of broom size if these are to be pruned. Infected trees are usually inspected annually or more frequently.

Surveys for dwarf mistletoe in conjunction with wildlife habitat are used for management (Marshall and others 2000) and research (Bennetts and others 1996, Parker 2001, Parks and others 1999a, Reich and others 2000). Information collected about mistletoe includes DMR and usually additional information on broom type, size, and location (Garnett 2002, Hedwall 2000, Tinnin 1998, Tinnin and Knutson 1985).

Table 6-2—Vegetation Structural Stages (VSS), an example of a classification system for describing dwarf mistletoe incidence and severity. (Table excludes VSS class 1, nonforested.)

VSS class	Size class (cm of d.b.h.)	Description
2	2–12.5	Seedlings/saplings
3	12.5–30	Young trees
4	30–45	Mid-age trees
5	45–60	Mature trees
6	60+	Old trees

Evaluations Using Dwarf Mistletoe Survey Data

After a survey is conducted to determine forest-level damage caused by dwarf mistletoe, one or more of several methods are used to project forest growth under different management regimes and evaluate impacts and potential benefits of management programs for dwarf mistletoes (see Power and D'Eon 1991).

One example of this type of evaluation is use of a whole-forest model such as FORPLAN or MUSYC. These models predict timber supplies and possibly other outputs such as wildlife habitat in infested stands under various management regimes. They determine potential returns and benefits of dwarf mistletoe control programs. Landscape or forest-level yield models require both extensive data on dwarf mistletoe occurrence and severity, and response curves based on individual land units or stands, similar to those proposed by Stage and others (1986) for root diseases.

To our knowledge, forest-level evaluations of dwarf mistletoe effects have not yet been reported but they should, however, be relatively simple to develop. Average curves can be developed for average stand conditions, using stand-level models with dwarf mistletoe effects. Growth curves for lodgepole pine infected by dwarf mistletoe are reported by Hawksworth and

Johnson (1989a) and van der Kamp and Hawksworth (1985) and are included in a review of forest growth models by Eav and Marsden (1988).

In evaluating effects of dwarf mistletoe, data used to construct the baseline or "healthy" stand growth curves should be examined. If temporary plot data were used, and plots were located without bias, then empirical growth curves may already include mistletoe effects. Stands that have been treated for dwarf mistletoe, therefore, should grow more than the baseline stands. Growth and yield data for landscape-level analyses, however, are often derived from remeasured plots selected to avoid dwarf mistletoe and other disturbances. If growth curves from these stands were used to represent operational conditions, they represent the growth of "healthy" stands or what is expected when dwarf mistletoe infestations are suppressed. In most analyses, these types of growth curves are usually reduced using one or more "operational adjustment factors" to account for unstocked or unproductive areas (such as swamps or rocky knolls). Tree volumes are also reduced using factors for waste and breakage during harvesting and internal wood decay in live trees. All of these factors and assumptions should be checked and verified as to the manner by which mistletoe effects were incorporated.

Another potentially important use of dwarf mistletoe survey data is to evaluate potential benefits of controlling or preventing effects of dwarf mistletoe on site productivity. Site productivity is one of the major factors affecting sustainability of the forest resource. For an example with lodgepole pine, mistletoe infection at moderate to severe intensities generally reduces growth to such an extent that a forest inventory based on mature trees would underestimate the site index or productivity. Foresters might not be particularly interested in dwarf mistletoe as such. If it were shown, however, that the productivity of the forest land base were substantially underestimated and underutilized and that it could be increased with sanitation, interest may rise.

Further Needs for Surveys and Evaluations

Large-scale, forest-growth projection methods need to be used and modified to accommodate analyses of the actual or potential benefits of dwarf mistletoe control programs. In many regions, more or supplementary data will have to be collected by well-trained personnel in conjunction with forest inventory sampling to provide a more credible basis for determining dwarf mistletoe effects and defining treatment opportunities.

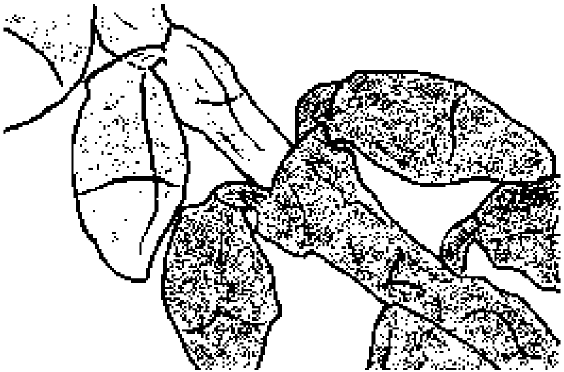
On an individual stand basis, information on spatial patterns of trees and autocorrelation of mistletoe need to be employed in more assessments (Robinson and others 2002). For many stands with complex structures and heterogeneity (see Reich and others 2000), an average DMR does not properly represent conditions where wildfire, windthrow, bark beetles, and mistletoe infestation have created a mosaic of canopy and gaps. Infected trees often occur in or at the edges of residual stands, strips, or patches, or as scattered individual trees; and spread of dwarf mistletoe from these sources is unlike that across a uniform stand (Muir 2002, Edwards 2002).

Detailed dwarf mistletoe surveys of land units are essential for determining effects on forest ecology, stand structure, and productivity or analyzing effectiveness and benefits of silvicultural treatment. These surveys and evaluations, however, are feasible only if foresters or specialists have access to methods or models endorsed by their agencies. Given the increasing complexity of forest management issues, comprehensive and detailed stand-level models are now essential to develop detailed prescriptions for harvesting and silvicultural treatments. These models are needed to ensure that forest ecosystems are managed sustainably and that these treatments do not detrimentally affect other management objectives such as visual quality, wildlife habitat, and recreation management. Although there have been considerable improvements in models in recent years, there is a continuing need for model development for new management scenarios. Access to several models is available from the British Columbia Ministry of Forests (2000) and Forest Health Technology Enterprise Team (2002); other vegetation management tools are at Forest Service (2002). Access to and support for various models are still needed for field foresters to conduct surveys and analyze potential benefits of treatment programs. This is particularly urgent with the increasing need to consider a wide array of effects and objectives such as wildlife and fuel reduction.

Finally, the increasing imperative to manage uneven-aged forest stands infested by dwarf mistletoe necessitates development of indices or measures of tree-to-tree variation of incidence and infection severity of dwarf mistletoe. New or drastically improved models are required to analyze the effects of dwarf mistletoes on trees and the efficacy of silvicultural treatments (including deployment of biological control agents) in these complex situations. Measurements of dwarf mistletoe occurrences and quantitative projections of effects of various forest and stand-level management regimes are essential to guide and help resolve the various, often-conflicting views of desirable forest-resource management strategies.

S. F. Shamoun
L .E. DeWald

Chapter 7



Management Strategies for Dwarf Mistletoes: Biological, Chemical, and Genetic Approaches

The opportunity and need for management of mistletoe populations with biological, chemical, and genetic approaches are greatest for application to the dwarf mistletoes. Although much information is available on these management strategies (see reviews by Hawksworth 1972, Knutson 1978), significant research and development are still required for these to become operational tools. In this chapter, we describe the potential for these tools and status of their research and development. Resource managers and practitioners interested in using these approaches can consult with forest pathologists and geneticists for specific applications.

Biological Control

Many fungi and insects are pathogens or herbivores, respectively, of dwarf mistletoes (Hawksworth and Geils 1996, Hawksworth and others 1977b, Kuijt 1963, Stevens and Hawksworth 1970, 1984). None, however, are sufficiently studied and developed for operational use as biological control agents (Anonymous 1982, Hawksworth 1972). Some fungal pathogens and insect herbivores (particularly lepidopteran larvae) are highly destructive to dwarf mistletoes in some areas and years. The factors that induce or regulate these outbreaks result from complex and often indirect interactions of weather and a multitrophic community of organisms. Dwarf mistletoe pathogens and herbivores are indigenous organisms that have coevolved with their hosts into relationships that are not readily amenable to human control. Nonetheless, given the potential number of agents and the advantages of the approach, development of biological control as a management option appears promising for the near future (Hawksworth 1972, Shamoun 1998).

Integrating Biological Control with Silviculture

Development of an effective biocontrol program requires technologies for mass production of the agent, an efficient delivery system, and a deployment strategy. The biocontrol agent does not have to eradicate all the dwarf mistletoe from the entire stand. A satisfactory strategy is to reduce mistletoe spread from residual trees in a regeneration area by timely introduction of biocontrol agents that kill or deflower the parasite. The selection of a treatment area and schedule is a silvicultural decision based an understanding of the epidemiology of the agent, the population dynamics of the mistletoe, and silvics of the host. The spatial-statistical model described by Robinson and others (2002) simulates mistletoe life cycles under various treatments and schedules and aids the selection of a preferred strategy. The objective is to protect new plantations from early mistletoe infestation where a significant number of infected residual trees are to be retained for various legacy values.

Insects

Initial research identifies several destructive insect predators that are apparently endemic to Pakistan (Baloch and Ghani 1980, Mushtaque and Baloch 1979), but no steps have been taken to test their applicability for introduction into North America. Other Asian dwarf mistletoes also harbor candidates for biological control of New World dwarf mistletoes (Tong and Ren 1980).

Fungi

The extensive literature on biological control of unwanted higher plants (weeds) is reviewed by DeBach (1964), TeBeest and Templeton (1985), Shamoun (2000), Wall and others (1992), and Wilson (1969). Mycoherbicides are developed practical tools in agriculture. Example mycoherbicides include: *Phytophthora palmivora* (DeVine,) for control of strangler vine in citrus (Ridings 1986), *Colletotrichum gloeosporioides* f. sp. *aeschynomene* (Collego,) for control of northern jointvetch in rice and soybean (Daniel and others 1973), and *Colletotrichum gloeosporioides* f. sp. *malvae* (BioMal, and Mallet WP™) for round-leaved mallow in field crops (Jensen 2000, Makowski and Mortensen 1992). *Chondrostereum purpureum*, a well-known primary wood invader, is being developed for biological control of woody vegetation in forests and rights-of-way (de Jong and others 1990, Shamoun and others 1996, Wall 1994). *Chondrostereum purpureum* (Chontrol™) may become the first biological control agent in North America used for integrated forest vegetation management (Shamoun and Hintz 1998). In South Africa, *Cylindrobasidium laeve* (Stumpout,) is used to clear Australian wattle tree (Morris and others 1998). Mortensen (1998) reviews a number of other products in development.

A particular challenge for application of mycoherbicides in controlling mistletoes is that death of the plant is not assured by destruction of the aerial shoots. The endophytic system of mistletoes within the host survives even when the shoots are killed back repeatedly; the endophytic system may persist for a century (Gill and Hawksworth 1961).

For a fungal parasite to be an effective biological control agent, it must possess a number of attributes (Mark and others 1976, Wicker and Shaw 1968):

1. It parasitizes only the target mistletoe, not the host or other vegetation.
2. Its activity seriously interferes with the life cycle of the mistletoe.
3. It produces abundant inoculum and significant infestations on the target mistletoe.
4. It has sufficient ecological amplitude to persistence throughout the range of the target mistletoe.
5. Its distribution coincides with that of the target mistletoe.
6. It exhibits high infectivity.
7. It shows high virulence.
8. It has an efficient mode of action for curtailing development of the target mistletoe.

Fungal parasites of dwarf mistletoe are of two general groups—those that attack aerial shoots and those that attack the endophytic system (canker fungi).

Although a large number of fungal parasites are associated with dwarf mistletoes (see Hawksworth and Geils 1996), there are no complete and comprehensive evaluations for most of these fungi, their hosts, and their interactions (Hawksworth and others 1977b).

Aerial Shoot Fungi—These fungi usually parasitize pistillate flowers, shoots, and fruits of certain spring-flowering species of mistletoe. Three of these fungi—*Colletotrichum gloeosporioides*, *Cylindrocarpon* (*Septogloeum*) *gillii*, and *Caliciopsis* (*Wallrothiella*) *arceuthobii*—are common and widespread in Western North America (Hawksworth and Geils 1996).

Colletotrichum gloeosporioides is commonly isolated from dwarf mistletoes in the United States and the Western Provinces of Canada (Kope and others 1997, Muir 1967, Wicker and Shaw 1968). Although different isolates of the fungus are distinct in mycelial growth, colony color, and sporulation, cross-inoculation experiments demonstrate that isolates are not host-specific (Scharpf 1964). *C. gloeosporioides* infections first appear as small, brown to black, necrotic lesions on the nodes of fruits and shoots (fig. 7-1 and 7-2). Lesions enlarge, coalesce, and cause dieback of the shoots (Parmeter and others 1959, Wicker and Shaw 1968). Parmeter and others (1959) observe that the fungus invades the endophytic system of *Arceuthobium abietinum*. Ramsfield (2002) did not detect the presence of the fungus in the endophytic system of *A. americanum*. Wicker (1967b) states that both sexes of *A. campylopodum* are attacked, and that from 35 to 67 percent of the plants or 24 percent of the shoots may be destroyed. Although the fungus may persist for years (Wicker and Shaw 1968), its occurrence is generally sporadic (Hawksworth and others 1977b). It can be destructive to *A. americanum* and *A. tsugense* subsp. *tsugense* in Western Canada (Muir 1967, 1977, Ramsfield 2002, Kope and others 1997). Muir (1977) concludes that it can exert significant natural control of *A. americanum*.

Figure 7-1—*Colletotrichum gloeosporioides* infecting shoots and fruits of *Arceuthobium tsugense*.

Figure 7-2—*Colletotrichum gloeosporioides* infecting shoots of *Arceuthobium americanum*.

Colletotrichum gloeosporioides is being developed as biocontrol agent of *Arceuthobium tsugense* and *A. americanum*. Successful projects to date include an *in vitro* bioassay system (Deeks and others 2001, 2002) and several laboratory and greenhouse experiments and field trials (Ramsfield 2002). The fungus is easily, inexpensively cultured and germinates over a wide temperature range (Parmeter and others 1959, Shamoun 1998). Its mode of action disrupts development of mistletoe shoots, thereby preventing reproduction. Because it attacks anytime after shoot emergence (Parmeter and others 1959), there is a broad window when the agent can be applied.

Cylindrocarpon gillii (formerly *Septogloeum gillii*) is a fungal parasite that causes anthracnose to staminate and pistillate shoots of dwarf mistletoes (Ellis 1946, Gill 1935, Muir 1973). The fungus and disease is recognized (fig. 7-3) by white eruptions at shoot nodes and conspicuous masses of hyaline, cylindrical to fusiform spores. The fungus parasitizes most dwarf mistletoes of Western North America (Hawksworth and others 1977b), including *A. americanum*, *A. douglasii*, and *A. tsugense* subsp. *tsugense* in Western Canada (Kope and Shamoun 2000, Shamoun 1998, Wood 1986). Mielke's (1959) inconclusive results from inoculating an isolate of a warm, dry climate to a cool, moist one suggest the need for proper climate matching when evaluating or using this fungus (Hawksworth and others 1977b).

Caliciopsis arceuthobii (formerly *Wallrothiella arceuthobii*) is the oldest known, fungal parasite of dwarf mistletoes. It attacks the spring-flowering mistletoes *Arceuthobium pusillum*, *A. americanum*,

Figure 7-3—*Cylindrocarpon gillii* infecting shoots and fruits of *Arceuthobium tsugense*.

A. douglasii, and *A. vaginatum* (Dowding 1931, Kuijt 1969b, Knutson and Hutchins 1979). Infection occurs at anthesis; stigmas are inoculated with ascospores carried by insects, wind, or rain. Within 2 months, hyphae penetrate the fruits to the ovary wall. Host cells deteriorate and are replaced by a black stromatic mass of hyphae (fig. 7-4). Normal fruit development and seed production are destroyed (Wicker and Shaw 1968). The fungus is widely distributed from Western Canada, United States, and Mexico (Hawksworth and others 1977b, Kuijt 1963). Parker (1970) demonstrates the fungus germinates and grows on artificial media. Its potential as a biocontrol agent, however, is limited by large, annual variations of infection. In a given location, natural infection will be high one year (80 percent of flowers infected) and fail (almost no infection) the next (Dowding 1931, Hawksworth and others 1977b, Weir 1915, Wicker and Shaw 1968).

Figure 7-4—*Caliciopsis arceuthobii* infecting the pistillate flowers of *Arceuthobium americanum*.

Other fungal parasites associated with aerial shoots of dwarf mistletoes are: *Alternaria alternata*, *Aureobasidium pullulans*, *Coniothyrium* sp., *Metasphaeria wheeleri*, *Pestalotia maculiformans*, *Pestalotia heteroercornis,* and *Phoma* sp. (Gilbert 1984, Hawksworth and others 1977b, Hawksworth and Wiens 1996, Kope and Shamoun 2000, Shamoun 1998). The potential use of these species as biocontrol agents requires additional evaluation.

Canker Fungi Associated with Endophytic System—The canker fungi of dwarf mistletoe attack both the cortex and endophytic system (Hawksworth and Geils 1996). More than 20 species of canker fungi are identified for *Arceuthobium tsugense* in British Columbia (Baranyay 1966, Funk and Baranyay 1973, Funk and others 1973, Funk and Smith 1981, Kope and Shamoun 2000, Shamoun 1998). Their potential as biological control agents includes both advantages and disadvantages. Because they attack the endophytic system, effects are immediate, pronounced, and likely to kill the mistletoe. Because the host tree may be damaged as well, additional laboratory study is required before field inoculations are attempted. Three canker fungi are good candidates for biological control.

Neonectria neomacrospora (formerly *Nectria macrospora*, *Nectria neomacrospora*) is characterized by a stroma with dark red perithecia containing eight-spored asci (Booth and Samuels 1981, Mantiri and others 2001). The conidial sporodochia (*Cylindrocarpon*) appear white and are found most commonly on freshly cankered swellings (fig. 7-5 and 7-6) caused by *Arceuthobium tsugense* (Funk and others 1973, Kope and Shamoun 2000, Shamoun 1998). Byler and Cobb (1972) report *N. neomacrospora* (as *N. fuckeliana*) is a virulent pathogen of *A. occidentalis* on *Pinus muricata*. The fungus is only weakly parasitic on pine and is secondarily parasitic on western gall rust cankers caused by *Peridermium harknessii*. *Cylindrocarpon cylindroides* is more virulent than *Colletotrichum gloeosporioides* on germinating seeds and callus of *Arceuthobium tsugense* (Deeks and others 2002).

The characteristics that recommend *Neonectria neomacrospora* as a biocontrol agent are its selectivity for dwarf mistletoe-infected host tissue, pathogenicity, ability to invade, rapid canker production, abundant spore production, reduction of shoot growth, girdling, and branch mortality. Further development involves improvements of formulation and delivery technologies (Funk and others 1973, Shamoun 1998, Smith and Funk 1980).

Cytospora abietis is the best known fungus associated with dwarf mistletoe cankers and is common (20 percent) on *Abies magnifica* and *A. concolor* parasit-

Figure 7-5—*Neonectria* canker of *Arceuthobium tsugense*. Note: symptoms of the disease are resinosis and necrosis of mistletoe shoots.

ized by *Arceuthobium abietinum* (Scharpf 1969a, Scharpf and Bynum 1975, Wright 1942). The fungus occasionally parasitizes nonmistletoe-infected branches. The overall interactions of the fungus, the mistletoe, and the host tree need to be evaluated. Although the fungus kills mistletoe-infected branches, it is not known how much the mistletoe population is reduced (Hawksworth 1972).

Resin Disease Syndrome—Resin disease syndrome is common on *Arceuthobium americanum* infecting *Pinus contorta* in the Rocky Mountains (Mark and others 1976). The symptoms include excessive resinosis of the mistletoe canker, necrotic lesions and discoloration of the host bark, and retention of dead needles, necrophylactic periderms, and dead mistletoe shoots. Numerous fungi are isolated from resin disease cankers. *Alternaria alternata* is the most consistent (recovered from 89 percent of cankers), but the syndrome appears to be a disease complex caused by *Alternaria alternata*, *Aureobasidium pullulans*, and *Epicoccum nigrum* (Mark and others 1976). However, Gilbert (1984) isolated these fungi from nonsymptomic mistletoe cankers and host wood; these fungi alone may not be the sole cause of the syndrome. Additional studies needed include: effects on reproductive potential of the mistletoe, comparisons for systematic and nonsytematic mistletoe infections, and assessments of environmental factors and each fungal component in disease development (Mark and others 1976).

Figure 7-6—*Neonectria neomacrospora* (anamorph: *Cylindrocarpon cylindroides*) infecting the basal cup and the swelling (endophytic system) of *Arceuthobium tsugense*.

Summary—Numerous studies of the mycobiotic associates of dwarf mistletoes are complete. The fungal parasites *Colletotrichum gloeosporioides*, *Cylindrocarpon gillii*, *Caliciopsis arceuthobii*, and *Neonectria neomacrospora* are effective in destroying aerial shoots or the endophytic system. They can disrupt the mistletoe life cycle and reduce dwarf mistletoe spread, intensification, and damage. Canker fungi are attractive biological control agents because they attack the mistletoe over a long period and infect the endophytic system. These canker fungi have the potential of killing the mistletoe in addition to reducing reproduction. The most promising biocontrol agents are *Colletotrichum gloeosporioides* and *Neonectria neomacrospora*.

Chemical Control

The development of a selective herbicide to control dwarf mistletoes has been a primary but elusive goal for decades. The fundamental challenge is to find a chemical that is easy to apply and kills the mistletoe without toxic effects to the host or other nontarget species. If the mistletoe cannot be killed, a second strategy is to cause abscission of shoots, thereby reducing and delaying spread and intensification.

Numerous lethal herbicides have been tested for control of dwarf mistletoes (Gill 1956, Quick 1963, 1964, Scharpf 1972). The most common chemicals investigated in early studies are various formulations of 2,4-D and 2,4,5-T. Typically, these chemicals are not effective at killing the mistletoe without also injuring the host. At low rates that do not damage the host, the endophytic system is not killed, and resprouting occurs. The most promising herbicide from a large study by Quick (1964) is an isooctyl ester of 2,4,5-T; but it is now banned for concerns over adverse, nontarget effects.

Hawksworth and Wiens (1996) review a series of tests from 1970 to the early 1990s with a number of herbicides and growth regulators including Dacamine, MCPA, Butyrac, Goal, Thistrol, D-40, Weedone, Emulsamine, DPX, Prime, and Florel. Although these chemicals cause high shoot mortality with minimal host injury, they also do not kill the endophytic system. Experiments to date with systemic chemical are inconclusive.

The most promising chemical for inducing shoot abscission is ethephon (Florel, active ingredient 2-chloroethyl phosphoric acid). The mode of action of ethephon releases ethylene, a natural growth-regulating chemical that causes early abscission of flowers, fruits, and shoots (Hawksworth and Johnson 1989b). Ethylene is a natural substance that dissipates quickly and shows few nontarget effects. It has been evaluated for numerous mistletoe–host combinations (Frankel and Adams 1989, Hawksworth and Johnson 1989b, Livingston and Brenner 1983, Livingston and others 1985):

- *Arceuthobium americanum* on *Pinus banksiana* in Manitoba
- *Arceuthobium americanum* on *Pinus contorta* in Colorado and California
- *Arceuthobium campylopodum* on *Pinus ponderosa* in California and Idaho
- *Arceuthobium campylopodum on Pinus jeffreyi* in California
- *Arceuthobium divaricatum* on *Pinus edulis* in New Mexico
- *Arceuthobium douglasii* on *Pseudotsuga menziesii* in Oregon
- *Arceuthobium laricis* on *Larix occidentalis* in Oregon
- *Arceuthobium pusillum* on *Picea mariana* in Minnesota
- *Arceuthobium vaginatum* on *Pinus ponderosa* in Colorado and New Mexico

An important consideration is achieving adequate coverage. Ground application can be effective (Johnson 1992, Johnson and others 1989, Nicholls and others 1987a, 1987b). Robbins and others (1989) and Baker and others (1989), however, report aerial applications by helicopter are not effective due to poor penetration. Most mistletoe infections are in the lower crown and protected from the spray by overhead host foliage.

With good coverage, shoot abscission rates of 90 to 100 percent are achieved (Johnson 1992). Limited, premature browning of older host needles may occur, but serious side effects on the nontarget host are few (Nicholls and others 1987a). Resprouting from the endophytic system, however, limits effectiveness (Parks and Hoffman 1991). When resprouting is rapid and extensive, long-term protection from mistletoe spread and intensification is not provided. With good control, mistletoe seed production is delayed 2 to 4 years; but it is not a permanent cure. Ethephon may be used to protect understory trees beneath an infested overstory in high-value areas (Adams and others 1993).

Summary

Investigations for chemical control of dwarf mistletoes have considered numerous herbicides intended to selectively kill the parasite or cause shoot abscission. No material tested warrants widespread application. Although the growth-regulating chemical ethephon is approved by the U.S. Environmental Protection Agency for control of dwarf mistletoes, it has limited use. Because the chemical does not affect the endophytic system, new shoots and fruits develop 3 to 5 years after application (or sooner). This chemical is most useful for high value trees at homes, offices, and parks, where frequent applications are possible, but pruning is not acceptable. A chemical treatment regime can be supplemented with various other cultural techniques such as underplanting immune species.

Management Through Selection for Genetic Resistance

Hanover (1966) describes the need for identification of heritable resistance and development of a controlled breeding program for genetic resistance to mistletoes. In the past, the relative low cost and ease with which mistletoes were controlled silviculturally delayed the development of these programs (Hawksworth and Wiens 1996). In general, trees suspected to be resistant to mistletoe are identified in the process of other management activities rather than through a deliberate search (Roth 1974a). A few scientists such as Frank G. Hawksworth, Lewis F. Roth, and Robert F. Scharpf have made consistent efforts to identify genetically resistance trees.

Native mistletoes can be relatively destructive in natural forests, and because tree species have been coevolving with mistletoes for 25 million years (Hawksworth 1978a), we can expect trees to have developed genetic resistance (Roth 1978). The existence of host-specific mistletoes and variation in host preference suggests a genetic basis of resistance, at least at the species level. *Arceuthobium douglasii* does not infect *Pinus ponderosa* (Hawksworth and Wiens 1996). Scharpf (1984) notes that two-thirds of dwarf mistletoes parasitize hosts in addition to a principal species; the levels of infection in these hosts are highly variable from secondary to rare for factors other than escape. *Arceuthobium pusillum* exhibits variation in ability to infect *Larix laricina*, *Picea glauca*, *Picea rubens*, *Pinus resinosa,* and *Pinus strobus* — all species naturally exposed to the mistletoe (Tainter and French 1971).

In contrast to our knowledge of species-specific susceptibility, within-species susceptibility to mistletoe has been less rigorously examined. Field observations of mistletoe-free trees in areas with high levels of mistletoe infection are reported for several host–mistletoe combinations. In Western North America, these reports include healthy *P. ponderosa* in areas heavily infected with *A. vaginatum* subsp. *cryptopodum* (Arizona and New Mexico, Hawksworth 1961); *P. ponderosa* and *P. jeffreyi* free of *A. campylopodum* (Oregon, Roth 1953; California, Scharpf 1984, 1987, Scharpf and Parameter 1967, Wagener 1965); *Pseudotsuga menziesii* var. *glauca* free of *A. douglasii* (Arizona, Nowicki and others, unpublished research); *A. americanum*-free *P. contorta* (Colorado, Hawksworth and Wiens 1996); healthy *Tsuga heterophylla* in areas heavily infected with *A. tsugense* (Vancouver Island, Smith and others 1993); and *Pinus hartwegii* free of mistletoe in heavily infected areas of Mexico (De la Puente 1966). Although the progeny of these “resistant” trees have not generally been tested for resistance, these field observations suggest variation of genetic resistance within host populations exists.

When trees suspected to be resistant to mistletoe are identified in the field, they may be tested by artificially inoculating grafts and out-planting grafted scions in a mistletoe-infested area. Scharpf and Roth (1992) report high correlation between resistant *Pinus ponderosa* parents and their scions grafted and out-planted in areas with heavy mistletoe infection. Artificially inoculated grafted *Tsuga heterophylla* trees from resistant and susceptible parents also show resistance correlations (Smith and others 1993). Although results of these studies using grafted material do not prove heritable resistance, they do verify resistance is being controlled genetically rather than environmentally. These sources represent good candidate trees for progeny tests of heritable resistance.

Progeny tests for inherited genetic resistance to mistletoes show mixed results. Some cases of field resistance represent escapes or other nonheritable mechanisms of resistance. The work of Roeser (1926) and Bates (1927) represents one of the first attempts to breed forest trees for disease resistance in the United States. Regrettably, there are no differences after 50 years in the incidence of infection between slow-growing, susceptible and fast-growing, resistant selections (Hawksworth and Edminster 1981). These results suggest that growth rate is not a reliable indicator of mistletoe resistance. Hawksworth and Wiens (1996) discuss the early results of an unpublished study by G. Fechner examining putative resistance of selected *P. contorta* seedlings. The infection rates 10 years after inoculation for putatively resistant families and susceptible families are similar (Geils, personal communication). Other progeny tests for mistletoe resistance show more positive results. Roth (1971, 1974a, 1974b) demonstrates that *Pinus ponderosa* seedlings from resistant parents have fewer infections and faster growth rates than those from more susceptible parents. Examination of these progeny tests 20 years later shows the same result (Scharpf and Roth 1992). Scharpf (1987) identifies *P. jeffreyi* trees with variation in field resistance; artificial inoculations on 7-year-old progeny from these parents indicate the resistance is heritable (Scharpf and others 1992). Finally, *Pseudotsuga menziesii* var. *glauca* progeny from healthy parents in heavily infested areas had fewer infections than progeny from infected parents. Subsequent genetic laboratory analysis using allozymes support a heritable basis for this apparent resistance (Nowicki and others, unpublished research).

Attempts to identify inherited mechanisms controlling resistance to mistletoe are few. Genetic resistance to pathogens and insects in general is classified as “vertical,” where specific resistant genes have developed, or as “horizontal,” where aggregate combinations of genes have developed to create a phenotypic response. Roth (1974a and 1974b) suggests that horizontal resistance is more likely controlling resistance to mistletoe in Western conifers. Age-related changes may confer some resistance to mistletoe in pines (Roth 1974b, Scharpf and Roth 1992), but younger true fir trees appear to be more resistant to mistletoe than older individuals (Scharpf 1984). Anatomical changes associated with age are under a high degree of genetic control and may serve as a clue for locating genetically controlled resistance mechanisms. In *Larix laricina*, the formation of a wound periderm that restricts endophytic growth of *Arceuthobium pusillum* is identified as a resistance mechanism (Tainter and French 1971); however, inheritance of the wound periderm response has not been demonstrated. Atsatt (1983a) suggests resistant hosts may produce chemicals that inhibit mistletoe or lack chemicals needed by the mistletoe to initiate and/or develop haustoria formation. In general, production of secondary chemicals is a common, genetically controlled, defense strategy used by plants; secondary chemicals may play a role in genetic resistance to mistletoe.

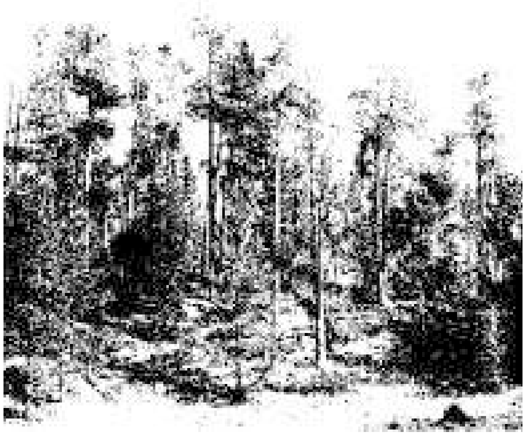
Summary

Despite the relatively limited investigation, there are field observations, progeny tests, and graft studies that all point to the presence of some degree of resistance to mistletoe in North American conifers. The recent need to develop options to traditional, even-aged silvicultural treatments has led to the renewed interest in developing genetic and breeding programs for resistance to dwarf mistletoe. Field identification of resistant sources, progeny testing to confirm heritably, plus screening and breeding programs such as exists for blister rust (*Cronartium ribicola*) are critically needed for a genetic strategy to become a viable. A screening program is being developed by Ringnes and others (1996). The objectives of this program are to identify trees exhibiting resistance to dwarf mistletoe, to evaluate testing methods for screening candidates, to identify resistance levels of candidates and their progeny, and to determine the mode and strength of inheritance for resistance mechanisms. Additional mistletoe resistance screening programs for *Pseudotsuga menziesii* var. *glauca* (DeWald and Nowicki Northern Arizona University, Flagstaff, AZ), and *Tsuga heterophylla* (Shamoun, Canadian Forest Service, Pacific Forestry Centre, Victoria BC, Canada) have been initiated. Finally, biotechnology approaches (including tissue culture, see Deeks and others 2001, Marler and others 1999) can be used to supplement traditional resistance screening and breeding programs. Trees whose resistance to mistletoe has been confirmed can be searched for molecular DNA markers. These markers can then be used in marker-aided selection for mistletoe resistance to eliminate the long generation times currently needed to confirm genetic resistance.

J. A. Muir
B. W. Geils

Chapter 8

Management Strategies for Dwarf Mistletoe: Silviculture



Although there are numerous sources for information on the practice of silviculture (Forest Service 2002), special considerations are required for control of dwarf mistletoe (Scharpf and Parmeter 1978). Mistletoe-infested forests, stands, and trees develop and respond to treatment differently than their uninfested counterparts (chapter 5). The spread, intensification, damage, and impacts of dwarf mistletoe can be reduced, maintained, or enhanced by silvicultural treatments alone or in combination with other control techniques (chapter 7). Silvicultural treatments discussed here include:

- Harvest, retention, and regeneration by clear-felling (even-aged silviculture), or selection harvesting to establish and maintain uneven or all-aged stand structures.

- Design and layout of harvest and treatment blocks.
- Site preparation and vegetation management by brushing, prescribed burning, and other methods.
- Planting or retaining residual and advanced regeneration.
- Thinning and sanitation.
- Pruning brooms and infected branches.

General guidelines for silvicultural treatment that integrate dwarf mistletoe information are presented in symposium proceedings (Scharpf and Parmeter 1978), regional directives (British Columbia Ministry of Forests 1995), and compendia (Alexander 1986). New strategies may be suggested and examined with simulation models (Robinson and others 2002), then tested and evaluated in practice at demonstration forests (Besse and others 2001, Edwards 2002, Nevill and Wood 1995).

The choice to initiate a silvicultural action, and the subsequent selection of techniques, timing, and location, are dictated by considerations in three major areas. First, each dwarf mistletoe species, forest type, and region present different situations. Some mistletoes have a wide distribution and cause serious damage; others are rare curiosities, spread slowly, cause little damage, or even enhance some aspect of the environment (chapter 5). Second, management objectives and constraints for individual stands (or sites), compartments (planning units), and whole forests determine the intended purpose of the treatment. Different objectives require different approaches. Objectives may be to produce timber and fiber (British Columbia Ministry of Forests 1995), enhance wildlife habitat (Reynolds and others 1992), or even promote wild mushroom production (Amaranthus and others 1998). Finally, any action must be consistent with an overall plan of forest regulation and a silvicultural system for regeneration. With even-aged silviculture, clear-felling, shelterwood, and seed tree harvests, planting, sanitation, and intermediate thinning all provide opportunities to direct stand and mistletoe development. With uneven-aged silviculture, tree and group selection determine forest character. Fuel management and prescribed burning may be used in both systems. Aesthetic values and economics may allow special cultural practices such as pruning to be used on high value trees such as found in recreation areas.

In this chapter, we describe silvicultural treatments that have been recommended or are used to prevent, mitigate, or encourage dwarf mistletoe development and effects. We provide examples of frequently encountered management situations. The discussion is organized into six topics. In *Designing Silvicultural Treatments*, we describe biological and ecological factors that apply to silvicultural decisions, especially the features that make mistletoes amenable to treatment. We also identify sources for species-specific guidelines. For *Management of Even-aged Stands*, we describe the strategies used primarily to prevent or reduce detrimental effects of dwarf mistletoes on timber and fiber production. The first and best opportunity is to prevent mistletoe spread into a clean, regenerated stand. Established stands with mistletoe present can still be treated with sanitation, thinning, harvesting, or be reestablished. In the discussion of *Uneven-aged Silviculture and Selection Cutting*, we recognize a shift in forestry to management for ecosystem structure and functions, retention of old-growth forest character, wildlife habitat, recreation, and other amenity values. Although we have less research and management experience for this kind of management, mistletoe can play a large role in determining whether those objectives are met. Techniques and tools are available for influencing the patterns and rates of mistletoe spread and intensification. *Prescribed Burning* is an especially useful tool for either even-aged or uneven-aged silvicultural systems. Regardless of the treatment considered, a manager needs to be aware of the likely responses to a proposed action. Because mistletoes add complexity and because the consequences of specific decisions may not be apparent for decades, managers can use *Models to Assess Treatment Opportunities*. Finally, in *Management for Recreation, Wildlife, and Ecosystem Values*, we describe some of the special requirements and techniques applicable to infested stands and trees managed with these objectives.

Designing Silvicultural Treatments

Dwarf mistletoes markedly affect the growth, form, and survival of infected trees and therefore how these trees and their stands develop and respond to silvicultural treatment (chapter 5). Effects to trees include: distorted growth from branch and stem infections, changes in wood quality, reduced overall tree growth, increased susceptibility to attack by secondary insects and fungi, and increased mortality. These damages aggregate over time, affecting forest health, sustainability, and productivity (DeNitto 2002, Hawksworth and Shaw 1984, Monning and Byler 1992). Consequently, mistletoes affect the basic ecological processes of primary productivity, biomass allocation, mortality, mineral recycling, and succession (Kipfmueller and Baker 1998, Mathiasen 1996, Tinnin and others 1982, Wanner and Tinnin 1989, Zimmermann and Laven 1984). Because significant infestations of dwarf mistletoe have profound, fundamental, and particular effects on stands, mistletoes need to be specifically considered in designing silvicultural treatments on infested sites (fig. 8-1).

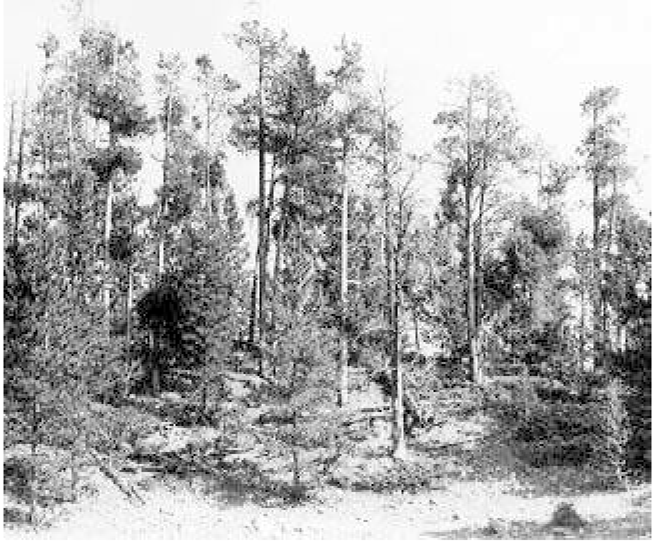


Figure 8-1—A portion of lodgepole pine stand in the Bighorn Mountains, Wyoming. As evidenced by the numerous, large witches' brooms, most trees are severely infected with *Arceuthobium americanum.* If the management objective were timber-oriented, this stand is a good candidate for regeneration and a poor candidate for commercial thinning. Fuel distribution and canopy structure depart greatly from what would be expected in an uninfested stand with significant consequences to fire and wildlife objectives.

Dwarf mistletoes and the forest stands at risk of infestation develop at a pace that appears slow from a human perspective but not from that of the host trees. For example, a rule of thumb for spread of a mistletoe infestation is 10 m per decade (Dixon and Hawksworth 1979); intensification in trees is one DMR class per decade (Geils and Mathiasen 1990); half-life of DMR class-6 trees is one decade (Hawksworth and Geils 1990). [Note: many factors influence rates of spread, intensification, and mortality. These rules of thumb are meant only to suggest the magnitude of the rate of change and are not intended as specific management guidelines.] With stand replacement times of one to two centuries, mistletoes are able to produce tens of generations and increase unchecked at a low exponential rate. Noticeable effects are delayed until infection reaches a moderate level, but damage accumulates at an increasing rate after that point (Hawksworth 1961, Tinnin and others 1999).

The potential impacts of dwarf mistletoe infestation and their dynamics have several implications for designing silviculture treatments. First, over time a treated stand that remains infested will develop differently than an uninfested stand. Second, early and frequent interventions provide greater opportunities to affect stand and infestation dynamics and impacts than later or infrequent entries. The timing and number of entries are, of course, determined by other factors as well. Therefore, an early treatment assessment (such as immediately after completion) may not provide a satisfactory indication of its long-term consequences without an adequate model.

Several biological and ecological features make dwarf mistletoes especially amenable to silvicultural treatment (Hawksworth 1978a, Parmeter 1978). The epidemiological bases of these features are discussed in chapters 4 and 5; here we suggest their silvicultural implications:

- *Obligate parasitism*. Dwarf mistletoes require a living host to survive and reproduce. When an infested tree or branch dies (or is cut), the attached mistletoe plants die as well. There is no need to burn or destroy slash or pruned branches to kill and sterilize the pathogen.
- *Host specificity*. Dwarf mistletoes generally infect only a single, susceptible host species or group of related species. Retained immune and less susceptible hosts reduce spread and severity of damage.
- *Extended life cycles*. Life cycles of dwarf mistletoes are relatively long compared to other tree disease agents; a generation ranges from 2 to 10 or more years. Dwarf mistletoe spread from tree to tree, and increase within tree crowns is relatively slow. Because numerous infections are required to cause serious damage, the effects accumulate slowly. Time is available to plan and implement a treatment regime.
- *Limited seed dispersal*. Dwarf mistletoe seeds are dispersed a maximum horizontal distance of only 10 to 15 m; gravity and foliage limit effective spread in the vertical and horizontal planes; animal vectoring of dwarf mistletoe (with one or two exceptions) is rare enough to be ignored other than from ecological and evolutionary perspectives. Consequently, mistletoe tends to occur as pockets of infestation. Spatial variation in mistletoe abundance provides numerous patches in which different, appropriate treatments can be applied. Even with severe infestations, the amount of mistletoe seed produced is limited; small, young understory trees present a minimum target. There is an opportunity to regenerate a stand under an infected overstory before the young trees are infected.
- *Slow intensification within tree crowns*. Dwarf mistletoe infection typically begins in the lower tree crown, and vertical spread is slow enough that trees with rapid height growth can outgrow or at least keep pace with mistletoe intensifica-

tion (Hawksworth and Geils 1985, Roth 1971). Good sites for tree growth allow rapid height growth at higher stand densities, which has several effects on mistletoe. Greater crown closure reduces light within the canopy, reducing mistletoe reproduction and increasing the rate of crown lift; the distance of seed dispersal in a dense stand is also reduced (Shaw and Weiss 2000). At some point, however, for each stand, competitive effects impact tree growth, and eventually trees reach their height limit. Density management and pathological rotation allow silviculturalists to influence the balance between growth of the host and the pathogen (Alexander 1986, Barrett and Roth 1985, Muir 1970, Safranyik and others 1998).

The silvicultural guidelines and treatments we discuss here can only be of a general nature. The literature on damage and control is already summarized by Hawksworth and Scharpf (1978) and suggests that different mistletoes in different regions require different approaches. Recent silvicultural guides with recommendations for mistletoe-infected trees and infested stands are available for some of the principal conifers of North America (table 8-1). There are also regional guides: British Columbia Ministry of Forests (1995), Conklin (2000), Hadfield and Russell (1978), Knutson and Tinnin (1980), and Wicker and Hawksworth (1988). Numerous older publications emphasize methods for reducing dwarf mistletoe populations and damage including: Buckland and Marples (1953), French and others (1968), Gill and Hawksworth (1954), Hawksworth and Lusher (1956), Kimmey and Mielke (1959), Korstian and Long (1922), Wagener (1965), and Weir (1916b). Although dwarf mistletoes cause significant growth losses and mortality in Mexico, we know of only a few publications that discuss silvicultural treatment of Mexican conifers in general terms (Hernandez and others 1992, Reid and others 1987).

Where silviculture dwarf mistletoe management is conducted, treatments to mitigate mistletoe impacts can be integrated with other activities to reduce susceptibility to forest insects, other diseases, and fire. The complex interactions between mistletoes and bark beetles are reviewed by Stevens and Hawksworth (1970, 1984) and include situations where reduction of mistletoe also results in reduction of hazard to bark beetles. Thinning stands to reduce bark beetle hazard presents an opportunity for mistletoe sanitation. Although the effect on the mistletoe infestation was minimal, Vandygriff and others (2000) describe an attempt to relocate bark beetle attacks with aggregant baits to mistletoe-infected trees. Marsden and others (1993) explore the options for management in a stand infested with both root disease and mistletoe. This is

Table 8-1—Silviculture guides for management of North American conifers with dwarf mistletoe.

Forest type	Host species	*Arceuthobium* sp.	References
Black spruce	*Picea mariana*	*A. pusillum*	Johnson (1977) Ostry and Nicholls (1979)
California true fir	*Abies concolor* *Abies magnifica*	*A. abietinum*	Filip and others (2000) Scharpf (1969b)
Douglas-fir	*Pseudotsuga menziesii*	*A. douglasii*	Hadfield and others (2000) Schmitt (1997)
Lodgepole pine	*Pinus contorta* var. *latifolia*	*A. americanum*	Hawksworth and Johnson (1989a) van der Kamp and Hawksworth (1985)
Pinyon pine	*Pinus edulis* *P. monophylla*	*A. divaricatum*	Mathiasen and others (2002a)
Sugar pine	*Pinus lambertiana*	*A. californicum*	Scharpf and Hawksworth (1968)
Western hemlock	*Tsuga heterophylla*	*A. tsugense*	Hennon and others (2001) Muir (1993)
Western larch	*Larix occidentalis*	*A. laricis*	Beatty and others (1997) Taylor (1995)
Western pines	*Pinus jeffreyi* *Pinus ponderosa*	*A. campylopodum*	Schmitt (1996) Smith (1983)
Rocky Mountain ponderosa pine	*Pinus ponderosa* var. *scopulorum*	*A. vaginatum* subsp. *cryptopodum*	Conklin (2000) Lightle and Weiss (1974)

an especially complex situation because trees killed by mistletoe or cut for mistletoe reduction provide stumps, which are the food base for root disease; simulation models are especially useful in such cases. We later discuss prescribed burning as a tool for mistletoe management, but it can be noted here that fuel reduction by cutting or burning can also reduce mistletoe. Applications of direct mistletoe control by chemical and biological means and genetic selection (see chapter 7) can be considered an adjunct to traditional silviculture treatments with the chain saw, planting bar, and drip torch.

An important consideration in the design of a silvicultural entry is whether dwarf mistletoe treatment is necessary. In many cases the presence of dwarf mistletoe poses no threat to stand objectives. The mistletoe may be infrequent and have a low potential for increase and damage. Mistletoes may not be a concern at their altitudinal or geographic range limits (Trummer and others 1998) or where conditions permit rapid tree growth (such as with ponderosa pine in southern Colorado). Where wildlife objectives take precedence, retention of some dwarf mistletoe may even be desired to generate snags (Bennetts and others 1996) or mistletoe brooms (Parks and others 1999a).

Management of Even-Aged Stands

Even-aged, single-storied stands composed of one or two tree species are the simplest to treat for mistletoe. Prevention of dwarf mistletoe infestation in a regenerated stand is essentially guaranteed where all susceptible host trees are harvested or killed soon after harvest.

Most early guidelines assume the objective of management is timber production, and the purpose of treatment is the timely and economical eradication of dwarf mistletoe (Korstian and Long 1922, Weir 1916a). The traditional recommendation for dwarf mistletoe has been clear-cut harvesting with relatively large blocks, followed, if necessary, by intermediate thinning and sanitation to create even-aged stands free of mistletoe (Wicker and Hawksworth 1988). This method has been used extensively and successfully for many Western and Northern species (but see Johnson 1994, Stewart 1978). Treatment before or after harvest removes or kills infected and suspect trees to prevent the young stand becoming infested.

Prevention of Spread Into Cut Blocks

One of the primary issues of dwarf mistletoe treatment in even-aged silviculture is the design and layout of cut blocks (treatment units) to prevent or reduce invasion of dwarf mistletoe from adjacent infested areas. Preventative measures recommended by previous authors and some agencies include:

- Wherever possible, locate cutting boundaries in noninfested stands, nonsusceptible timber types, and natural or created openings, and take advantage of natural or constructed barriers such as roads, streams, openings, or meadows.
- Design cut blocks within infested stands to create large ratios of area to perimeter and minimize the length of infested border; avoid long, narrow blocks and units of less than 8 ha, but compromise where required for natural regeneration of heavy-seeded trees (Alexander 1986).
- Unless local, long-term, successful plantings have been demonstrated, do not plant barriers of nonsusceptible tree species around the cut block perimeter. In the majority of cases, this strategy fails because of rapid natural regeneration and fast growth of the susceptible tree species; however, in a few exceptions, a mixture of nonsusceptible tree species has retarded mistletoe spread.
- If infected trees are to be left on the boundary, avoid leaving fringes or narrow strips but rather maintain dense blocks of trees and leave a relatively uniform, abrupt (nonfeathered) margin. In British Columbia and Alberta, mistletoe spread into an adjacent young stand appears retarded from dense stands with abrupt edges (Muir 1970). Where spread and infection of young trees occurs, remove or kill infected trees at the next treatment entry.
- Avoid leaving single trees or small clumps of residual infected trees scattered throughout the harvested area. Scattered overstory trees are a significant inoculum source for young, understory regeneration, because improved light or growing conditions favor production and dispersal of dwarf mistletoe seeds (Muir 1970, 2002). Remove or destroy these trees.
- When regenerating stands with seed tree or shelterwood systems, select residual trees that are mistletoe-free or only lightly infected (DMR 2 or less). If infected trees are left, remove them before regeneration reaches 1 m in height or about 10 years of age, or prune residual seed trees to remove infected branches. Because of its deciduous habit and ability to produce epicormic, adventitious branches, larch can be severely pruned.

Silvicultural Treatments of Young Stands

When an even-aged, immature stand is already infested by dwarf mistletoe, management options are available to reduce mistletoe at one or more stages of early stand development. Factors involved in evaluating the need, kind, and timing of treatment include stocking level, growth rate, and disease level. Although mistletoe may kill some small trees in young stands, infections are usually too recent and too light to cause much growth loss; damage is a poor management indicator. More important is the potential for future, unavoidable damage as indicated by the areal extent of the infestation, the percent of trees infected, and the rate of spread. In general, treatment options for mistletoe control are to remove infected overstories, favor nonsusceptible tree species, sanitation, and thinning.

Recently Harvested and Regenerated Stands—The best opportunity for preventing reinfestation of an area by dwarf mistletoe is through complete harvest, removal, or killing of infected trees of the previous stand. This opportunity may be exercised during or soon after the harvest and regeneration period. Although the length of time and size of seedlings before which they are at serious risk of infection vary by species and site, few are infected before they are 5 to 15 years old or about 1 m tall (Wicker 1967a). The decisions to be made on the basis of management objectives and specific situation are the number of infected residual trees to be retained and the length of time they remain.

The most important means by which a regenerated stand becomes infested is through infected residual trees left on site. In decreasing order of importance, infected advanced regeneration, spread from adjacent stands (see above), and long-distance animal vectoring play lesser roles. Trees are intentionally retained for a number of reasons, even though some of these trees may happen to be infected. For example, visual quality, screening, and wildlife objectives may call for the retention of “legacy” trees. The potential for these trees to survive and fill their role must be weighted against their possible contribution to the infestation of the new stand. Total eradication of mistletoe-infected trees is neither realistic nor necessary; a sufficient goal of sanitation can be to allow for effective mistletoe management. A new stand with some infested legacy trees can still be treated with periodic sanitation thinning (see below) to selectively remove more severely infected trees and by pruning infected branches.

Some residual trees are left not for legacy objectives but because they have no merchantable value. Many timber contracts and silviculture prescriptions stipulate the felling of diseased, nonmerchantable trees for safety and forest health reasons. If undesired residual trees remain after harvest, remedial work may be appropriate. For mistletoe control purposes alone, only residuals over 3 m in height with branch infections need to be felled; shorter trees and those with only bole infections have limited potential for spreading the pathogen (Mark and Hawksworth 1974).

Another option for controlling mistletoe infestation in a new stand is to regenerate with a mixture of species including trees less susceptible to mistletoe. Robinson and others (2002) report on simulations of stands infested by *Arceuthobium tsugense* and regenerated under three different scenarios including a 20 percent mixture of an immune species (cedar). Their simulations suggest that over time, mistletoe incidence (percent infected) and severity (DMR) are less for the 20 percent mixture compared to the other scenarios. Different mixtures may be better in other situations.

Sanitation Thinning—The purpose of sanitation thinning is to reduce mistletoe incidence. As trees increase in size, stands can benefit from silvicultural thinning to select crop trees and distribute growth to those individuals. Sanitation is conducted in young stands; silviculture thinning with sanitation is practiced in precommercial and commercial stands. Sanitation is most practical in young stands after initial infection appears but before subsequent spread occurs. A postregeneration survey is useful to determine stocking and the distribution and incidence of infection (see chapter 6). A decision is required as to whether there is sufficient stocking of noninfected, potential crop trees. The options are for sanitation or for destruction and reestablishment of the stand. A third option is, of course, to redefine management objectives that reset the decision criteria for selecting a treatment. Each situation requires appropriate assessment because of the ecological and economic constraints of different management objectives, different hosts, and mistletoes with different potentials for growth and damage. Numerous sanitation and thinning studies and computer simulations suggest a few general guidelines where the manager wishes to minimize mistletoe damage and maximize tree growth.

Sanitation is most effective in lightly infested stands younger than 15 to 30 years old. At early ages, infection percentages are less; at later ages potential crop trees can be selected. In the past, most timber stands less than 30 years old were sufficiently stocked (over 1,200 stems per ha) and infested at a low enough percentage (10 to 20 percent) that sanitation was feasible. A sanitation treatment that removes all visibly infected trees can significantly reduce an infestation (Hawksworth and Graham 1963b); but due to latent infections, missed trees, and spacing requirements, complete elimination of mistletoe is unlikely (Conklin 2002). A sanitation treatment usually retains the best, apparently mistletoe-free trees and whatever additional lightly infected trees are required to meet stocking and spacing standards. Mistletoe is sometimes found as a light or moderate infection (DMR 2 or 3) in the larger of the young trees. Given the potential for future spread and growth loss, these initially larger trees may not be as desirable for retention as smaller healthy trees. For stands about 40 years old and with few patches of infected trees, approximately 1,200 healthy stems per hectare on good sites are sufficient to retard mistletoe spread.

The effectiveness of sanitation is doubtful in heavily infested young stands. Although stands about 20 years old with half or more of the stems infected may sometimes be encountered, they are poor candidates for sanitation (Scharpf and Vogler 1986). These stands generally do not have a sufficient number of healthy trees to stock the site. Severely infected trees (DMR 3 to 6) do not sufficiently respond to spacing, and reducing stand density may increase mistletoe spread and intensification. Generally, the degree of infestation in the stand, not strictly stand age, is the best criterion to decide whether sanitation is practical. For example, a general rule for lodgepole pine is that stands with more than 40 percent of the trees infected (average stand rating greater than DMR 0.5) are too heavily infested for sanitation. In these stands, removing all infected trees reduces stocking below minimal standards and depresses yields (Hawksworth 1978b). An alternative is stand replacement by clear-cutting, roller chopping, or prescribed burning.

Thinning Precommercial Stands—Whether or not an early sanitation treatment was conducted, the standard practice of precommercial thinning conducted in some forests—even for healthy stands—provides an opportunity to promote tree growth and reduce mistletoe spread and intensification. For infested stands, the usual criteria for scheduling and marking thinning treatments are supplemented with several mistletoe-related considerations. The silvicultural evaluation that precedes the drafting of a prescription can include an assessment of the size and location of patches of infected trees within a stand, approximate number and location of infected residual trees, and number of potential crop trees. An intensive, systematic survey can provide these data (see chapter 6).

Silviculturalists need to balance two results of thinning that work in opposition to one another. First, spacing reduces tree-to-tree competition and over a density range stimulates height growth and crown lift. Second, opening a canopy also stimulates mistletoe shoot growth, seed production, spread, and intensification (Hodge and others 1994). In practice, thinning is most likely to favor the host where trees are no more than moderately infected (less than DMR 3) and growing in height faster than the vertical spread of the mistletoes (Barrett and Roth 1985, Parmeter 1978, Roth and Barrett 1985). In a similar finding, Hawksworth (1978b) found that thinning in stands less than moderately infested (40 percent incidence) and on better quality sites can produce satisfactory volumes, but not on more severely infested stands or on poor quality sites. As with sanitation, replacement and acceptance are options for stands that cannot be satisfactorily thinned. The sale of merchantable timber may be available to help offset cleaning and reforestation of immature, severely infested stands. Simulation models are useful for particular situations (Hawksworth 1978b, Strand and Roth 1976) and help managers to better understand the range of outcomes that are likely to follow from specific activities.

Sanitation—removing as many infected trees as practical—is usually an integral part of precommercial thinning. For stands where average tree diameter exceeds 5 cm, the prethinning evaluation can include an assessment of potential crop trees. The priority for crop trees depends on species but is often set as:

1. Noninfected dominant and codominant trees.
2. Dominant and codominant trees with mistletoe confined to branches in the lower one-third of live crown (DMR 2 or less).
3. Dominant and codominant trees with mistletoe confined to less than one-half of the branches in the lower two-thirds of the live crown (DMR 3 or less).
4. Intermediate trees with no visible infection.

In mixed species stands where immune or less-susceptible species are available, their priority for retention can be determined by their intrinsic value plus their disease-mitigation value. If acceptable stocking cannot be obtained, alternative objectives and treatments can be considered. Thinning crews must be able to recognize mistletoe infections if a sanitation objective is to be realized. Economics may permit a single precommercial treatment but are unlikely to support additional entries until there is a commercial opportunity. Although usually considered in the context of uneven-aged management, forest health and fuel reduction treatments may be justified as well in young or old even-aged stands.

Commercial Thinning Treatments

As trees reach commercial size and the stand approaches harvest (rotation) age, a different set of concerns and opportunities are presented to the manager. As before, information on mistletoe distribution is useful, but as the infestation develops, disease level as average DMR becomes more relevant than percent of trees infected. Trees rated with a DMR of 3 or greater exhibit growth loss, greater mortality, reduced reproductive capability, and increased potential for mistletoe spread. Trees may be harvested at intermediate thinnings, shelterwood cuts, or at rotation. Simulation programs that project final, cumulative yields can be used to assess the number, timing, and severity of thinnings, to select the kinds of trees to harvest at various entries, and to set the regeneration schedule. Mistletoe factors can be integrated into these simulations to address specific situations.

Thinning trials and simulations suggest three general guidelines for management at this stage (Filip and others 1989, Hawksworth 1978b, Hawksworth and others 1977a, Knutson and Tinnin 1986, Tinnin and others 1999). Intermediate thinning in stands with an average DMR rating of 3 or greater is not practical. As most trees are infected, stocking requirements cannot be met with healthy trees; many trees are so severely infected that growth responses are poor. These stands can be considered for early harvest and regeneration. Because severely infected trees of DMR 5 or 6 show little growth and have a high risk of mortality, they can be removed at any opportunity. Within 10 to 20 years of harvest, however, other sanitation and thinning treatments may be deferred. An important consideration is the early selection of potential seed trees for regeneration; uninfected host trees and nonsusceptible species are usually preferred.

Uneven-Aged Silviculture and Selection Cutting

Because the spread and intensification of dwarf mistletoe in uneven-aged, multistory strands can be quite rapid, management of these stands is a serious challenge. But they also present opportunities. Dwarf mistletoe spread is greatest when seeds rain down from an infested overstory to a susceptible understory. With greater crown closure and competition, understory trees do not increase rapidly in height and are less likely to outgrow the mistletoe. Managers, however, do have several factors to work with. Uneven-aged, multistory stands are usually a mosaic of different size and density of trees and mistletoes. These patches can be used to isolate pockets of mistletoe. Such stands are also often composed of several tree species with a range of susceptibility to the prevalent mistletoe. Nonhost species provide not only immune stocking but also screening, which reduces mistletoe spread. Selection for greater species diversity has numerous, ecological benefits.

Management in uneven-aged stands consists of frequent entries for harvest or improvement thinning. If these entries are timely and removals sufficient, sanitation can check mistletoe spread, intensification, and damage. Several cautions are warranted, however. Mistletoe spread can be several times faster than managers expect from their experience in even-aged strands. Overtopped or severely infected trees (DMR 3 or greater) grow at reduced rates and do not outgrow mistletoe. Periodic entries at 10- to 20-year intervals with modest sanitation may be adequate to check mistletoe; but in 30 to 40 years without control, it can spread throughout the stand. Writing a prescription and marking trees in these stands requires a high skill level to detect mistletoe, recognize its potential, and select the proper action.

Guidelines for uneven-aged management are available (Mathiasen 1989, Conklin 2000). In principle, many of the suggestions described in previous sections for even-aged stands are applicable here also. The goals are to maintain individual tree ratings at DMR 3 or less and prevent infection in the top of the crown. Diligence and thoroughness can be major obstacles in applying treatments, and monitoring is important (Merrill and others 1998). One of the key considerations in uneven-aged management is whether silvicultural treatment (cutting trees) maintains the height growth of remaining trees at a rate that exceeds mistletoe vertical spread. Where trees outgrow the mistletoe and infections remain in the lower crown, impacts on tree growth are generally insignificant (Hawksworth 1978b, Parmeter 1978). For coastal hemlock, Richardson and van der Kamp (1972) suggest that trees growing 36 cm per year outgrow the mistletoe. Parmeter (1978) suggests a rate of 20 cm per year for lodgepole pine. For ponderosa pine in the Pacific Northwest, Barrett and Roth (1985) and Roth and Barrett (1985) report that infected ponderosa pine saplings outgrew the effects of dwarf mistletoe for 20 years at 25 cm annual height growth. Similarly, Wicker and Hawksworth (1991) state that after thinning, western larch grew 37 cm per year, while the larch dwarf mistletoe spread upward only 9 cm per year. Because mistletoe spread and effects vary with stand density, site quality, and other factors, these are only approximate rates (Bloomberg and Smith 1982).

Management of mistletoe-infested uneven-aged stands is discussed in detail by Mathiasen (1989) and Conklin (2000). At each entry they recommend that: more severely infected trees (DMR 5 and 6) are cut; healthy trees and those with a DMR of 1 and 2 are retained; moderately infected (DMR 3 and 4) trees are retained only where height growth is expected to exceed 30 cm per year or where the next cutting entry is scheduled within 20 years. Pruning infected branches or large witches' brooms from moderately to severely infected trees reduces spread, intensification, and damage. Pruning, however, is expensive (see section on Management for Recreation Values).

The practice in the Southwestern United States for management of pine stands with dwarf mistletoe is to consider uneven-aged management where 25 percent or fewer of the stems are infected. Individual tree selection is used where fewer than 15 percent of stems are infected; and group selection of trees in patches of less than 1 ha where 15 to 25 percent of stems are infected. Where more than 25 percent of trees are infected, even-aged management is used. Because larger trees tolerate more dwarf mistletoe infection without deleterious effects, Conklin (2000) proposes cutting and selection guidelines based on tree size and infection severity (table 8-2).

One of the major challenges for management of infested uneven-aged stands is the dispersal of dwarf mistletoe seed from infected overstory trees to the understory (Mathiasen 1989, Bloomberg and Smith 1982). Although the predominant opinion has been that dwarf mistletoe intensifies rapidly after a partial cutting or disturbance such as windthrow, there are exceptions. Shaw and Hennon (1991) and Trummer and others (1998) describe the relatively slow spread and intensification of hemlock mistletoe in Alaska. Situations such as these are good candidates for uneven-aged management. Geils and Mathiasen (1990) provide equations for the increase in DMR for Douglas-fir in uneven-aged, multistory stands. Maffei and others (1999) describe an exercise to develop similar equations for other species and incorporate the results in the Dwarf Mistletoe Model (Forest Health Technology Enterprise Team 2002). Because spatial relations are paramount in uneven-aged, multistory stands, the spatial-statistical model (Robinson and others 2002) provides another means for determining expected mistletoe spread.

In view of the uncertainties and potential adverse effects from selection and partial cutting in infected stands, use of the appropriate criteria for selecting and retaining trees is especially important. Overcutting reduces growing stock and possibly accelerates spread of dwarf mistletoe; undercutting and leaving more infected trees allows severe damage and unacceptable impacts. Cutting cycles and intensity of cutting can be adjusted to maintain healthy stands. Monitoring stand and infestation characteristics is especially important, as is the employment of well trained and highly skilled individuals who can recognize and evaluate dwarf mistletoe infection and apply complex marking guides. Although it is a challenge, management of infested, uneven-aged stands is possible (Hawksworth 1978a, Roth and Barrett 1985).

Table 8-2—Dwarf mistletoe ratings for leave trees in selection cuttings in Southwestern ponderosa pine.

Tree dbh (cm)	Maximum DMR per tree
<10	0
10-15	1
16-20	2
>21+	3

Based on Conklin (2000), acceptable rating of leave trees assumes a 20-year cutting cycle; a maximum of rating of 3 is allowed for trees that are intended for timber purposes.

Prescribed Burning

Prescribed burning is a potential silvicultural treatment applicable to even-aged and uneven-aged stands or forests. Historically, wildfire is an important ecological factor in many Western forest ecosystems and a strong determinant of mistletoe distribution and abundance (chapter 5 and Zimmerman and Leven 1984). In recent years, burning has been prescribed to maintain or reestablish desired stand conditions. Prescribed burning for treatment in dwarf mistletoe-infested stands can be used for stand replacement or mistletoe reduction.

Muraro (1978) and Zimmermann and others (1990) describe the use of fire as an economical method for replacing lodgepole pine stands that are overstocked and severely infested. Lodgepole pine, however, has a number of unusual silvicultural and fire ecology characteristics that make this species suitable for such treatment but that are not shared by all forest types.

Prescribed burning is usually a silvicultural tool for reduction of fuels where forest type and condition permit. Moderately to severely infected trees may be more vulnerable to fire because of lower crowns, witches' brooms, and accumulation of debris and resin. A goal of prescribed burning can be the differential killing of infected trees with discrimination of more severely infected trees and consequently a reduction in average stand infestation (Conklin and Armstrong 2001). Fire intensity and distribution can be directed at specific trees or groups of trees using techniques such as removing or piling duff and selecting upslope/upwind or down slope/downwind ignition points. In some stands, dwarf mistletoe infestation generates openings or gaps where infected trees survive fire (Wanner and Tinnin 1989). An approach for infected lodgepole pine or Douglas-fir stands is to replace these with more fire-resistant species such as ponderosa pine by a series of light fires over a period of several years. In any case, prescribed burning requires careful design and execution by experts (Muraro 1978). Numerous variables such as fuel loading and condition, stand structure, objectives for burn, weather, and other factors must be considered. Although prescribed fire will remain primarily a treatment for other forest management purposes, additional research and development (for example, on fire behavior, fuel distribution, and brooms) can enhance its potential as a tool in dwarf mistletoe infested stands.

Models to Assess Treatment Opportunities

When considering more complex or controversial silvicultural treatments such as sanitation and selection cuttings in uneven-aged stands or thinning of immature, even-aged stands, it is helpful to undertake a detailed, site-specific analysis of potential impacts and benefits. Such evaluations typically include a summary of current conditions, potential growth of an infested stand, costs and effects of treatments, and projected outcome with treatment. A variety of factors are important to consider, such as tree age, stand structure, stand density, species composition, site index, and years to next treatment. Useful mistletoe data are incidence (percent of stems infected), severity (DMR), area and pattern of infestation, and length of time the stand has been infested. The most feasible approach for summarizing information, making projections, and displaying results is with a forest growth and yield simulation model that includes the dynamics and effects of dwarf mistletoe infestation.

Numerous computer models are available that simulate various aspects of tree or stand development for dwarf mistletoe infected trees or infested stands. Strand and Roth (1976) describe a population model for young pine with *Arceuthobium campylopodum*. Baker and others (1982) predict stand impacts on spruce from *A. pusillum*. For hemlock forests with *A. tsugense*, Bloomberg and Smith (1982) model second-growth stands and Trummer and others (1998) model old-age stands. Myers and others (1971) introduce a growth and yield program of mistletoe-infested pine that, through many iterations and updates, has become the Dwarf Mistletoe [Impact] Model (DMIM) described by Hawksworth and others (1995). The DMIM is an operational tool supported by the U.S. Department of Agriculture, Forest Service and available on the Internet (Forest Health Technology Enterprise Team 2002). The DMIM functions with the Forest Vegetation Simulator (FVS) to model tree and stand dynamics and provide a number of presimulation and postprocessor features for data preparation, simulation control, and display (Forest Management Service Center 2001). Development currently under way for the DMIM includes improvement of overstory to understory spread (Maffei and others 1999). Robinson and others (2002) describe a process-oriented simulation model derived from the same origin as the DMIM but with additional capabilities to represent features of the mistletoe life cycle and crown canopy. This spatial-statistical model has a potential for examining such integrated mistletoe treatments as the silvicultural deployment of biological control agents.

The conversion of mistletoe control from eradication with large clear-cuts for timber production to sustained, uneven-aged management for ecological services has greatly increased the complexity of silvicultural assessments. Dwarf mistletoe simulation models are most useful to silviculturalists for addressing these complex situations, in which numerous factors interact over a long period. In chapter 5, we identify some of these interacting factors and effects; in chapter 6, we describe some procedures for acquiring data; in chapter 7 and earlier in this chapter, we outline treatments available to silviculturalists for managing infested stands. Simulation models permit planners to evaluate a number of treatment alternatives and to compare the long-term results before committing on the ground to a single, “experiment” in the sense of adaptive management (Holling 1978). Elaborate simulation models such as the DMIM–FVS incorporate a huge volume of research and experience. These models simplify an analysis by conducting the tedious bookkeeping and arithmetic required for such processes as computing statistics and applying growth functions. Because these processes are coded in the program, they are documented and can be reexecuted numerous times. The analyst is able to focus on formulating the problem, generating possible solutions, evaluating results, and documenting the overall activity.

Models are a simplification of a reality that is more or less “correct” and hopefully at least insightful. Although models are especially useful for novel situations, confidence in their predictions is supported by comparisons to the actual performance of benchmark stands. A useful set of benchmark stands represents the range of conditions and treatments silviculturalists are likely to consider (Taylor and Marsden 1997). Models are usually evaluated for sensitivity to a number of factors (Chen and others 1993). Knowledge of which factors a system is sensitive or insensitive to is useful to the planner, as these suggest what data are required to achieve high levels of accuracy or precision, and what treatments may be effective. The DMIM has numerous stochastic functions and is apparently sensitive to mistletoe incidence (percent of infected trees) at low levels (Chen and others 1993). This may well reflect real situations where a small infestation of only several trees could either spread throughout the stand or be isolated in one packet and eventually expire. A single simulation represents one likely outcome. Gregg and Hummel (2002) describes a bootstrapping facility for FVS that simplifies execution of multiple simulations to obtain information on the distribution (mean and dispersion) of outcomes. It is not necessary to simulate every infested stand to be managed. Most stands can be clustered into groups with similar conditions and treatment regimes. An analysis of these typical situations provides local guidelines that can be applied to all similar stands. Special analyses are then conducted for unusual cases and may contribute to the portfolio of guidelines.

Although the scope, availability, and applicability of current models for dwarf mistletoes are limited, their chief value is in the ability to determine quantitative effects and impacts of dwarf mistletoes under various stand conditions and treatment regimes. In so doing, models provide forest managers with a rational framework for decisionmaking.

Management for Recreation, Wildlife Habitat, and Other Ecosystem Values

It is becoming increasingly evident that active forest management by silvicultural treatment is necessary to sustain or enhance desirable stand conditions where trees or stands are infested by dwarf mistletoe. The particular conditions desired for different objectives vary: for recreation sites, live trees that are not a hazard; for some wildlife species, dense tree cover for screening; for other wildlife species, large openings with a few big trees and mistletoe brooms for nesting and roosting. Forests are not static, and trees, especially mistletoe-infected trees, have short lives. Forest management, working with the opportunity and capability provided by a site or stand, can influence vegetation development, including mistletoe, to meet a variety of objectives.

Management of dwarf mistletoe in recreation, administration, and home sites has the fundamental objective to maintain a safe and pleasant environment (Scharpf and others 1988). Although in these areas there is a low tolerance for mistletoe damage, trees are sufficiently valuable to justify repeated, individual treatment such as pruning branches. Methods are outlined as *Treatments in Developed Recreation Sites*.

Where wildlife habitat is an important consideration, it may be desirable to maintain or encourage features resulting from mistletoe infections, such as snags and witches' brooms. The same factors that can be manipulated to reduce mistletoe spread, intensification, and effects can also be used to enhance these processes and produce a continuing supply of dead and diseased trees. Examples are outlined in the section *Treatments for Wildlife Habitat and Other Ecosystem Values*.

Treatments in Developed Recreation Sites

In developed, intensively managed sites, treatments of dwarf mistletoe are needed to protect human life and property, and aesthetic and recreational values. Scharpf and others (1988) outline general principles and strategies for managing infested recreation sites and for maintaining individual trees or stands. They emphasize that specific management objectives and constraints for each site should be carefully considered and incorporated in the action plan.

The primary interests in developed, intensively used sites are to reduce the negative effects of dwarf mistletoe on tree vigor, longevity, and hazard, and to prevent mistletoe spread into healthy trees (Wood and others 1979). The first opportunity to do this is at the time of site selection and establishment. Spread from adjacent infested areas is slow and easy to control. Site planning and layout can achieve eradication by sanitation of light or patchy mistletoe infestations; hardy, immune species can be planted. The value of early control is appreciated when long-term costs of treatment and site replacement are recognized. Recreation sites range in size and level of intensity from campgrounds to National Parks (Hansen 1997, Lightle and Hawksworth 1973, Maffei 1984). Various techniques and concepts of even-aged or uneven-aged silviculture can be adapted for special uses. For example, a site may be laid out to remove an infested block of trees; or a portion of the infected trees may be removed on a periodic schedule to encourage establishment of healthy trees (Johnson 1998, Pronos 1995). A common feature of recreation sites is inspection and treatment of potentially hazardous trees on a relatively frequent schedule. Although branch pruning is rarely done in commercial forests to produce clear bole wood, pruning infected branches and brooms in high value sites is a common practice.

Pruning mistletoe-infected and broomed branches is used to maintain and improve tree vigor and to reduce hazard (Hawksworth and Johnson 1993, Maffei 1992). The most suitable candidates for branch pruning are trees having: infections in the lower half of the crown only; a DMR of 3 or less, and if smaller than 13 cm in diameter, with no bole infections or branch infections closer than 10 cm from the bole. Mark and Hawksworth (1974) have concluded that infections on tree boles larger than 13 cm have little effect on growth and produced few seeds, and they are therefore not a management concern. Aerial shoots on a branch but within 10 cm of the bole probably emerge from an endophytic system that has already reached the bole. Because most trees can tolerate removal of up to half the live crown, general practice is to prune all live branches to two whorls above the highest visibly infected branch. Mistletoe infestations in a tree usually include a number of latent (invisible, incubating infections) and other easily overlooked infections. Most of the missed infections appear in 3 to 5 years; reinspection and repeated pruning are appropriate. Such treated trees often show dramatic recovery in crown vigor. Trees with severe infections, however, such as those with infections throughout the lower crown or in the upper crown, are not likely to respond but likely to soon die. The proper consideration for these trees is whether the value of retaining them for a few more years is greater than the risk they pose for infecting other trees.

Broom pruning can also prolong the life and crown vigor of individual pine trees (Lightle and Hawksworth 1973, Scharpf and others 1988). In this method, the emphasis is on removing branches with witches' brooms rather than removing all visibly infected branches. Hadfield (1999) describes the hazard in high traffic areas from breakage of brooms in species with large or brittle witches' brooms. Pruning these may also be justified.

Treatments for Wildlife Habitat and Other Ecosystem Values

From certain perspectives and in some situations, dwarf mistletoe infestations have beneficial impacts for associated species and communities (Mathiasen 1996, Monning and Byler 1992, Tinnin and others 1982). In old-growth forests, dwarf mistletoes may exert a different set of effects on infected trees and display different dynamics (Hawksworth and others 1992a, Trummer and others 1998). Special management strategies and silvicultural treatments for infested stands are required where the objectives are to maintain and enhance wildlife habitat, old-growth character, and other ecosystem values.

As described in chapter 5, dwarf mistletoe infection produces mistletoe shoots, fruits, diseased branches, brooms, distorted crowns and boles, detritus, diseased and insect-infested trees, snags, and eventually logs. Infestations alter succession, disturbance regimes, and vegetation pattern of the landscape. Within limits, these features favor some species (or groups), inhibit other species, and are essentially neutral to most (Watson 2001). By influencing the spread and intensification of mistletoe and the environment around infected trees, managers are able to affect mistletoe infestations and ecological effects. The specific goals of a treatment depend on specific management objectives such as identification of featured species. For example, Reynolds and others (1992) describe guidelines for the northern goshawk that include consideration of mistletoe and other forest disturbance agents (also see Steeger and Hitchcock 1998).

Most of the recent interest in research and development of management recommendations has focused on snags, brooms, birds, and mammals. Bennetts and others (1996) describe a study of passerine bird diversity in a Colorado Front Range ponderosa pine forest. They suggest greater bird diversity is associated with increased mistletoe infestation (24 of 28 species positively associated); the key limiting resource for the birds in this situation may be snags. Parker (2001) reports a similar study in a northern Arizona ponderosa pine forest. He finds, however, a more complex situation with four species positively associated with mistletoe (cavity-nesting birds), five species with a negative association (avoiding infested areas), and seven with no relation (indifferent). Fairweather (1995) and Parks and others (1999b) describe mistletoe control treatments in which infected trees were killed but left standing for woodpeckers and other cavity-nesting animals. Although these snags are used, they remained standing for only a few years. Studies of broom use by wildlife include work by Parks and others (1999a), Hedwall (2000), and Garnett (2002). These studies identify which birds and mammals use witches' brooms, how they use it (for nesting and roosting), and what kinds of brooms are preferred. This information is useful to determine if retaining certain brooms is a potential benefit for a favored species. Information still lacking is knowledge of how the number and distribution of snags and brooms relates to levels of mistletoe infestation and to wildlife populations and the dynamics (rates of generation and loss) of these features.

Marshall (1996) discusses management lessons, implications, and research needs from a project to manage infested stands for northern spotted owl in southwestern Oregon. Maffei (2002) presents results of an analysis for a similar situation also in Oregon, and for maintaining owl habitat. Although owls use mistletoe brooms for nesting, vegetation changes and disturbance stimulated by the mistletoe (such as fire) lead to loss of critical owl habitat. The analyses demonstrate use of an infection index that represents desired condition (relative to owls and mistletoe) and application of the FVS-DMIM in a landscape planning exercise. These projects illustrate how mistletoe information can be integrated with wildlife criteria to design treatment regimes that benefit long-term survival of a featured species. Complex situations involving numerous ecological relationships are not amenable to simple guidelines defining which trees to cut and which to retain; rather, they require an adaptive management process of analysis, simulation, experimenting, monitoring, and revision (Holling 1978).

Appendices

Appendix A: References

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Appendix B: Scientific and Common Names of Trees

Abies amabilis Douglas ex J. Forbes[a]	Pacific silver fir
Abies balsamea (Linnaeus) Miller[a]	balsam fir
Abies bifolia A. Murray[a]	Rocky Mountain subalpine fir
= *Abies lasiocarpa* var. *arizonica* (Merriam) Lemmon	corkbark fir
Abies concolor (Gordon & Glendinning) Hildebrand[a]	white fir
Abies durangensis Martinez[c]	Durango fir
Abies grandis (Douglas ex D. Don in Lambert) Lindley[a]	grand fir
Abies lasiocarpa (Hooker) Nuttall[a]	subalpine fir
Abies lowiana (Gordon) A. Murray[a]	Sierra white fir
= *Abies concolor* var. *lowiana* (Gordon) Lemmon	
Abies magnifica A. Murray[a]	California red fir
Abies procera Rehder[a]	noble fir
Abies religiosa Lindley[c]	sacred fir
Abies religiosa var. *emarginata* Loock & Martinez[c]	
Abies vejarii Martinez[c] [as *vejari*]	Vehar fir
Abies vejarii subsp. *mexicana* (Martinez) A. Farjon[c]	Mexican fir
=*Abies mexicana* Martinez	
Calocedrus decurrens (Torrey) Florin[a]	incense-cedar
Cupressus arizonica Greene[a]	Arizona cypress
Cupressus arizonica var. *montana* (Wiggins) Little[c]	cypress
Cupressus bakeri Jepson[a]	Baker cypress
Cupressus benthami Endlicher[c]	cypress
Cupressus goveniana Gordon[a]	Gowen cypress
Cupressus lusitanica Miller[c]	cypress
Cupressus macnabiana A. Murray[a]	MacNab cypress
Cupressus macrocarpa Hartweg[a].	Monterey cypress
Cupressus sargentii Jepson[a]..	Sargent cypress
Juniperus ashei J. Bucholtz[a]	Ashe juniper
Juniperus ashei var. *saltillensis* (H.M. Hall) Silba[c]	
Juniperus californica Carrière[a]	California juniper
Juniperus deppeana Steudel[a]	alligator juniper
Juniperus flaccida Schlechtendal[a]	drooping juniper
Juniperus monosperma (Engelmann) Sargent[a]	one-seed juniper
Juniperus occidentalis Hooker[a]	western juniper
Juniperus osteosperma (Torrey) Little[a]	Utah juniper
Juniperus pinchotii Sudworth[a]	Pinchot juniper
= *Juniperus erythrocarpa* Cory	
Juniperus scopulorum Sargent[a]	Rocky Mountain juniper
Larix decidua Miller[c]	European larch
Larix leptolepis (Sieb. & Zuccarini) Gordon[c]	Japanese larch
=*Larix kaempfer* (Lambert) Sargent[c]	
Larix laricina (Du Roi) K. Koch[a]	tamarack
Larix occidentalis Nuttall[a]	western larch
Picea abies (Linneaus) H. Karsten[a]	Norway spruce
Picea breweriana S. Watson[a]	Brewer spruce
Picea engelmannii Parry ex Engelmann[a]	Engelmann spruce
Picea glauca (Moench) Voss[a]	white spruce
Picea mariana (Miller) Britton, Sterns, & Poggenburg[a]	black spruce
Picea mexicana Martinez[c]	Mexican spruce
Picea pungens Engelmann[a].	blue spruce
Picea rubens Sargent[a]	red spruce
Picea sitchensis (Bongard) Carrière[a]	Sitka spruce
Pinus albicaulis Engelmann[a]	whitebark pine
Pinus aristata Engelmann[a]	Colorado bristlecone pine
Pinus arizonica Engelmann[b]	Arizona pine
= *Pinus ponderosa* var. *arizonica* (Engelmann) Shaw[a]	
Pinus arizonica var. *stormiae* Martinez[b]	pino real
Pinus attenuata Lemmon[a].	knobcone pine
Pinus ayacahuite C. Ehrenberg ex Schlechtendal [b]	Mexican white pine
Pinus ayacahuite var. *brachyptera* Shaw[b]	
Pinus balfouriana Greville & Balfour[a]	foxtail pine
Pinus balfouriana subsp. *australis* Mastoguiseppe & Mastoguiseppe	Sierra foxtail pine
Pinus banksiana Lambert[a]	jack pine
Pinus bungeana Zuccarini[c]	lacebark pine
Pinus californiarum D. K. Bailey[c]	singleleaf pinyon
Pinus californiarum subsp. *fallax* (Little) D. K. Bailey[c]	Arizona singleleaf pinyon
Pinus caribaea Morelet	Caribbean pine
Pinus caribaea var. *hondurensis* (Sénécl) Barr. & Golf.[b]	Honduras Caribbean pine
Pinus cembroides Zuccarini[b]	Mexican pinyon
Pinus cembroides subsp. *orabensis* D. K. Bailey[b]	Orizaba pinyon
=*Pinus orizabensis* (D. K. Bailey) D. K. Bailey & Hawksworth	
Pinus contorta Dougl. ex Loudon[a]	lodgepole pine

Pinus contorta var. *contorta*[a]	shore pine
=*Pinus contorta* subsp. *bolanderi* (Parlatore) Critchfield[a]	Bolander pine
Pinus contorta var. *murrayana* (Grenville & Balfour) Engelmann[a]	Sierra lodgepole pine
Pinus contorta var. *latifolia* Engelmann in S Watson[a]	lodgepole pine
Pinus cooperi Blanco[b]	pine amarillo
Pinus coulteri D. Don[a]	Coulter pine
Pinus culminicola Andresen & Beaman[b]	Potosi pinyon
Pinus discolor Bailey & Hawksworth[b]	border pinyon
Pinus douglasiana Martinez[b]	pino
Pinus durangensis Martinez[b]	ocote
Pinus edulis Engelmann[a]	pinyon
Pinus engelmannii Carrière[a]	Apache pine
Pinus flexilis E. James[a]	limber pine
Pinus halepensis Miller[c]	Aleppo pine
Pinus hartwegii Lindley[b]	Hartweg pine
Pinus herrerai Martinez[b]	ocote
Pinus jaliscana Perez de la Rosa[b]	Jalisco pine
Pinus jeffreyi Greville & Balfour in A. Murray[a]	Jeffrey pine
Pinus lambertiana Douglas[a]	sugar pine
Pinus lawsonii Roezl ex Gordon & Glendinning[cb]	pino
Pinus leiophylla Schiede & Deppe[a]	pine chino
Pinus leiophylla var. *chihuahuana* (Engelmann) G.R. Shaw[a]	Chihuahua pine
Pinus longaeva D. K. Bailey[a]	Intermountain bristlecone pine
Pinus lumholtzii Robins & Fern.[b]	pino triste
Pinus maximinoi H. E. Moore[b]	pino
Pinus michoacana Martinez[b]	pino lacio
Pinus monophylla Torrey & Fremont[a].	singleleaf pinyon
Pinus montezumae Lambert[b]	Montezuma pine
Pinus monticola Douglas ex D. Don[a]	western white pine
Pinus mugo Turra[c]	dwarf mountain pine
Pinus muricata D. Don[a]	Bishop pine
Pinus oaxacana Mirov[b]	pino chalmaite
Pinus occidentalis Swartz[c]	West Indian pine
Pinus oocarpa Schiede[b]	pino prieto
Pinus oocarpa var. *ochoterenia* Martinez[b]	
Pinus oocarpa var. *microphylla* Shaw[b]	
=*Pinus praetermissa* Styles & McVaugh[c]	
Pinus palustris Miller[a]	longleaf pine
Pinus patula Schl. & Chamisso[b]	pino triste
Pinus pinea Linneaus[c].	Italian stone pine
Pinus ponderosa Douglas ex Lawson & C. Lawson[a]	ponderosa pine
Pinus ponderosa var. *scopulorum* Engelmann in S. Watson[a]	Rocky Mountain ponderosa pine
Pinus pringlei Shaw[b]	pino rojo
Pinus pseudostrobus Lindley[b]	pino
Pinus quadrifolia Parlatore[b]	Parry pinyon
Pinus radiata D. Don[a]	Monterey pine
Pinus resinosa Aiton[a]	red pine
Pinus rudis Endlicher[b]	pino
Pinus sabiniana Douglas ex D. Don in Lambert[a]	digger pine
Pinus strobiformis Engelmann[a]	southwestern white pine
Pinus strobiformis var. *potosiensis* Silba[c]	
Pinus strobus Linnaeus[a]	eastern white pine
Pinus sylvestris Linnaeus[a].	Scotch pine
Pinus tecunumanii (Schwertfeger) Equiluz & Perry[b]	pino
Pinus teocote Schl. & Chamisso[b]	ocotl
Pinus thunbergii Parlatore	pine
Pinus torreyana Parry ex Carrière[a]	Torrey pine
Pinus virginiana Miller[a]	Virginia pine
Pinus washoensis H. Mason & Stockwell[a]	Washoe pine
Pseudotsuga macrocarpa (Vasey) Mayr[a]	bigcone Douglas-fir
Pseudotsuga menziesii (Mirbel) Franco[a]	Douglas-fir
Pseudotsuga menziesii var. *menziesii*	coast Douglas-fir
Pseudotsuga menziesii var. *glauca* (Mayr) Franco[a]	Rocky Mountain Douglas-fir
Taxodium distichum (L.) Richard var. *mexicanum* Gordon[a]	Mexican bald-cypress
=*Taxodium mucronatum* Tenore	
Tsuga heterophylla (Rafinesque) Sargent[a]	western hemlock
Tsuga mertensiana (Bongard) Carrière[a]	mountain hemlock

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[a] Flora of North America Committee (1993)
[b] Perry (1991)
[c] Plant Names Project (1999)

Appendix C: Acknowledgments

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Appendix D: Glossary

Baranyay and others (1971) provide a complete glossary of terms and special definitions that apply to mistletoes. Although most of our readers ought to be familiar with the concepts and terms of forestry, they may be less comfortable with a number of other terms used here. These are primarily botanical and plant pathology terms or words with a special application in this context.

Abundance. See incidence.

Acuminate apex. Tapering to a point with the sides more or less pinched in before reaching the tip.

Adnate. The union of unlike parts, as an inferior ovary to the calyx tube.

Allozymes. Similar proteins that provide a physiochemical trait for investigating the population genetics of groups of plants (hosts or parasites).

Anamorph. An imperfect stage of a fungus that is taxonomically described and provides a basis for identification and referral.

Anthesis. Period when the flower is open.

Ascospore. A spore of a fungus produced within an ascus, a saclike cell of ascomycetes in which, following meiosis, a specific number (usually eight) of ascospores is produced.

Autocorrelation, spatial. A quantification of a relation between two entities whereby the similarity of a feature depends on the distance between the entities. Because of mistletoe spread and intensification, the severities of mistletoe infection on two neighbor trees tend to be more or less similar, or spatially autocorrelated.

Bark strand. A structure that ramifies throughout the inner bark of the host and from which shoots and sinkers of the mistletoe are derived.

Blight. Rapid discoloration and death of all parts of a plant.

Bootstrapping. A statistical processing method using iteration and repeat calculation to estimate variation.

Branch girdle, segment. Girdle refers to a region on a vegetative branch or main stem of a conifer between two annual growth segments; segment refers to a single year's growth of a vegetative branch or main stem.

Brooming. See witches' broom.

Callus. Undifferentiated plant tissue, usually as grown in a laboratory with artificial media.

Calyculus. A floral structure of the Loranthaceae, a vestigial whorl of bracts of the suppressed flowers of a lateral branch inflorescence that have become adnate to the inferior ovary.

Canker, mistletoe canker. The structure and malformation of a host stem or branch caused by a disruption of the cambium and bark as a result of dwarf mistletoe infection.

Cordate. A shape of a leaf like a stylized heart.

Cortex. Ground-tissue region of a stem or root bounded externally by epidermis and internally by the vascular system; a primary-tissue region.

Decussate. Of leaves or scale-like leaves that are arranged in pairs that alternately cross each other.

Disjunct. Pertaining to a discontinuous range having two or more potentially interbreeding populations separated by a distance that precludes genetic exchange by pollination or dissemination.

Dyads. See monads.

Endemic. The kind of distribution for taxa that is geographically small.

Endophytic system. The root system parts of a dwarf mistletoe within host tissues. The endophytic system consists of bark strands within the inner bark and "sinkers" that are embedded in successively formed layers of xylem, referred to as haustorial root system or haustorium.

Endosperm. A tissue, containing stored food, that develops from the union of a sperm nucleus and the polar nuclei of the central cell; it is digested by the growing sporophyte either before or after the maturation of the seed; found only in angiosperms.

Epigynous. Growing, or appearing to grow, on the summit of the ovary.

Flabellate branching. Fan shaped, a branching pattern produced by the continued development of superposed axillary buds.

Flowering, direct and indirect. Indirect flowering is the result of an intervention of a rest period between initiation of a floral bud and anthesis, whereas direct flowering is the result of uninterrupted development of floral buds from initiation to anthesis.

Frass. Solid larval insect excrement.

Fusiform. Spindle-shaped; broadest at the middle and tapering at both ends.

Glabrous. Smooth, no hairs present.

Glaucous. Covered with a whitish or bluish waxy covering.

Growth loss. An expression of yield reduction that includes both lost annual production on still living trees and lost volume to tree death.

Growth, primary and secondary. The growth of shoots and roots from inception until completion of their expansion is primary growth. This growth is the result of apical meristems and their three primary derivative meristems (protoderm, ground meristem, and procambium). Secondary growth results from divisions of secondary meristems (typically the vascular cambium and phellogen) and adds circumference to the plant body.

Haustorium, primary and secondary. The primary haustorium is a wedge-like projection, arising from the circular attachment disc of the radicle, that penetrates the outer bark extending to the host xylem. Secondary haustoria are “sinkers” produced by bark strands that grow radially to the vascular cambium.

Holdfast. A disc-like swelling at the distal end of the radicle through which infection of the host occurs.

Host susceptibility. A subjective classification system based on the percentage of trees of the host species in question that are infected by dwarf mistletoe within 6 m of a principal host heavily infected with the same species of dwarf mistletoe.

Hyphae. Tubular threads of the mycelium of a fungus or similar organism.

Hypocotyl. Region of an embryo that is between the radicle and the attachment point of the cotyledons.

Incidence, abundance, distribution, severity. Incidence refers to the frequency of which host trees in a given stand are infected by a given species of mistletoe (usually measured as percent of trees infected). Abundance refers to the relative quantity of mistletoe in a stand or on a host (not usually quantified). Distribution describes the spatial extant and pattern of a mistletoe species or population within a given area. Severity is a qualitative term describing the disease situation (see infection class); high incidence along with large abundance would result in a severe disease situation.

Incubation period. That period from infection to production of first shoots. See latency.

Infection class. A measure (generally from 0 to 6) of the relative severity of dwarf mistletoe infection for individual trees, in contrast to host susceptibility class.

Infection, secondary infection, localized and systemic infections. Infection refers to that process in which dwarf mistletoes successfully penetrate host tissue and initiate establishment of the endophytic system; infection also refers to the mistletoe plant and the associated diseased host tissues. Secondary infection is reinfection by dwarf mistletoe of already infected tissue. Localized infections (anisophasic) are those in which the endophytic system is generally restricted to within or near (such as a few centimeters) the swollen portion of the host, whereas systemic infections (isophasic) are those in which the endophytic system occurs within the host terminal bud, and growth keeps pace with that of the host’s shoot apices.

Infestation. A condition in which one or more trees of a stand or group are infected.

Intensification. Increase in the number of dwarf mistletoe infections within a tree (see spread).

Internode. See node.

Latency. Phenomenon in which host tissues are infected by dwarf mistletoe but either visible symptoms of swelling or brooming are not apparent or shoots are not present. Infections are latent during the incubation period and when environmental conditions induce a cessation in production of shoots.

Lenticel. A group of loose corky cells formed beneath the epidermis of woody plants; allows gas exchange to occur across the periderm.

Ligulate. A property of a leaf, petal, or similar structure whereby the structure possesses a small membranous appendage.

Meiosis. The chromosome reduction stage in formation of gametes.

-Merous. A suffix indicating division into parts; a five-merous flowers would have five sepals, five petals, five stamens and a five-carpellate pistil (providing all these structures were present).

Monads, dyads, triads. Sets of flowers arising from a common peduncle, in singles (monads), pairs (dyads), or triples (triads).

Mycelial stroma. A mass of vegetative hyphae in or on which spores are produced.

Mycoherbicide. A plant-killing substance based on the action of live fungi that induce disease.

Mycorrhizae. Fungus-root, a symbiotic relation of a fungus and plant root.

Node, internode. A region of the stem where a leaf or leaves diverge; the region in between nodes is an internode.

Obovate. A shape of a leaf like an oval, wider at one end (stylized egg).

Parasite, parasitism. A parasite is an organism, such as a mistletoe, that obtains sustenance from another organism, and also completes all, or at least some, of its life cycle on that host organism. Parasitism is the typical mode of existence or behavior of a parasite.

Pathosystem. A biotic combination consisting of a host and a pathogen; the reference is to the pair of organisms rather than the nature of their relationship.

Pedicel. The stalk of an individual flower.

Peduncle. The stalk of an inflorescence (basal to a pedicel).

Penetration wedge. A structure in dwarf mistletoes that develops from the holdfast and initiates the infection process.

Pericarp. The wall of the ripened ovary (fruit); consists of three layers, the exocarp (outer), mesocarp (middle), and endocarp (inner).

Periderm, necrophylatic. A bark, cortex tissue that reacts to invasion by rapid, localized necrosis (isolating the potential pathogen).

Phloem, primary and secondary. The principal food-conducting tissue of a plant composed mainly of sieve elements, various kinds of parenchyma cells, fibers, and sclereids. Primary and secondary phloem are formed during primary and secondary growth, respectively.

Phyllotaxy. The morphological arrangement of leaves.

Pistillate, stigma. Referring to the female flower, which includes an ovary, pistil, style, and stigma (which receives the pollen).

Primary growth. See growth.

Pubescence, trichomes, puberulent, papillate-hispid, stellate. Hair-like structures on a plant surface are epidermal glands called trichomes. A surface that bears trichomes is pubescent or puberulent if the hairs are thin and sparse or papillate-hispid if it has “hairy bump.” Stellate hairs have a stalk and three or more branches from a common point.

Radicle. See holdfast.

Severity. See incidence.

Sessile. Of a leaf that appears attached directly to the stem, without a petiole.

Sinker. A radially oriented structure, composed of tracheary and parenchymal elements, that originates from a dwarf mistletoe bark strand and grows centripetally to the cambium where it becomes embedded by successive layers of xylem.

Source–sink. In the context of the mistletoe–tree interaction, the tree is the source or supplier of water and nutrients to the mistletoe, and the mistletoe plays the role of sink or depository of water and nutrients taken up by the host tree.

Spike, determinate, indeterminate spike. The unbranched inflorescence of a mistletoe of indeterminate type when flowering proceeds from the base while younger flowers are formed as the spike continues to elongate or of determinate type otherwise.

Sporodochia, conidial. An asexual reproductive structure of a fungus that produces spores by a budding process.

Spread, vertical spread. Increase in the area of mistletoe infestation by infection of additional host trees. Vertical spread refers to the net result of dispersal of mistletoe seeds to higher portions of the host crown.

Staminate. Referring to the male flower, which produces pollen.

Stigma. See pistillate.

Symbiont. A member of a close biotic relation whereby both species benefit, such as in mycorrhizae, and in contrast to a pathogen that benefits to the harm of the host. The terms of these forms of mutualisms — symbiosis and parasitism — are relative and contextual.

Sympatry. The condition in which the distributions of two species overlap and hybridization between taxa would be possible if they were not reproductively isolated by factors other than spatial separation.

Synonymy. See taxonomy.

Systematics. See taxonomy.

Systemic infection (isophasic). Infection in which growth of the endophytic system keeps pace with the growth of the infected host branch. See infection.

Taxon (plural, Taxa). A taxonomic unit of any rank (order, family, genus, species, subspecies, and so forth).

Taxonomy, systematics, synonymy. Taxonomy refers to the valid assignment of names to organisms based on natural relations and rules of convention; systematics refers to the natural relations based on decent from a common ancestor. Several (taxonomic) names may be used for an individual plant or population of plants. One name will be preferred (for reasons dealing with the inferred relations and application of conventions); other names are synonyms.

Terete. Of a stem, approximately cylindrical but tapering at ends.

Trichomes. See pubescence.

Triads. See monads.

Verticillate branching. Whorled, a branch pattern produced by the continued development of superposed axillary buds.

Vertical spread. See intensification.

Viscin. Sticky material contained in the viscin cells of dwarf mistletoe fruit, which acts as the initial means of seed attachment to the host.

Witches' broom. An abnormally profuse, dense mass of host branches. This is a common symptom induced by dwarf mistletoe infection, as well as other parasites and abiotic agents.

Woodrose. An ornamental object composed of the host wood deformed by a mistletoe haustorium and exposed by removing the mistletoe tissue.

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RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

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Forest Insect
& Disease
Leaflet 54

Revised February 2000

U.S. Department of Agriculture • Forest Service

Douglas-Fir Dwarf Mistletoe

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Douglas-fir dwarf mistletoe, *Arceuthobium douglasii* Engelm., is a destructive native parasite of Douglas-fir and is the primary disease agent affecting this tree over most of its range. With the exceptions noted below, its distribution essentially coincides with that of Douglas-fir from southern British Columbia to central Mexico. The parasite is not found in the Douglas-fir stands east of the Continental Divide in Montana, most of Wyoming, northern Colorado, and west of the Cascade Range (except near the crest) and north of the Siskiyou Mountains of Oregon. It is the only dwarf mistletoe that occurs in all of the western states (Figure 1). The dwarf mistletoe occurs on many different Douglas-fir ecologic, successional, and topographic types.

Douglas-fir is the principal tree species affected by Douglas-fir dwarf mistletoe. True firs and spruces are rarely infected where they are associated with infected Douglas-firs, but the parasite is of little or no economic importance on these species. Douglas-firs are rarely infected by mistletoes other than Douglas-fir dwarf mistletoe.

Douglas-fir dwarf mistletoe has increased in abundance since the late 1800s. Douglas-fir stands are much more widespread in the Inland West largely as a result of nearly a century of fire suppression. Prior to this time, fires restricted the

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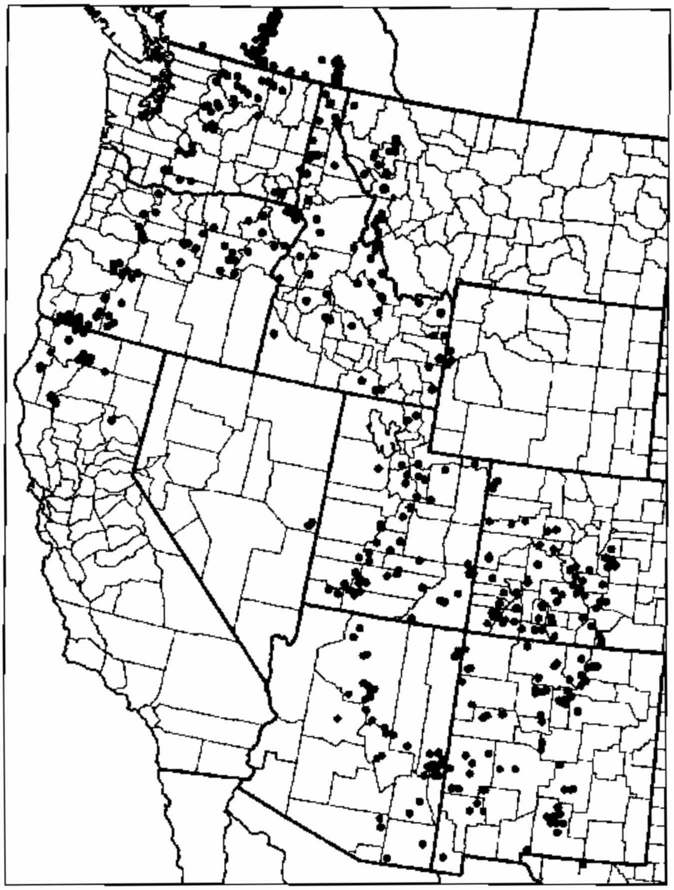

Fig. 1. Distribution of Douglas-fir dwarf mistletoe in the western United States and Canada.

distribution of Douglas-fir and dwarf mistletoes, especially on drier sites dominated by ponderosa pines. Frequent fires killed the small Douglas-firs, especially those infected by dwarf mistletoe. Fire suppression has enabled Douglas-fir to survive and dominate on millions of acres where once it was a relatively minor stand component.

A history of selective harvesting with removal of more valuable ponderosa pines, western larch, and large diameter Douglas-firs has also contributed to the increases in dwarf mistletoe by leaving small or poor quality infected Douglas-firs in which the parasite flourished and spread.

Life History

Douglas-fir dwarf mistletoe is a small, inconspicuous, seed-bearing parasitic plant. The aerial system of this parasite found on infected branches and stems consists of slender, olive-green, perennial shoots. They are most commonly found nestled among needles on infected branches. The average length is only 0.75 in. (2 cm), about the length of fir the needles, but they are rarely up to 3 inches (8 cm) (Figure 2). Although shoots contain chlorophyll, they produce little food for the parasite. The major function of the aerial shoots is reproduction. Individual aerial shoots can live for several years.

Aerial shoots arise from a network of root-like strands imbedded in host tissues. This network, called the endophytic system, consists of cortical strands growing within the living bark and sinkers embedded in the wood. The endophytic system takes nutrients and water from the host tree. The endophytic system lives as long as adjacent host tissues are alive and may produce aerial shoots for many years.

Male and female flowers are small and produced on separate plants. Flowering takes place in May and June. Insects and wind are both involved in pollination. Fruits complete their development 17 to 18 months after pollination. Only the female plants bears the fruits and seeds that spread the parasite. Berry-like fruits are olive-green and contain one seed averaging less than 0.1 inch (2 mm) long.

At maturity in September and October, the elastic outer case of the fruit, which is under high internal water pressure, abscises from its base, contracts rapidly, and explosively propels the seed into the air.

Most seeds are shot upward and outward. Initial seed velocity is about 72 feet (22 m) per second. Seeds may travel 30 to 40 feet (10-13 m), but most land within 10-15 feet (3-5 m) of the disseminating shoot.

Seeds have a sticky hygroscopic coating called viscin which enables them to stick to most objects they strike. Foliage is the most common receiving surface.

Viscin, when first moistened by rains, acts as a lubricant. Seeds slide downward and either fall off needles or become lodged at the base of needles. Seeds are fastened in place when the viscin dries and they overwinter in a dormant state. Many of the seeds are removed by rain, snow and ice or are eaten by birds, insects and fungi.

The seeds germinate in early spring. Radicles grow along twig surfaces until an obstruction, usually a needle base, is encountered or the food supply is exhausted. When radicle extension is obstructed small mounds of tissue called holdfasts are formed. Infection pegs that develop from the holdfasts then infect the host by penetrating through the thin bark during the summer. After the bark has been penetrated the mistletoe's root or endophytic system grows in the cortex and wood of the host. Infection occurs most readily in twigs and stems less than 5 years old.

About 2 to 5 years pass before the first aerial shoots appear at infection sites. Infections on branches exposed to direct sunlight probably produce shoots quicker than shaded infections. Infections that have not yet produced aerial shoots are termed latent infections.

The typical length of time needed for female plants to complete their life cycle from initial establishment to dissemination of the first seed crop is 4 to 6 years.

Symptoms of Infection

The first symptom of Douglas-fir dwarf mistletoe infection is a slight swelling at the infection site 1 to 2 years after infection occurs. Initially these can be difficult to see. As time passes and the endophytic

Fig. 2. Aerial shoots of Douglas-fir dwarf mistletoe.

system of the parasite becomes more extensive, the form of the infected branch or stem becomes distorted.

Douglas-fir dwarf mistletoe typically becomes systemic within the host when the endophytic system invades tree buds at the infection site. Masses of invaded buds are stimulated to grow and develop long twigs, which eventually form witches' brooms. The mistletoe endophytic system grows apically at the same rate as the infected twigs. Aerial shoots can be found on branch growth segments ranging from 2 to 7 years old.

Fig. 3. Large witches' broom in a Douglas-fir.

The most striking symptoms of dwarf mistletoe infection on Douglas-fir are witches' brooms, which are noticeable within 10 years after infection takes place. Broom shapes vary but start out as fan-shaped and eventually tend to become somewhat spherical.

Branches in witches' brooms may become long and droopy and attain lengths of 10 feet (3 m), but are typically only about one-quarter inch in diameter (these are locally called "rat tails"). Large brooms may be several feet in diameter and compared to healthy branches have very large surface areas.

Broom development is most rapid in infected branches exposed to direct sunlight. Witches' brooms on lower branches in dense stands develop slowly and tend to be small.

Trees may have one to many witches' brooms. Most extensive development of witches' brooms is usually in the lower half of tree crowns. Brooms can become so large and numerous that they make up entire tree crowns (Figure 3). Branches with big witches' brooms develop large diameters at their junction with the main stem to support the weight, which can be several hundred pounds. Infected branches are kept alive because of the ability of the parasite to obtain food and water from the tree. In severely infected trees, branches with witches' brooms are generally the last to die.

Severely infested Douglas-fir stands typically have many trees with stunted growth, witches' brooms, dying and dead tops, and dead trees.

Spread and Intensification

Spread is movement of mistletoe from one tree to another; intensification is the increase of mistletoe populations within a tree. Nearly all Douglas-fir dwarf mistletoe spread is local and results from explosive discharge of seeds. Wind exerts a minor influence on distance and direction of seed travel. Birds and other animals are responsible for some long-distance spread when seeds that stick to them are later rubbed off onto susceptible trees.

Several factors affect spread of Douglas-fir dwarf mistletoe. These include stand structure, tree size, species composition of stands, tree spacing, infection position, and topography. In single storied stands, horizontal spread averages 1.5 to 2 feet (0.5-0.6 m) per year. Spread in multistoried Douglas-fir stands is more rapid because understory firs are showered with dwarf mistletoe seeds from infected overstory trees. Seeds discharged from plants high up in tree crowns travel farther than those originating from lower positions.

Presence and arrangement of nonsusceptible tree species can slow the spread of Douglas-fir dwarf mistletoe. Spread rates in dense stands are less than in more open stands because dwarf mistletoe seed production is usually lower due to more shading and poorer host vigor, and many seeds are trapped within the foliage of the infected trees rather than escaping to adjacent trees. Spread tends to be more rapid from ridgetops than narrow valley bottoms. Douglas-firs less than 4 feet (1.2 m) tall are small targets for seed deposition and have low infection rates, even though trees of all sizes and ages are susceptible .

The 6-class dwarf mistletoe rating (DMR) system is commonly used to categorize intensity of infection in Douglas-fir trees and stands. For this system, the live crown of the tree is visually divided into thirds and each third rated as: 0 = no visible infection, 1 = light infection (less than half of the branches infected), or 2 = severe infection (more than half of the branches infected). The three ratings are then added to obtain a tree rating.

A tree severely infected in each third would be rated class 6. Because Douglas-fir dwarf mistletoe shoots are small and often difficult to observe, particularly in large trees, witches' brooms are usually used as an indication that a branch is infected when determining the rating for each crown third. The tree ratings of all live trees (including uninfected ones) are averaged to obtain a stand or plot rating.

Douglas-fir dwarf mistletoe infection increases about one DMR class per decade for individual trees, however this can be highly variable. Infection intensifies most rapidly in saplings and pole- size trees under infected larger trees in stands with openings. Mistletoe populations increase within trees as a result of continued deposition of seeds from adjacent infected trees and from seeds produced by plants in the trees.

Most initial infections are located in the lower portions of crowns because this material is older and has been exposed to infection longer and represents a larger surface area for seeds to strike. Infections resulting from these initial plants tend to spread upward in the crowns at a rate of 4 to 6 inches (10-15 cm) per year.

Effects of Infection

Infection of Douglas-fir by dwarf mistletoe alters tree form, reduces vigor and growth rates, reduces seed production, increases susceptibility to other damaging agents, and results in topkilling and tree death. These effects result from the parasite taking food and water from the host, thus reducing the amount of energy available for the tree's normal growth, reproductive, and protective processes.

The effects of Douglas-fir dwarf mistletoe infection are progressive. Lightly infected trees do not differ much from healthy trees, however they become moderately then severely infected with the passage of time, resulting in gradual tree and eventually stand deterioration.

The effects of dwarf mistletoe on tree growth increase with severity of infection. In western Montana it was found that light infection resulted in a 14 percent reduction in basal area growth. Medium and severe levels of infection caused reductions of 41 and 69 percent, respectively. Height growth was similarly affected.

In the Southwest, severely infected (tree ratings of DMR 5-6) sawtimber size trees have 50 to 65 percent less 10-year periodic annual volume increment than lightly infected (DMR 1-2) or healthy trees. Because severe Douglas-fir dwarf mistletoe infection causes marked reductions in height and radial growth, severely infested sites look less productive than they actually are.

Topkill is common in severely infected trees. Foliage in tops of trees with large witches' brooms lower in the crowns gradually become sparse and off-color as the dwarf mistletoe plants and brooms use large amounts of water and nutrients needed for tree growth. Eventually the tops become so weakened they die.

Mortality of Douglas-fir in severely infested stands (stand ratings of DMR 4 or higher) is 3 to 4 times greater than that in comparable non-infested stands in the Southwest. Even stands with mean dwarf mistletoe ratings of 2 or 3 show increased mortality rates over uninfested or lightly infested (stand DMR 1) stands.

Seedlings and saplings, especially those with main stem infections, readily succumb to the parasite. Those weakened by numerous branch infections or large witches' brooms cannot compete successfully with surrounding trees and die.

Severely infected trees typically produce few cones and those that are produced are smaller than normal. Cones from severely infected trees weigh only about one-third of those from healthy trees and have about half as many viable seeds.

Other forest values are affected adversely by Douglas-fir dwarf mistletoe. Risk of wildfires is increased because of the long, thin twigs in witches' brooms in the lower portions of crowns, accumulation of fallen witches' brooms around the bases of infected trees, and increased tree mortality.

Witches' brooms provide fuel ladders for flames to spread upward into tree crowns. The small diameter dead twigs in brooms ignite easily and can serve to spot fires well ahead of the main fire. Mistletoe infected trees are less likely to survive fires than healthy trees.

Large witches' brooms can increase the hazard potential in recreation sites because they are more prone to break and fall than healthy branches as a result of collecting snow and ice or presenting large dense surface areas for wind to blow against.

Dead and dying trees detract from visual quality. Severely infected trees are less capable of resisting attacks by other diseases and insects.

There seems to be no strong relationship with the Douglas-fir beetle *(Dendroctonus pseudotsugae)* but severely mistletoe-infected trees are frequently attacked and killed by secondary insects, such as the flatheaded fir borer *(Melanophila drummondi)*.

Benefits of Douglas-fir dwarf mistletoe have been recognized. The shoots and fruits are eaten by some birds, especially grouse. They also serve as a food source for several species of insects, fungi, rodents and mammals.

Some rodents, such as porcupines and squirrels, feed on bark tissues at infection sites because of the accumulations of starch and nutrients at these locations. The large witches' brooms caused by the parasite are used for hiding, thermal cover, and nesting sites by grouse, hawks, owls, squirrels, porcupines, martens and other wildlife. Northern spotted owls east of the Cascades show an attraction to Douglas-fir witches' brooms for nest sites.

Management

Management of Douglas-fir dwarf mistletoe should consider the role that it plays in the tree, stand, and overall ecosystem in which it resides. Douglas-fir dwarf mistletoe can serve as an important disturbance agent, food for other species, and provide habitat for a variety of organisms. It is a "pest" only when it interferes with accomplishment of management objectives.

In stands where good timber production or intensive recreation use are major considerations, control of dwarf mistletoe may be necessary in order to meet management objectives. However, in areas where timber production or high recreation use are not the principal concerns, Douglas-fir dwarf mistletoe may not adversely influence management objectives and actions could be developed to maintain or possibly increase Douglas-fir dwarf mistletoe populations for wildlife habitat.

The presence of Douglas-fir dwarf mistletoe can thwart accomplishment of tree, stand, and forest management objectives. When this occurs, control of the parasite should be considered. Many traits of Douglas-fir dwarf mistletoe can be used to develop successful management practices: 1) the parasite is host specific, essentially only infecting Douglas-fir, 2) it is an obligate parasite that requires a living host for its survival, 3) spread and intensification are slow and predictable, 4) it is more vigorous in full sunlight than under shade and 5) the disease is rather easily detected because it causes distinct symptoms, the witches' brooms.

Douglas-fir dwarf mistletoe can be managed with cultural treatments that change the vegetative conditions of the tree, stand, or forest. No practical chemical or biological controls are available for treating infected trees and stands.

Good timber volume production is almost impossible in multi-storied, infested Douglas-fir stands. Treatments designed to produce stands with a single canopy layer of Douglas-firs offer the best prospects of preventing unacceptable losses to dwarf mistletoe.

The most effective methods for managing Douglas-fir dwarf mistletoe in timber-producing stands involve killing of all infected trees by cutting (harvesting) and/or burning. Infected trees can be girdled and left standing if they are needed for snags. Dwarf mistletoe plants in a single overstory tree with a crown diameter of 30 feet (10 m) could cast seeds over 6,400 square feet (0.15 acre or 0.06 ha).

To slow invasion of young Douglas-fir stands by dwarf mistletoe from infected border trees, the ratio of perimeter to area of treatment sites should be as low as possible. They should not be long, narrow strips. Advantage should be taken of any potential barriers to dwarf mistletoe spread, such as roads, treeless ridge-tops, natural openings, and changes in timber types when laying out the boundaries of treatment units.

Where clearcutting of dwarf mistletoe-infested Douglas-fir stands is not appropriate, shelterwood and seed tree harvests can be effective alternative even-age management methods. Trees selected to provide shelter or seeds should be uninfected or only lightly infected (DMR less than 3).

Infected shelterwood or seed trees should be removed as soon as Douglas- fir seedlings become established. Failure to remove infected overstory trees in a timely manner will contribute to rapid infection of the developing understory Douglas-firs.

As a general rule, it is desirable to remove the infected overstory before the Douglas-firs in the young stand are 3 feet (1 m) tall or ten years old (whichever comes first). However, in the Southwest few Douglas-firs are infected until they reach heights of 4 feet (1.2 m) or 20 years in age.

In mixed species stands that contain Douglas-firs infected by dwarf mistletoe, silvicultural treatments should retain other tree species. Non-hosts left between infected and non-infected Douglas-firs prevent or slow spread and intensification of the parasite.

Sanitation by removal of infected trees can be an effective treatment in young (10 - 30 years old), lightly infested stands. Lightly infested is defined as those stands in which the numbers of desirable dwarf mistletoe-free trees are sufficient to meet management objectives. Typically these stands would have a stand DMR no greater than 2.

Douglas-firs with one-third or more of their crowns infected by dwarf mistletoe generally decline rapidly about 10 years after they are exposed to full sunlight by thinning. Because of their rapid decline, lightly infected trees should not be left when stands are being sanitized unless they can be expected to reach merchantable size within 15 years.

Pruning of infected branches, in conjunction with sanitation, can further reduce dwarf mistletoe populations, but is seldom effective in eliminating the parasite because latent infections will be missed. Re-examination of stands 5 years after sanitation is desirable to determine if additional sanitation is needed. Moderately and severely infested stands (stand DMR greater than 2) should not be sanitized because many trees with latent infections will be missed, and once these trees are released from competition, the number of dwarf mistletoe plants will increase rapidly within their crowns. Such stands should either be regenerated or left unthinned to avoid their rapid decline.

Latent dwarf mistletoe infections in trees in densely stocked stands and in shaded reproduction are very difficult to detect. It should be assumed that understory trees more than 3 feet (1 m) tall that have been overtopped by infected trees for at least 15 years are probably infected.

Retention of living infected trees, particularly those with large witches' brooms, for use as nesting sites and cover for wildlife is a consideration for some stands. Large diameter trees with brooms confined to the lower halves of trees will survive longer than smaller infected trees overtopped by large trees.

The risk of losing the stand or large numbers of trees to wildfires and other damaging agents can be reduced by clumping the distribution of infected trees into small groups separated by much larger areas free from infection.

Stands that have a uniform distribution of Douglas-fir dwarf mistletoe will experience higher rates of tree mortality from the parasite than those where clumps of infected trees are widely separated from each other. Infected trees with large witches' brooms can be killed by girdling and left standing for use by wildlife.

Forested recreation sites, such as campgrounds, with Douglas-fir dwarf mistletoe infestations may need to be treated to maintain Douglas-firs on the sites for many years and to reduce the risk of injuries and damage to users from breaking branches. Pruning infected trees can prolong their lives and slow or even stop spread of mistletoe to adjacent Douglas-firs. Witches' brooms exert a large drain on infected trees, so their removal by pruning can improve tree vigor and longevity.

All branches with witches' brooms should be cut. Branches below brooms and two whorls above them are also likely to be infected, and should also be pruned, even if brooms are not obvious. Trees may have to be repruned occasionally to remove developing witches' brooms.

The best candidates for pruning are trees with infections only in the lower half of their crowns. In addition to prolonging tree life, pruning can reduce the danger of branches and trees breaking and causing accidents. Pruning branches with large witches' brooms should not be done from January through July to avoid attracting Douglas-fir beetles to the pruned trees. Trees too severely infected to be pruned should be removed if they pose an infection threat to adjacent Douglas-firs or a serious safety hazard to users.

There are natural factors which limit Douglas-fir dwarf mistletoe, including wildfire which has been nature's primary control agent. Several species of insects and fungi attack and kill dwarf mistletoe shoots or fruits. Some of the fungi are common pathogens that can exert considerable local but temporary control of dwarf mistletoe. Environmental factors, currently not completely understood, limit the effectiveness of these fungi to small areas for short durations.

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R6-NR-FID-PR-003-00

May 2004
12.0
WEB Feb 2010

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Forest Health Protection and State Forestry Organizations

Management Guide for
Dwarf Mistletoe

Arceuthobium spp.

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Dwarf mistletoe parasitism reduces the growth, wood quality, seed production ability, and life span of infected host trees. Most western conifer species are host to one or more species of dwarf mistletoe.

Parasitic Plants that cause significant damage to trees

Dwarf mistletoes are small, leafless plants. They are entirely dependent upon their hosts for water, nutrients, and support. These parasites can infect trees of all sizes and ages. They are generally host specific, but the eight dwarf mistletoe species present in the forests of the Northern and Intermountain Regions can infect 21 tree species (See page 12). While they are generally host specific (occur on one principal host species), cross-over does occur into other tree species.

Dwarf mistletoes are the most widely dispersed pathogens in the western United States. Several forces have influenced their distribution across the landscape. Historically, fire has been the foremost factor in affecting dwarf mistletoe population dynamics.

In terms of acres affected, the major tree species impacted by dwarf mistletoes in the Northern and Intermountain Regions are lodgepole pine, Douglas-fir, and western larch (See page 11).

Key Points

- Dwarf mistletoes affect tree growth and form.
- Dwarf mistletoe plants and brooms may be important ecosystem components.
- Control is accomplished by killing infected trees and preventing spread to young trees.

Features of dwarf mistletoes that make them relatively easy to control.

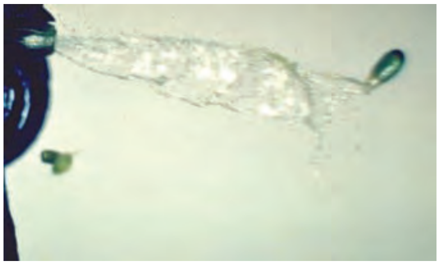
- ⇒ **Dwarf mistletoes are obligate parasites, always requiring a living host in order to survive.**
- ⇒ **They are generally host specific.**
- ⇒ **Dwarf mistletoes have long life cycles (2 to 8 years).**
- ⇒ **Spread and intensification of dwarf mistletoes is slow in a newly infected stand averaging 1 to 2 feet / year.**
- ⇒ **Dwarf mistletoe infections in both trees and stands are easy to detect because of the presence of witches’ brooms, branch and stem swellings, and presence of the mistletoe shoots.**

Life History

According to fossil records, dwarf mistletoes have co-evolved with their hosts for at least the past 40-million years, meaning they have likely filled many ecological niches in many forest landscapes over time.

Both male and female plants can be produced upon the same host tree. Mature fertilized female shoots produce fruits from which seeds are explosively discharged in the late summer and early fall. The average horizontal distance of seed flight is about 20 feet with 90% of the seed landing within 30-feet. The seeds have a sticky coating that enables them to adhere to any surface they contact. Seeds that land on needles and twigs of susceptible species may germinate the following spring and penetrate the bark resulting in new infections.

The equivalent of a dwarf mistletoe root system that develops within the host is called the endophytic system. Growth of this "root-like"system gives rise to specialized structures called "sinkers" that develop within the host wood, providing the parasite with nutrients and water. Success and spread of the sinkers causes a visible swelling on the twig due to distortion of the annual rings and cambial tissues. Several years after infection, dwarf mistletoe shoots emerge on the twig. New shoots require a couple years of maturity to produce seeds.



Dwarf mistletoe seed is explosively discharged.

Management objectives determine desirability of dwarf mistletoes

We are just beginning to value dwarf mistletoes as unique biological species in their own right and to recognize and define their roles as functional components of ecosystems.

It is only during the last 100 years that the roles of dwarf mistletoes in forest ecosystems were defined by humans as being counter to the predominant forest management goal of maximizing timber production.

Dwarf mistletoe parasitism reduces the growth, wood quality, seed production ability, and life span of infected host trees. Stem infections also provide entrance points for decay fungi. For these reasons, and the fact that they infect so many acres, dwarf mistletoes are considered serious pathogens of the forests in the Northern and Intermountain Regions.

Wildfire risk is greatly increased because of dwarf mistletoe infestations, especially in Douglas-fir stands. The large, pendulous brooms usually occur in the lower portion of the crown and are filled with small twigs and dead needles that provide a fuel ladder for upward spread into tree crowns. Brooms broken off by winter storms accumulate around the base of infected trees and increase the fuels on site. It has also been reported by firefighters that large witches' brooms can fall off burning trees on steep hillsides and quickly spread fire downhill via "flaming pinwheels."

On the positive side, dwarf mistletoe seeds and shoots and dwarf mistletoe–affected branches are used in a variety of ways by many animal species.

Ecology: *Fire and Dwarf Mistletoes*

Fire is the foremost factor in affecting dwarf mistletoe population dynamics. Generally any fire event that kills their host trees will reduce the population of dwarf mistletoes, at least in the short term. Large, high intensity burns will greatly reduce dwarf mistletoe populations across a landscape and may even eliminate small, localized populations. Smaller, but more frequent light intensity fires will temporarily reduce segments of a dwarf mistletoe population. However, infected residual trees that survive a fire provide a source of dwarf mistletoe seeds to infect newly developing regeneration. Large and numerous brooms in dwarf mistletoe infected-stands increases the fire potential on a site, greatly increasing the likelihood of returning the forest to an early successional stage through a stand-replacing fire event.

Human influences, including fire suppression and logging have affected dwarf mistletoe distribution and disease severity.

Ecology: *Successional Effects*

In areas where dwarf mistletoes infect trees that are early seral species, dwarf mistletoe-related mortality will advance forest succession toward the climax species. Mortality of large, mature seral individuals provides an opportunity for the release of the shade-tolerant species. Significant mortality generally does not occur until trees are 100+ years of age, when height growth has slowed, allowing infections to move upward and intensify throughout the entire tree crown. Seedlings and saplings of seral species growing under a heavily infected overstory of the same species will be killed at an accelerated rate, further increasing the rate of stand succession toward the climax species.

Dwarf mistletoe shoots and seeds are consumed by a variety of birds, mammals and insects.

Ecology: *Animal Utilization*

There is increasing evidence that important interactions exist between dwarf mistletoes and animals living in the forested ecosystems where the parasitic plants occur. Bird species, including black-capped chickadees, sparrows, ruffed grouse and blue grouse, are reported to eat dwarf mistletoe seeds, and porcupines and squirrels preferentially eat the bark associated with dwarf mistletoe infection. Dwarf mistletoe shoots can be an important winter food source for many animals including porcupines, mule deer, elk, Abert's squirrels, ruffed grouse and blue grouse. Several insect species are also reported to feed on various parts of dwarf mistletoe plants. Cavity-nesting birds utilize trees killed by dwarf mistletoe, and witches' brooms provide cover and nesting sites for many different birds and mammals. Many species of songbirds and owls are attracted to mistletoe brooms for nesting.

Dwarf mistletoes affect tree growth and mortality

Western larch with brooms caused by dwarf mistletoe infection.

Dwarf mistletoe witches' brooms extract water and nutrients from their hosts thereby reducing the amount of available stored photosynthetic energy that is necessary for tree maintenance and growth. Consequently, witches' brooms grow at a faster rate than the rest of the tree, causing reduction in both tree stem diameter growth and height. Ultimately the witches' brooms become such a drain on the host tree that both the vegetative and reproductive tissues die from the top down.

The more severely infected a tree, the more severe the growth impacts are. Once the dwarf mistletoe has spread throughout the entire tree crown, it usually takes 10+ years for tree mortality to occur. Growth effects and mortality rates generally increase as site quality decreases. Growth loss, as expressed in terms of cubic foot volume, can be quite significant. In addition to direct tree mortality, infected trees are predisposed to attack by other pathogens and/or insects.

Management Strategies

Dwarf mistletoe impacts can be effectively reduced through timing the use of any silvicultural treatments that emphasize the removal or killing of infected branches or trees.

⇒ **Regeneration operations**: The greatest opportunity to control dwarf mistletoes is by the removal of infested stands and replacement with mistletoe-free regeneration.

⇒ **Precommercial thinning**: Lightly infested precommercial stands can be brought through to rotation age using sanitation thinning operations but heavily infested stands may not benefit from sanitation thinning.

⇒ **Commercial thinning**: Select leave trees with a dwarf mistletoe rating (DMR) of 3 or less, preferably those with infections in the lower crown.

⇒ **Chemical control**: The chemical, Florel ® is registered for dwarf mistletoe control. It doesn't kill the parasite but prevents seed production for a short period of time(one to three years).

⇒ **Prescribed fire**: Western dwarf mistletoe (*A. campylopodum*) has been reduced somewhat in ponderosa pine stands using prescribed underburning. Heavily infested trees were less than half as likely to survive underburning than their healthy counterparts.

Assessing Dwarf Mistletoe Infection in Stands

Dwarf mistletoe management should only be considered after an analysis of the impacts that the parasite has in the trees, stands, and ecosystems they inhabit. One tool has been used for over 25-years to standardize the quantity of dwarf mistletoe parasitism within a stand. The Hawksworth 6-class dwarf mistletoe rating system (DMR) provides a quantitative reference scale for determining the relative population status of a dwarf mistletoe infestation within a stand and its potential for spread and intensification.

Partial cutting creates multi-storied stands, which serves to increase the distribution and intensity of dwarf mistletoe.

The 6-class dwarf mistletoe rating system (DMR)

(Hawksworth 1977)

Instructions

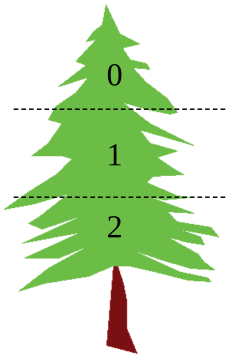
STEP 1. Divide live crown into thirds.

STEP 2. Rate each third separately. Each third should be given a rating of 0, 1 or 2 as described below.

- (**0**) No visible infections.
- (**1**) Light infection (1/2 or less of total number of branches in the third infected).
- (**2**) Heavy infection (more than ½ of total number of branches in the third infected).

STEP 3. Finally, add ratings of thirds to obtain rating for total tree.

Example



If this third has no visible infections, it's rating is (**0**)

If this third is lightly infected, it's rating is (**1**)

If this third is heavily infected, it's rating is (**2**)

The tree in this example will receive A rating of **0+1+2=3**.

Dwarf mistletoe management is based on the five biological characteristics of this parasite

(See "Features of Dwarf Mistletoes… on page 1).

Management of Dwarf Mistletoe in Stands

Human influences, including fire suppression and logging have also affected dwarf mistletoe population dynamics. In many cases, dwarf mistletoe intensity has been increased by partial cutting. Conversely, dwarf mistletoe populations may have been reduced in certain age-classes, habitat types, elevation zones, or topographic positions that have been intensively managed. Fire suppression and cutting practices that encouraged shifts in species composition may increase or decrease disease severity depending on the species of trees and dwarf mistletoes present on the site.

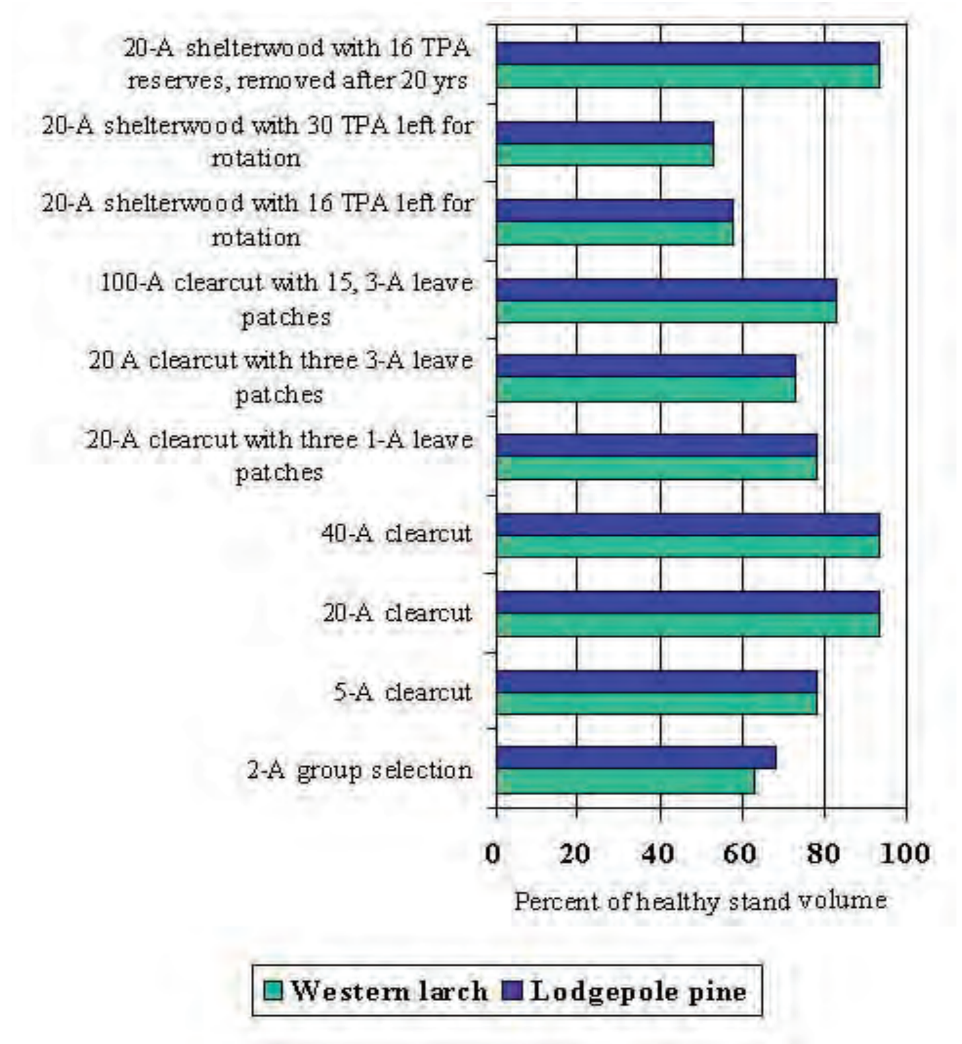
Dwarf mistletoe impacts can be effectively reduced through timing the use of any silvicultural treatments that emphasize the removal or killing of infected branches or trees. Direct control is usually only necessary when the parasite interferes with accomplishment of clearly defined land management goals.

Management

Regeneration Operations -

These methods include the use of clear cuts, and seed tree and shelterwood operations. A possible downside of clearcutting in some ecosystems is that it leads to the establishment of an even-aged stand. However, if mistletoe control is successful at time of regeneration, it is usually possible to convert the stand to an uneven-aged state in subsequent rotations.

Clear cuts in infested stands should have as large of an area/perimeter ratio as possible to minimize edge effects and reinvasion from bordering stands (see graph below). Preferably, the harvest unit should be at least 20-acres in size, and narrow strips should be avoided.



Expected productivity of western larch and lodgepole pine stands with moderate initial dwarf mistletoe infection rates with a variety of management methods. Analysis results for western larch using northern Idaho variant of the Forest Vegetation Simulator (Wykoff and others 1982), and for lodgepole pine using the eastern Montana variant. Percent of non-infected stand merchantable cubic-foot volume at 120 years of age.

The dwarf mistletoe spread rate is fastest in multi-storied stand conditions where mistletoe seeds from infected overstory trees "rain down" on susceptible understory trees.

In evenaged stands, the spread rate is faster in single species stands than in mixed species stands, and the rate decreases as stand density increases.

The Forest Vegetation Simulator (Wykoff and others 1982) is a stand based tree growth regeneration and mortality model developed by the US Forest Service.

This model is widely used to predict forest productivity and composition under a variety of site and management conditions.

Wykoff, W. R., N. L. Crookston, A.R. Stage. 1982 User's guide to the Stand Prognosis Model. USDA-Forest Service, Intermountain For. And Range Exp. Sta., Gen. **Tech. Rep. INT-133. 112P.**

Management: Regeneration Operations

Whenever possible, cutting unit boundaries should be located in non-infested stands, and take advantage of natural and/or manmade barriers such as roads, meadows, natural openings and species type changes.

In shelterwood and seed tree operations, it is essential to leave non-infected trees. However, if only infected trees are in the treated stand, silvicultural objectives may be met by retaining trees with a dwarf mistletoe rating (DMR) of 3 or less, providing they are felled, girdled, or removed before the regeneration is 3 feet tall or 10-years old. If non-susceptible species are present, it may be desirable to favor these species as leave trees for shelter, to meet management objectives, or for regeneration purposes. Infected overstory trees may be left if the site is regenerated with a non-susceptible species. This is frequently the best option in recreation or riparian areas.

It is essential to leave only uninfected seed trees or shelterwood trees unless they will be removed before the regeneration is three feet tall or ten years of age.

Management: Thinning Operations

Precommercial Thinning

Lightly infested precommercial stands can be brought through to rotation age using sanitation thinning operations. The stand should be surveyed to determine the degree of infestation when deciding whether or not sanitation thinning is practical. If an acceptable stocking level of noninfected trees will be left following thinning little growth loss will occur. If heavily infested stands remain, severe growth losses may occur. It is generally recommended that sanitation thinning should be attempted only if < 40% of the trees of the susceptible species are infected and the average stand DMR is 3 or less. In stands with higher infection levels, the removal of infected trees will reduce stocking below acceptable levels. In these cases, it would be better to adjust the spacing guidelines to retain more trees per acre on the site. A denser stand will slow both individual tree growth and the expansion of dwarf mistletoe intensity within the stand.

Commercial Thinning

Stands should be surveyed for the level of dwarf mistletoe infestation before treatment is prescribed. If timber growth and yield are not the objectives of the stand, it is possible that control measures will not be warranted at this time. However, if growth and yield are major concerns, the following guidelines can be followed. It is known that significant growth losses do not occur until trees reach a DMR >3. Therefore, it is advisable to select trees for removal that have a DMR > 3. Trees with DMR 3 and less, especially those with infections limited to the lower 1/3 of the crown, will probably not incur major growth effects, as the anticipated growth of the thinned trees should exceed the dwarf mistletoe impacts. It is also important to consider the time of harvest and site quality. If time until harvest is short, or if the site is good, leave trees with moderate levels of dwarf mistletoe infection to maintain stocking.

Management: Chemical Control

Florel ® (active ingredient, ethephon) doesn't kill dwarf mistletoe but does slow the spread.

The only chemical approved by the Environmental Protection Agency (EPA) for use in controlling dwarf mistletoes is Florel (the active ingredient is ethephon), an ethylene-releasing growth regulator that causes mistletoe shoot abscission. Unfortunately ethephon doesn't kill the root-like endophytic system of the dwarf mistletoe, and the parasite resprouts quickly. However, the chemical does delay production of dwarf mistletoe seeds, which postpones spread of the parasite by 2 - to 4-years. High-valued trees in recreation, residential, or commercial sites may benefit from applications of ethephon to control dwarf mistletoe spread and intensification.

Management: Prescribed Fire

Dwarf mistletoe brooms may provide fuel ladders to move fire from the ground to the crown.

Fire has long been recognized as the most important single factor governing the natural distribution and abundance of dwarf mistletoes, however, there are few studies and papers on fire-mistletoe interactions. Dwarf mistletoe-infested stands have been measured and demonstrated to have higher total fuel loadings compared to un-infested stands. Moreover, dwarf mistletoe-infected branches are larger, more resinous, and persist longer than healthy branches. In these ways dwarf mistletoe infections increase the fire risk within an infected stand.

Direct Control by fire:

Western dwarf mistletoe can be partially sanitized from both thinned and unthinned ponderosa pine stands using prescribed understory fires. It is essential, though, to attain scorch heights 30- to 60% of the crown length to significantly reduce dwarf mistletoe infestations. On ponderosa pine on the south rim of the Grand Canyon infected with southwestern dwarf mistletoe, it was found that a larger proportion of tree crowns were scorched because infected trees have highly flammable witches' brooms in the lower portion of the live crown. With equal amounts of crown scorch in the 40 to 90% range, the probability of survival of heavily infested trees was less than half that of healthy trees. Mortality of dwarf mistletoe infected trees following the prescribed fires ranged from 9% to 36%.

Indirect effects of fire:

The effects of heat and smoke from fires need additional study. One study found southwestern dwarf mistletoe seed germination was reduced to almost zero by exposure to smoke for 60-minutes or longer, but exposing seeds to smoke for 30-minutes had little effect on their germination. Seeds of lodgepole pine dwarf mistletoe were unaffected by 40-minutes of exposure to smoke from fuels with a high moisture content, and germination was even enhanced by 30-minutes of smoke exposure from dry fuels.

Modeling Dwarf Mistletoe Spread and Effects

Growth and yield simulation models have been developed which can be used in the planning of silvicultural decisions. One of the most widely used models throughout the USDA Forest Service in the western United States is the Forest Vegetation Simulator (FVS) model. The dwarf mistletoe impact model is initiated through FVS automatically when mistletoe data is encountered. This process allows the user to estimate dwarf mistletoe effects on yield in stands under different silvicultural treatments.

Analyses of the effects of silvicultural treatments on the estimated volume reduction from dwarf mistletoe in infected western larch and lodgepole pine were presented in the graph on page 6. For the comparison, certain conditions were assumed: 120-year rotation, regenerated stand is 90-100 percent host species, cutting unit edge contains infected residuals, leave-patches and reserve trees are infected, and no sanitation treatments occur during the rotation.

Projected Productivity of Dwarf Mistletoe-infected Stands

	Percent of non-infected stand volume (merchantable cubic feet) at 120 years	
Treatment	**Western larch**	**Lodgepole pine**
2-acre group selection	60-65	65-70
5-acre clear cut	75-80	75-80
20-acre clear cut	90-95	90-95
40-acre clear cut	90-95	90-95
20-acre clear cut with reserves (Three 1-acre leave patches)	75-80	75-80
20-acre clear cut with reserves (Three 3-acre leave patches)	70-75	70-75
100-acre clear cut with reserves (Fifteen 3-acre leave patches)	80-85	80-85
20-acre shelterwood with reserves (16 trees/acre left for rotation)	55-60	55-60
20-acre shelterwood with reserves (30 trees/acre left for rotation)	50-55	55-60
20-acre shelterwood with reserves (16 trees/acre, removed after 20 years)	90-95	90-95

Analysis for larch was done using the northern Idaho variant of the Forest Vegetation Simulator. For lodgepole pine, the eastern Montana variant was used.

Modeling Dwarf Mistletoe Spread and Effects

These simulations suggest that the impacts of dwarf mistletoe on merchantable cubic foot volume increase as the size of the cutting unit decreases and if infected residuals are left standing throughout the rotation. If cutting units are at least 20-acres in size, and residual trees are removed before the regeneration is 10- years old, growth losses may be reduced to as little as 5-10 percent when compared to volume produced in a non-infected stand growing under similar conditions.

Dwarf mistletoes are widespread and damaging in many forest types throughout the northern and central Rocky Mountains.

Distribution of Dwarf Mistletoes

Surveys in the northern and central Rocky Mountains have demonstrated the widepread distribution and, often, damaging effects of dwarf mistletoes in conifer forests. The overall distribution and intensity of these parasites changes slowly through time as host age and abundance changes. The following tables show the estimated percent of area by forest types on National Forest lands which are infested by dwarf mistletoes.

Distribution of Dwarf Mistletoes in the northern and central Rockies

UTAH	Percent Acres Affected by Forest Type			
National Forest	**Lodgepole pine**	**Ponderosa pine**	**Douglas-fir**	**Western larch**
Ashley	45	0	8	0
Dixie	__	20	10	__
Fishlake	__	0	9	__
Uinta	12	0	10	__
Wasatch-Cashe	34	0	9	__

(Continued on page 11)

Distribution of Dwarf Mistletoes in the northern and central Rockies

(continued from page 10)

WYOMING				
National Forest	**Lodgepole pine**	**Ponderosa pine**	**Douglas-fir**	**Western larch**
Bridger-Teton	53	—	14	—

NEVADA				
National Forest	**Lodgepole pine**	**Ponderosa pine**	**Douglas-fir**	**Western larch**
Humboldt	*	*	*	*
Toiyabe	17	20	15	—

IDAHO	**Percent Acres Affected by Forest Type**			
National Forest	**Lodgepole pine**	**Ponderosa pine**	**Douglas-fir**	**Western larch**
Boise	40	20	30	10
Caribou	52	—	21	—
Clearwater	9	*	1	55
Idaho Panhandle	10	*	10	55
Nez Perce	40	*	55	50
Payette	40	28	30	21
Salmon	49	0	45	—
Sawtooth	70	0	53	—
Targhee	60	—	40	—

MONTANA	**Percent Acres Affected by Forest Type**			
National Forest	**Lodgepole pine**	**Ponderosa pine**	**Douglas-fir**	**Western larch**
Beaverhead	52	*	—	—
Bitterroot	44	*	43	40
Custer	28	*	—	—
Deerlodge	47	*	—	—
Flathead	18	*	1	34
Gallatin	42	*	—	—
Helena	35	*	1	15
Kootenai	23	*	10	50
Lewis & Clark	37	*	—	—
Lolo	23	*	17	30

*** insufficient survey data available; — dwarf mistletoe not found on this Forest**

Dwarf mistletoes in the Northern and Central Rockies

Dwarf mistletoe species	**General location**	**Principal Host**	**Secondary Host**	**Occasional (o) or Rare (r) hosts**
A. abietinus, f.sp. concoloris White fir dwarf mistletoe	Southern Utah and Nevada	White fir		Subalpine fire (o)
A. americanum Lodgepole pine dwarf mistletoe	Idaho, Montana, Wyoming, Northern Utah and far western Nevada.	Lodgepole pine		Ponderosa pine (o) Whitebark pine (o) Limber pine (o) Engelmann spruce (o) Blue spruce (r) White spruce (r) Douglas-fir (r)
A. campylopodum Western dwarf mistletoe	Western Nevada and, rarely, in northern Idaho.	Ponderosa pine and Jeffrey pine		Lodgepole pine (o)
A. cyanocarpum Limber pine dwarf mistletoe	Dispersed in Idaho, Montana, Utah, Wyoming and Nevada	Limber pine, Whitebark pine,Great Basin bristlecone pine	Western white pine Mountain hemlock	Engelmann spruce (r) Lodgepole pine (r) Ponderosa pine (r)
A. divaricatum Pinyon pine dwarf mistletoe	Nevada and Utah	Singleleaf pinyon and common pinyon pines		
A. douglasii Douglas-fir dwarf misteltoe	Idaho, western Montana, Utah and one location in eastern Nevada	Douglas-fir		Grand fir (o) Subalpine fir (r) Engelmann spruce (r) Blue spruce (r) Limber pine (r)
A. laricis Larch dwarf mistletoe	Northern Idaho and western Montana	Western larch	Lodgepole pine Mountain hemlock Subalpine fir	Grand fir (r) Engelmann spruce (r) Ponderosa pine (o) Western white pine (r) Whitebark pine (o)
A. vaginatum**, subsp. **cryptopodum Southwestern dwarf mistletoe	Southern Utah	Southwestern ponderosa pine		Rocky Mountain bristlecone pine (o) Southwestern white pine (r) Limber pine (r)

Recognizing Dwarf Mistletoe infections

Dwarf mistletoe plants appear as perennial shoots, either simple or branched. Length varies from less than 1-inch in the case of Douglas-fir dwarf mistletoe, to nearly a foot-long in the case of southwestern dwarf mistletoe in Utah. They may occur as tufts or be scattered along the young twigs. Shoots are jointed with opposite pairs of scale-like leaves at the top of each segment. Color varies from yellow to purple to brownish-green or olive-green. If the shoots have dropped, the small basal cups from which they developed often remain on the bark.

It is far easier to identify dwarf mistletoe infections from the symptoms they cause to their host trees than to look for the plants. Even from a long distance, infected stands can be noticed by the presence of deformed, stunted, spike-topped, dead and dying trees. Infected trees are most easily recognized by witches' brooms, a pendulous dense cluster of small twigs on a branch, and/or swellings or other abnormalities on the branches and tree stems.

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An Ecologically Integrated Approach to Management of Dwarf Mistletoe (*Arceuthobium*) in Southwestern Forests

Southwest Forest Alliance
May 5, 1995

by
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An Ecologically Integrated Approach to Managing Dwarf Mistletoe (*Arceuthobium*) in Southwestern Forests

Abstract

Dwarf mistletoes (*Arceuthobium* species) are a group of vascular plants that parasitize conifers. These plants are integral part of forested ecosystems, and have existed as part of the coniferous forests of North America since the Miocene. Dwarf mistletoe is important to the ecology of these systems. The fruit, foliage and pollen of dwarf mistletoe are a food source for numerous bird, mammalian and insect species. Dwarf mistletoe alters the growth patterns of infected trees, creating structural complexity within forests in the form of witches brooms and snags, both which are used by numerous wildlife species for nesting, roosting and cover. These mistletoes are considered serious pests (by silviculturalists) throughout much of Western North America because they infect, and can reduce the growth rates of commercially important conifers. In the Southwestern United States, ponderosa pine is the primary commercially important species infected by dwarf mistletoe. Land use activities in Southwest forests during the past 125 years have encouraged the spread of dwarf mistletoes. Many of the silvicultural challenges created by these parasites are exacerbated by ecologically insensitive land management policies such as fire suppression, livestock grazing, and inappropriate silvicultural techniques. In general, dwarf mistletoe only becomes a problem when land managers attempt to create highly productive forests or tree farms to grow timber far in excess of historical production rates. The damaging effects of mistletoe can best be minimized, and their ecological benefits maximized, by recreating forest stands with age, size and density distributions similar to the original, presettlement forests.

Introduction

Dwarf mistletoes (*Arceuthobium* species) are an integral component of most coniferous forests in western North America. Dwarf mistletoe range from central Canada and southeast Alaska to southern Mexico (Fig. 1). The western United States and northwestern Mexico are the center of diversity for this genus, containing 24 of the known 32 species in the world 31. *Arceuthobium* utilize a wide variety of conifers as their hosts, although most species prefer pines 31. Two important *Arceuthobium* species quite prevalent in the Southwest are *A. vaginatum* and *A. douglasii*, which infect ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*), respectively. This paper examines the ecology of these and other parasite-host complexes, but is primarily focused on applying this information to the management of Southwest ponderosa pine forests.

Arceuthobium are well known to most silviculturalists in the Southwest because they diminish the cash value of Douglas fir and ponderosa pine, the regions most commercially important conifers60. Accordingly, concerted efforts have been made to rid forests of these plants on federal lands. However, such a strategy is not wise (or feasible). Fossil records clearly show that *Arceuthobium* species have been associated with North American coniferous forests since the Miocene (12-26 million years BP) 39. Over this vast expanse of time, many species have adapted to and are perhaps even dependent on mistletoes. Numerous species of birds, mammals and arthropods have been observed feeding on the fruits and foliage of mistletoe, while other birds and mammals utilize the witches brooms created by the mistletoe as nesting platforms or roosting sites (Appendices 1 and 2). Witches brooms are abnormal branches found on trees infected by *Arceuthobium*. These brooms contain dense patterns of interconnecting twigs and branches, forming a unique structural element in the forest that has many ecological benefits.

Although dwarf mistletoe and witches brooms are integral components of Southwest forests, the primary focus of forest managers in the National Forests has been to eliminate them. Because of the agencys overwhelming focus on timber production, most dwarf mistletoe research sponsored by the Forest Service has been focused on control methods, with little attention being paid to their ecological importance (e.g. see symposia proceedings by Scharpf and Parmeter 1978, Hawksworth and Scharpf 1984). Dwarf mistletoe control projects have traditionally been pursued by the Forest Service in order to maximize timber production. As a result, attention has been focused on management techniques to produce more merchantable trees at the expense of managing for ecosystem health. There is an urgent need for the Forest Service to reevaluate its current strategy for managing dwarf mistletoe, and to adopt an integrated ecosystem perspective that manages for forest ecosystem integrity, rather than waging a war (sensu Wicker, 1984) against dwarf mistletoe 74. In this paper we examine three crucial issues related to dwarf mistletoe in Southwest forests in the hopes of bringing a more enlightened approach to the management of these forests: (1) The biology and ecological importance of dwarf mistletoe, (2) how fire suppression, livestock grazing and silvicultural practices have altered the interaction of dwarf mistletoe with its environment, and (3) integrated, ecosystem-based strategies for managing dwarf mistletoe.

The Importance of Dwarf Mistletoe to the Ecology of Southwestern Forests

Figure 1. Distribution of *Arceuthobium* in North America (from Hawkinsworth & Wiens 1972)

Dwarf mistletoe interacts with other plants and animals in Southwest forests in several ways: (1) their fruit and foliage provide a food source to animals (2) the brooms they help form adds short-term structural complexity to the forest, and (3) by hastening the death of trees, they help to create snags, which are an important source of long-term structural complexity and wildlife habitat. Additionally, by influencing the amount of dead wood in a forest, they indirectly affect fire intensities, and thus the successional dynamics of forests. This latter topic will be covered under Fire and Dwarf Mistletoe.

Consumers of Dwarf Mistletoe
There are a number of animals that have been observed eating the fruit and foliage of dwarf mistletoe (Appendix 1). Such species include elk, deer, squirrel, grouse, pygmy nuthatches and mountain chickadees, as well as a number of arthropods [7-11, 16, 23, 40, 71-74]. The relative importance of dwarf mistletoe as a food source for such species is not known, but given the prevalence of mistletoe, it is likely that certain species have come to rely upon it as a food source during certain times of the year. It is known that the foliage of dwarf mistletoe provides a source of food in the winter for grazers, when fresh foliage is scarce. Witches brooms create ideal platforms for trapping snow, making them susceptible to breakage. These breakages provide mistletoe foliage to animals such as elk and deer [9]. Nutritional analyses of dwarf mistletoe indicate that the foliage and berries have high nutritional value for deer, and likely for other species as well [73]. Dwarf mistletoe also helps to provide food for other species early in the spring. Branches of conifers such as Douglas fir, that are infected with dwarf mistletoe,

break bud (bud out) earlier in the spring than do uninfected twigs, providing a food source for certain insect groups [70], which in turn provide food for insectivores.

Witches Brooms as Wildlife Habitat

The habitat created by witches brooms is important to a number of birds and mammals. Forests infected with mistletoe have been strongly correlated with the biodiversity of birds in Ponderosa pine forests [8], in part because of the brooms, which provide ideal platforms for nesting and cover. It is well documented that birds of prey such as accipiters and owls use witches brooms as nesting sites [20, 40, 53, 45, 46, 12, 11]. These birds seem to prefer the large brooms found up high in older trees. The formation of such a broom requires infection of a large tree, because young trees that are infected tend to die before they reach a large size. These large brooms provide visual protection from predators both above and below. It is quite difficult to determine whether a broom contains a nest when viewed from the ground (as many researchers have discovered). A well-disguised nest in a large broom can also be difficult to detect from the air, providing protection against predators such as the great horned owl [46].

Available evidence suggests that the size of the broom needed for nesting is a function of bird size [40, 53, 45, 46, 12, 11]. Therefore, it is likely that current logging practices, which preferentially remove large trees, tend to have a disproportionately larger impact on big birds of prey. This habitat need may partially explains why two birds of the Southwest which use brooms as nesting sites, the Mexican spotted owl and the Northern goshawk are listed as endangered and as sensitive, respectively, by the U.S. Fish and Wildlife Service and the U.S. Forest Service. Several recent studies have demonstrated that the spotted owl shows a marked preference for witches brooms as nesting sites [68, 24, 65]. Of all the nests examined in these studies, 153 out of 359, or 43%, were associated with witches brooms [68, 24, 65]. This is particularly remarkable in light of the fact that large brooms of sufficient size for nesting are rare in Southwest forests. It is quite possible that given an abundance of brooms to choose from, an even higher percentage of spotted owls would nest in these structures.

The list of animals known to utilize brooms as nesting platforms is extensive, but not exhaustive. There have been no thorough studies to determine which Southwestern birds and mammals use brooms. They may well be crucial habitat for other endangered species. Other birds known to use brooms as nesting sites include the Coopers hawk, great gray owl, long-eared owl and others (see inset and Appendix 2).

It is well known that species associated with ponderosa pine forests are declining in numbers and that bird diversity is decreasing. Bird surveys conducted yearly since 1968 in logged ponderosa pine forests in New Mexico indicate that 75% of all bird species are declining [44]. Overall, about 25% of all species associated with ponderosa pine forests are declining [21, 32]. How much of this is attributable to the loss of witches brooms is uncertain, but the growing list of birds that use witches brooms as nesting sites that are also experiencing population declines, suggests that the loss of this important habitat feature may at least in part be contributing to the loss of biodiversity in Southwest forests.

Dwarf Mistletoe and Snag Formation

Dwarf Mistletoe as Food forWildlife

For numerous birds and mammals, dwarf mistletoe is an important part of their diet. The foliage and berries of these plants are highly edible. Twelve wildlife species have been documented in the scientific literature as eating dwarf mistletoe, including game animals such as elk, deer and grouse. It is known that dwarf mistletoe is highly nutritious, and if more research efforts were put towards learning about their ecology (rather than studying ways to eliminate them), we would likely find that many more wildlife species use these plants as a food source.

Wildlife known by science to eat dwarf mistletoe.

Mammals
Elk
Porcupine
Mule Deer
White-tailed Deer
Yellow Pine Chipmunk
Red Squirrel

Birds
Blue Grouse
Spruce Grouse
Band-tailed Pigeon
Thrushes
Black-headed Grosbeak
Black-capped Chickadee

One of the most important ecological functions of dwarf mistletoe is to increase the rate of snag formation in Southwestern forests. Mistletoe has always existed as a stand replacing mechanism that has helped to create ecologically important large snags, while simultaneously opening up the canopy to allow for the establishment of young trees. Mistletoe infections eventually result in death for many trees, and the average life span of infected trees is considerably shorter than uninfected trees [29]. In general, infected large trees live longer than infected small trees, although precise relationships between tree size or age and post-infection longevity are not known. Snags are an important resource for many species of cavity nesting birds and mammals [63, 52, 48]. The number of snags and cavity nesting birds in Southwest forests are correlated to the degree of mistletoe infection 8. Much of the recent decline in cavity nesting birds in southwest forests has been attributed to the loss of large snags. Bird species diversity and numbers in the Southwest have been positively correlated with the density of mature live ponderosa pines and snags [3]. Snags are used by 85% of North American birds [37], at least 49 species of mammals, and many reptiles, amphibians and invertebrates [19]. Thirty percent of all North American birds nest in snags [47] and forty bird species nest in ponderosa snags [64]. Secondary cavity nesters alone make up 33% of breeding bird species, and 40% of total breeding bird pairs in ponderosa pine forests [4]. Eighty two percent of secondary cavity nesters breed exclusively in dead and dying trees [4], while between 60 and 94% of overwintering ponderosa pine-associated birds require snag roosts [69]. In addition to nesting and roosting sites, snags and broken-tops are used as drumming posts, song perches, hawking platforms and foraging.

Large snags are preferred by primary and secondary cavity nesters. Seventy five percent of cavity nests on the Coconino National Forest are in trees > 24 inches dbh 17, while the mean dbh for trees containing cavity nests on the Apache-Sitgreaves National Forest is 23 inches [63]. The availability of suitable nesting cavities is the primary limiting factor in secondary cavity nester populations sizes [2, 28, 13, 51, 76, 5]. Studies demonstrate that where unlimited nesting and roost sites are available, other factors such as availability of food, do not affect population sizes [41]. Mature forests are the most favorable to cavity nesters because of their abundance of large dead and dying trees. The removal of these trees in managed forests dramatically decreases the number and diversity of secondary cavity nesters. The loss of natural bird diversity in managed forests has been well documented, and the general decline is largely accounted for in the disappearance of cavity nesting species [27].

Because large trees infected with dwarf mistletoe have been viewed as infection centers for nearby smaller trees, the Forest Service has promoted a policy of removing these large trees [55]. Such a management strategy removes the next generation of large snags, leading to the long-term loss of prime rearing habitat for cavity nesting birds.

Witches Brooms and Wildlife

The witches brooms created by dwarf mistletoe are important nesting sites for birds and mammals. Scientists have determined that where these structures are abundant in Southwest forests, bird diversity is very high and where they are absent, diversity is low. Brooms create an ideal platform for nesting, especially for large birds such as raptors. The dense cover provided by brooms helps to conceal nests, making them hard to detect by predators on the ground and in the air. Eighteen wildlife species have been documented in the scientific literature as nesting in witches brooms, including such rarities as the Mexican spotted owl and the northern goshawk.

Organisms known to use witches brooms as nesting sites.

Mammals

Aberts Squirrel
Pine Squirrel
Red Squirrel

Birds

Mexican Spotted Owl
Northern Goshawk
Long-eared Owl
Great Gray Owl
Sharp-shinned Hawk
Coopers Hawk
Gray Jay
Western Tanager
Chipping Sparrow
American Robin
Hermit Thrush
Cassins Finch
House Wren
Pine Siskin
Red Crossbill

Fire and Dwarf Mistletoe

Fire was historically an integral component of forest development in the Southwest, and helped to control the spread of dwarf mistletoe by: (1) keeping overall tree densities low, (2) selectively destroying infected trees and stands, and (3) pruning infected limbs from live trees. Additionally, smoke from fires may have inhibited dwarf mistletoe seed germination.

Today, the number of trees per acre on some southwestern pine forests are one to two orders of magnitude higher than during pre-European times 15. The reasons for this increase are discussed below under the Land Use Practices section. High stand densities contribute to the spread of dwarf mistletoe by placing more trees within the range of dwarf mistletoe seed dispersal from infected trees.

Estimates of pre-European tree densities range from 9.3 to over 150 trees per acre in the ponderosa pine type, depending upon growing conditions and method of measurement [14, 15, 38]. Forests tended to be more open at lower elevations, on southern exposures, and on poor soils. Forest were denser in wetter, cooler areas and on richer soils. While a complete picture of pre-European forests has yet to be established, it is clear that in many areas, todays ponderosa pine forest is thicker than in the past. As a result, mistletoe may spread from tree to tree more easily than in the past.

Additional evidence suggests that some ponderosa pine forests had a clumped distribution, with small clusters of trees imbedded in a grassland matrix [15]. The areas of grass between tree clusters likely formed barriers to the dispersal of mistletoe seed, helping to limit infections to isolated patches of trees. It must be emphasized that the density of presettlement southwest forests was quite variable and that some of the more productive forests were dense enough to facilitate the spread of mistletoe by direct dispersal. We simply use some estimates of presettlement tree densities to show that historically, there were many forests where the rate of spread of mistletoe infections was likely quite low, and infections were not as widespread as they are today.

There is also evidence to suggest that infected trees are weeded out by fires [1]. Because witches brooms contain highly resinous, flammable material, dwarf mistletoe influences the susceptibility of trees to fire. Often, brittle brooms break off of trees, forming a pile of inflammable material at the base of the tree. These broom piles can support a fire of sufficient intensity to kill a tree. In heavily infected stands, there may be enough broom piles and dead trees that the entire stand will conflagrate, killing all trees in a wide area. Such an event, provided it kills all infected trees, serves to sterilize the area of dwarf mistletoe, keeping it free from this parasite for decades [1]. If some infected overstory trees survive however, they can serve as infection centers, raining mistletoe down upon the emerging understory of young trees regenerating after the burn [56]. The historical record suggests that such large, stand destroying fires were rare in ponderosa pine forests [14], and it is likely that most fires stimulated by the presence of brooms and other dead wood resulting from mistletoe infections at most killed only single or small clusters of trees.

It also appears that prior to extensive fire suppression, the heat from frequent ground fires was sufficient to prune back mistletoe infected branches in the lower crowns of ponderosa pines [57, 58]. This served to limit the extent of mistletoe to the upper reaches of the forest canopy [57, 58]. This pruning approach to dwarf mistletoe control has been successfully employed by modern day foresters to increase the longevity of infected stands [62].

There is also evidence to suggest that the smoke from fires was deadly to mistletoe seeds. In an experimental study, researchers found that exposure of mistletoe seeds (*A. vaginatum, A. americanum and A. cyanocarpum*) to wood smoke resulted in a germination rate of less than 5% (as compared to a normal germination rate of 27%) when the seeds were exposed to smoke for an hour [78]. In general, exposure to smoke inhibited germination after 10 minutes, and virtually no seeds germinated after long exposure times (90 minutes). Although the importance of smoke to inhibiting dwarf mistletoe seed germination under natural conditions is not known, this study suggests that it could be important, especially in light of the documentation by early European explorers that ponderosa pine forests were often quite smoky during the summer months, when ground fires were burning [14].

The Biology of Dwarf Mistletoe

The Life Cycle of Dwarf Mistletoe and Short Distance Seed Dispersal

Arceuthobium species have a unique and interesting life cycle that is well adapted to surviving in coniferous forests. The life cycle is illustrated in Figure 2, and has been well described by

Hawksworth elsewhere [31]. The summary presented here is a synthesis of that information. The adult plant produces berries which contain a single seed. As the fruit matures, fluid pressure builds up inside, until the berry finally breaks off the stem. At this moment, the released pressure ejects the seed from the fruit at tremendous velocities, sometimes exceeding 60 miles per hour. Dwarf mistletoe can eject their seeds up to 100 feet under optimal wind conditions, but in general most seeds travel no more than 10-15 horizontal feet from their source, and a tree 40 feet from an infected tree is considered safe from infection. The average, long-term rate of spread for dwarf mistletoe by such short-distance seed dispersal is about 1-2 feet per year, in managed stands. The seed contains a viscous coat, which allows it to stick to any object with which it comes in contact, such as the needles of a conifer. The seeds remain stuck to the conifer needles until they absorb moisture (e.g. during a rainstorm), whereupon they slide down to the base of the needle, adjacent to a twig. Young, needle-bearing twigs are most susceptible to infection. Once in this position, they begin to grow a hypocotyl, or small root, and bore into the outer layers of the twig. At this stage, swelling occurs in the infected area on the tree. About two years after the infection, aerial shoots develop, and two years after that, the female plant develops mature fruit. Dwarf mistletoe are dioecious (literally, of two houses) meaning that the male and female flowers are found on separate plants. Although individual shoots of the plant die after four or five years, the vegetative part of the mistletoe continues to grow, and old colonies are recognizable by the dense and misshapen cluster of twigs and branches known as witches brooms [30].

Figure 2. The probability of being infected by mistltoe seed decreases exponentially as a function of the distance from the seed source (see text for sources).

Long distance seed dispersal

Although the seeds of mistletoe are spread to nearby trees by direct contact upon ejection, animals also serve as dispersal agents, and help to explain why mistletoe plants have been found far from the nearest potential seed source [49]. Birds and small mammals feed on and adjacent to mistletoe as ripe seeds are being ejected, and some of the seeds attach to their bodies. As the animals move to other trees, the seeds may detach. Birds such as mountain chickadees and pygmy nuthatches, which forage on the tips of branches and in the foliage, where seed germination is most likely to be successful, are thought to be particularly important agents of dispersal [33]. Birds apparently do not transfer viable dwarf mistletoe seeds through their feces. Most such seeds passing through the digestive systems of birds will not germinate [77, 33]. The success of seeds dispersed by birds is quite low. One study estimated that in a 150 ha plot of ponderosa pine, there was only one successful long distance infection every four years [33]. A number of birds and mammals, including Stellars jays, red crossbills, Cassins finches, red squirrels, flying squirrels and pine martens have been observed carrying mistletoe seeds on their fur or feathers. A complete list of dwarf mistletoe seed vectors is given in Appendix 3.

Pollination

Wind and insects are both important pollination mechanisms for *Arceuthobium*. There are no specialized pollinators of dwarf mistletoe. Instead they rely on general pollinators and wind. Hundreds of insect species have been identified as carriers of dwarf mistletoe pollen, but only a few dozen have been identified as being important pollinators [26, 50]. These pollinators include dipterans (e.g. flies), hymenopterans (e.g. ants) and coleopterans (beetles). The importance of dwarf mistletoe flower parts (e.g. the pollen and nectaries) as a food source for insects is not well studied. For those seeking more information, several excellent reviews on the pollination biology of dwarf mistletoe have been published [66, 25, 67].

Tree host selection

Whether some trees are more susceptible than others to dwarf mistletoe infestation has long been a subject of interest to silviculturalists. The dwarf mistletoe of the Southwest are fairly host specific, that is, one type of mistletoe only has one primary host. However, there are secondary hosts. For instance, *A. americanum* will sometimes infect ponderosa pine even though its primary host is lodgepole pine. Likewise, spruce and true firs will occasionally host *A. douglasii* even though Douglas fir is the primary host. *A. vaginatum*, which primarily infects ponderosa pine, occasionally infects lodgepole pine [31].

Large areas of apparently susceptible primary hosts are immune to mistletoe infection. For instance, ponderosa pines in the Black Hills area of south Dakota are uninfected *by A. vaginatum*, while *A. douglasii* is generally absent from the Douglas fir forests of the West Coast. Why these areas are immune to mistletoe infections is unknown, but it is thought to be related to climate [61].

Figure 3. Generalized six year life cycle of dwarf mistletoe. Modified from Hawksworth and Wiens (1972).

Climate is also thought to influence the distribution of dwarf mistletoe on a more local scale. Studies suggest that dwarf mistletoe infestations in ponderosa pine forests are most severe on the driest sites, where tree growth rates are slowest , and least severe in wetter habitats [18, 43]. Also, *A. americanum* is absent form the higher ranges of lodgepole pine, apparently because of low temperatures, while *A. vaginatum* is absent from lower elevation ponderosa pine forests, presumably because of high summer temperatures [75]. Topography also affects the distribution of dwarf mistletoe, as they are most abundant on ridges, upper slopes and moderate slopes, and least abundant on steep slopes and valley floors [43]. There is also evidence to suggest that dwarf mistletoe preferentially infect trees on slopes with west and southwest exposure, and prefer stands with moderate site indices and low basal areas [43]. Collectively, these studies suggest that dwarf mistletoe preferentially infect stressed or slow growing trees.

The Effects of Land-Use Practices on the Ecology of Dwarf Mistletoe

Fire suppression, livestock grazing and logging are the primary land use practices that have altered the ecology of mistletoe in the Southwest. Because these land use practices have so radically altered the overall condition of Southwest forests, the changed ecology of dwarf mistletoe is largely reflective of overall changes in Southwest forest conditions. Fire suppression and livestock grazing have both altered the effect of dwarf mistletoe by increasing its infection rate, primarily by increasing stand densities and thus facilitating the direct tree-to-tree transfer of mistletoe. Livestock grazing increases stand densities by removing grasses and exposing bare mineral soil, which is ideal for pine seedling germination . Additionally, the hooves of livestock press pine seeds into the soil, further facilitating germination. Livestock also trample seedlings, but overall, they promote seedling establishment.

Fire suppression has eliminated the fires that regularly swept through forest understories [14]. Historically, these fires were of sufficient frequency to kill most pine seedlings, helping to keep recruitment rates and stand densities low. Though fire suppression is commonly identified as the primary cause of high stand densities, scientific studies have determined that intensive livestock grazing preceeded active fire suppression policies by several decades. As a result of this grazing, fire occurance was greatly reduced long before active fire suppression occured. Other comparative studies also strongly suggests that livestock overgrazing, not fire suppression, is the primary factor that has allowed stands to become overstocked [59, 42, 79]. Studies of paired sites where fire has been suppressed in both sites, but where grazing has occurred in only one site, show that the ungrazed sites have little in the way of conifer regeneration though fire has been suppressed for many decades (e.g. 125 years). Grasses in these systems are known to contain allelochemicals (toxins) that can kill ponderosa pine seedlings [35, 54], further suggesting that competition with grasses is the primary reason why historically, ponderosa pine recruitment rates were low. Such findings strongly suggest that land use practices which destroy the native grass understory may be the primary cause for the rapid increase in pine seedling recruitment. Fire suppression may have played a secondary role in increasing seedling recruitment, as historically, fires only eliminated those seedlings that managed to grow where competition with grasses was minimal.

Past and current logging practices have also contributed to the spread of dwarf mistletoe in Southwest forests. Disturbing soils during timber harvesting, encouraging afforestation at tree densities well above historic levels, and selective harvesting have all contributed to a decline in forest health and encouraged the spread of mistletoe. When soils are disturbed and ground cover is removed during logging operations, stand densities increase because pine seedlings readily germinate and grow on bare mineral soil. Such disturbances are particularly prevalent when heavy machinery is used extensively during timber operations. In general, silviculturalists do not consider such disturbances a problem because undisturbed forests of the Southwest are considered to be stocked at numbers far below their productive capabilities. Thus any activity that artificially increases stand densities, whether it be fire suppression, livestock grazing, or logging activities, is considered beneficial.

Selective tree harvesting that leaves infected overstory trees standing, also contributes to the spread of mistletoe. These large trees rain seeds down upon the new stand that is emerging below, thus infecting an entire new generation of trees, and ensuring that their lives are short. Recognition of this overstory-to-understory transferal of mistletoe infections have lead foresters to conclude that removal of such large trees is the best way to prevent dwarf mistletoe from spreading. However, such thinning practices fail to consider that under normal conditions, there would be minimal tree regeneration (and thus minimal infections) near infected trees, because of fires and competition from grasses. It is more accurate to consider the unnaturally high numbers of regeneration trees as the problem contributing to the spread of mistletoe. Removing the large trees creates a forest that is quite unlike anything that historically existed. This thinning technique, where the largest, most ecologically important trees are removed from the forest, is known as sanitation salvage, and is being practiced by the Forest Service as way to improve ecosystem health. However, the idea that ecosystem health can be restored by simplifying forestsremoving the most important large structural elements in a forest and replacing them with a stand of even aged seedlingsis counter intuitive and ignores basic ecological principles. It is a basic tenet of ecological theory that structurally complex habitats are more diverse than simplified habitats [34], and habitats that are biologically diverse are generally healthy.

If the purpose of removing infected trees is to improve ecosystem health by preventing the spread of mistletoe, then the infected trees can simply be killed and left standing, as mistletoe will not survive on dead trees. Or better yet, simply creating a small donut shaped no tree zone around infected overstory trees, to serve as a barrier to mistletoe seed dispersal, should solve the problem without further impoverishing the forest.

Logging has not only increased the spread of mistletoe in small trees, but has also removed the ecologically important brooms created by dwarf mistletoe infections in large trees. Unfortunately, current forest practices encourage the removal of these structures. Even when the tree are not cut, thinning and pruning operations designed to save stands (so they can later be harvested) typically remove infected trees and limbs from infected trees. These tree and limbs often contain witches brooms, and many of the trees, because they are infected, will soon be snags. Thus, these well intentioned clean up efforts to improve the health of trees, actually reduce the structural elements of a forest that most greatly contribute to overall ecosystem health and biodiversity.

Integrated Management Strategies for Controlling Dwarf Mistletoe

MISTLETOE "CONTROL" AND

Although dwarf mistletoe is frequently referred to as a problem, that needs to be controlled, it is more correctly viewed as a component of Southwest forests that is increasing in abundance because of land use changes that have occurred in the past 125 years. The spread of mistletoe is symptomatic of the decline in the health of Southwest forests that has occurred because of these changes. Specifically, livestock grazing, fire suppression and certain logging practices have all contributed to the decline in forest health and to the spread of dwarf mistletoe. An integrated management strategy that restores some of the fundamental components and processes that historically existed in these systems would largely eliminate the mistletoe problem. We refer to this strategy as integrated because the components (outlined below) are interrelated. All components need to be incorporated into an overall management plan for any one of them to work correctly. Such an integrated strategy would include the following fundamental components:

1. *No cutting of large diameter trees and snags*. There is no justifiable ecological or forest health reason for removing large trees or snags. Mistletoe infections are a normal ecological process whereby large trees are converted into snags. The live infected trees today are the snags of tomorrow. Unfortunately, large trees and snags are relatively rare components of Southwest forests because of past and current timber harvesting activities. There really are very few truly large trees left. The smaller ranges of trees today classified by the Forest Service as large (17 in > dbh < 24 in) [36] were not even considered to be merchantable less than 90 years ago [3]. However, the largest existing trees do provide the best current habitat, and will provide a future source of large snags. Therefore, they should not be removed. If a tree is infected with mistletoe and it is determined that the tree should be killed because it poses a high risk of infection to other ecologically important trees, then it should be killed and left standing, to serve as snag habitat.
2. *Thin understory trees* to create stand structure and densities that approximate presettlement conditions. The overstocked young forests of today facilitate the spread of dwarf mistletoe and in some instances, present a fire hazard to large, ecologically important trees. Any thinning operation, however must leave the

THE DISAPPEARANCE OF LARGE TREES

The Elk Timber Sale

The Elk Timber Sale, on the Lakeside District of the Apache-Sitgreaves National Forest in eastern Arizona, is a classic example of mistletoe control being used as a rationale for cutting large trees. Because of previous logging, the Lakeside District has no remaining old growth at all. The few moderately sized trees which do exist are clumped in pockets of 3-10 trees surrounded by acres of young pines. Though much smaller than the giant pines which once blanketed this area, the largest trees remaining are still of exceptional wildlife and recreation value. On the Elk Timber Sale, trees larger than 16 inches dbh make up just 3% of the landscape, while trees less than 9 inches dbh cover 70% of the area (Fig. 4).

Figure 4. Although large trees make up a small percent of all trees in the Lakeside District, they continue to be disproportionately harvested at a non-sustainable rate.

With the Elk Timber Sale, however, the Forest Service chose to log many of the rare large trees for mistletoe "control" and to encourage the growth of vast numbers of small trees. According to their Environmental Assessments, "Large ponderosa pines can not only spread mistletoe downward if infected, but can effect growth of the understory (i.e. small trees) by shading and utilizing water and nutrients with the massive root systems." And, "Removal of infected trees will allow residual trees to live longer, allowing nearby stands with smaller diameter trees to grow faster..."

Tragically, many of the large trees logged for mistletoe control were in old growth reserves (mature forests to be left undisturbed so they can develop into old-growth forests) and protected Northern goshawk nesting territories. Twenty seven percent of the trees did not even have any verifiable infection. The Forest Service claimed

largest trees in a stand intact. The current Forest Service practice of removing large overstory trees during thinning operations is an ecologically destructive practice that degrades ecosystem health. Understory thinning will slow tree-to-tree spread of dwarf mistletoe or limit it to isolated clusters of trees. All downed small diameter trees and slash should be removed to reduce the forest floor fuel load and minimize fire hazards. Current and historic logging practices which leave large volumes of slash in the forest increase fire threats and beetle infestations.
3. *Reestablish regular ground fires* in order to minimize seedling survival and to prevent the accumulation of fuel. Although crown fires did occur on occasion, the historical record suggests that they were rare in ponderosa pine forests. Hence, crown fires should not be encouraged. Before fires are reintroduced, forest understories need to be thinned and accumulations of forest floor fuels must be removed to prevent intense fires from killing the few remaining large trees. Although fires, if controlled properly, will improve forest health, it is essential that large trees be protected or the ecological benefits that occur because of burning may be outweighed by the loss of the big trees that take centuries to replace. Given the rarity of large trees, it is extremely important to remove fuel near their bases to prevent their untimely demise. The frequency of ground fires should approximate presettlement fire frequencies.
4. *Reduce livestock densities* to a level that will allow a relatively continuous ground cover of herbs and grasses to develop where light, soil and moisture conditions would normally support such vegetation. Once forests are thinned and opened up, they will simply return to their pre-thinning densities if livestock remain to prevent the reestablishment of ground cover. In areas where the ground cover has been eliminated, livestock should be completely removed until the vegetation has recovered. Future introductions of livestock in such areas should occur on a limited basis and under careful monitoring. Should the ground cover begin to degrade, livestock should be removed again until vegetative recovery is complete. In general, livestock should only be grazed in forests where there is a relatively complete ground cover, and in these areas, only at densities and frequencies low enough to prevent increases in the extent of exposed mineral soil. Experimental evidence from other arid systems (e.g. eastern Oregon) suggests that removing livestock from degraded areas will improve foraging opportunities [22]. This suggests that removing livestock from damaged Southwest forests may, in the long run, improve ecosystem health *and* provide more livestock forage.

that these trees, had latent infections, or were in excess of the number of large trees needed, even though the District has no old growth and is deficient in all large tree classes.

Sources:
USFS. 1992. Environmental Assessement & 1994. Environmental Assessment Supplement Elk Timber Sale. USDA Forest Service, Apache-Sitgreaves National Forest, Springerville, AZ.

Continued on next page

Summary

The spread of dwarf mistletoe throughout Southwest forests is linked to the overall decline in forest health that has resulted from 125 years of excessive grazing, logging and fire suppression. Most problems associated with dwarf mistletoe can be solved by managing these forests for ecosystem integrity rather than timber protection or livestock forage. Much of the spread of dwarf mistletoe is directly attributable to artificial attempts at increasing timber yields above historic levels. Fire suppression, livestock grazing and logging have all contributed to the spread of dwarf mistletoe. Although there are legitimate concerns about the spread of dwarf mistletoe, management plans must recognize the importance of these plants to forest ecology. Dwarf mistletoe is an integral component of Southwest forests, providing food, shelter and nesting sites for wildlife, and in general

MISTLETOE "CONTROL" AND THE DISAPPEARANCE OF LARGE TREES

The Rocker Timber Sale

In 1991, the Forest Service announced plans to log a portion of the Gila National Forest in New Mexico, in what became known as the Rocker Timber Sale. Dwarf mistletoe, the announcement stated, was not a severe problem. A year later, the Forest Service unexpectedly announced that mistletoe was a severe problem on over 1,600 acres. Overnight, the Rocker Timber Sale was transformed into a mistletoe "control" project, and shortly thereafter the largest trees were logged under the guise of disease control. According to the increasing biodiversity. Land managers need to focus on maximizing the ecological benefits of dwarf mistletoe, while researchers need to learn more about the ecology of these species. Current attempts to improve ecosystem health by removing mistletoe-infected overstory trees does more harm than good, and the practice should be discontinued. An integrated ecosystem management strategy that restores the natural processes and stand conditions that historically occurred in these forest is the best approach for controlling dwarf mistletoe while simultaneously restoring ecosystem health.

Forest Service, approximately 90% of the area had previously been logged, virtually all the old growth was gone, there were very few large snags left and this habitat type was "on the threshold of losing community viability."

Prior to the sale, Forest Service biologists suggested that, "A long-term commitment will very much need to be made to work toward restoring this habitat community." They went on to predict the ecological impacts of logging in this area, stating that, The most likely nest trees would be those older-aged residual overstory ponderosa pine trees and the more disfigured older-aged dwarf mistletoe infected pine and mixed conifer trees. These trees are the most likely future snags and would be heavily removed..."

and that, "The potential for snag recruitment should decrease substantially. Stands remaining in the 4.3 wildlife habitat capability class are projected to decrease by an estimated 91% in ponderosa pine stands and 47% in mixed conifer stands."

Forest Service managers ignored the advice of biologists, and instead chose to maximize short-term timber production, admitting that mistletoe control was used to justify this goal. Six and half million board feet were logged on 2,564 acres. More than 12,650 trees over 16 inches dbh were cut. Rather than improving the health of the forest, this mistletoe management project further impoverished an area that had already been severely damaged by past logging activities.

Sources: USFS. 1992. Biological Evaluation Supplement, Biological Evaluation, Environmental Assessment, Timber Sale Cruise Report & Wildlife Assessement for the Rocker Timber Sale. USDA Forest Service, Gila National Forest, Silver City, NM (Five separate publications).

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Appendix 1. Organisms that are known to eat dwarf mistletoe

Organism	Reference
Mammals	
Red squirrel	Baranyay 1968, Wagner 1968 (cited in Tinnin et al. 1981)
Yellow pine chipmunk	Broadbooks 1958 (cited in Tinnin et al. 1981)
Porcupine	Taylor 1935
Elk	Craghead et al. 1973
Deer (Mule & white tailed)	Wright and Arrington 1950 (Cited in Tinnin et al. 1981), Urness 1969 Neff 1974, Currie et al. 1977
Birds	
Blue grouse	Beer 1943, Crawford et al. 1986, Severson 1986

Black-headed grosbeak	Marshall 1957
Band-tailed pigeon	Neff 1947
Black-capped chickadee	Wagner 1968
Thrush	Zakaullah and Badshah 1977 (cited in Tinnin et al. 1981)
Spruce grouse	Zwickel et al. 1974
Fungi	Hawkworth et al. 1977
Arthropods	
Insects	Stevens and Hawksworth 1970, Gregor et al. 1974, Penfield et al. 1976, Stevens and Hawksworth 1984
Mites	Stevens and Hawksworth 1970

Appendix 2. Organisms known to use witches' brooms as nest sites or cover

Organism	Reference
Mammals	
Red squirrel	Ostry 1978 (cited in Tinnin et al. 1981), Patton and Vahle 1986
Aberti squirrel	Ferentinos 1972, Hall 1981
Pine squirrel	Hatt 1943
Birds	
Spotted owl	Dicky 1914, Lignon 1926, Forsman et al. 1984
Northern goshawk	Reynolds 1978, Moore and Henny 1983
Long-eared owl	Bull et al. 1989
Great gray owl	Bull et al. 1989
Sharp-shinned hawk	Reynolds 1978, Moore and Henny 1983
Cooper's hawk	Reynolds 1978, Moore and Henny 1983, Henny 1984
Gray Jay	Warren 1899 (cited in Tinnin et al. 1981)
Blue grouse	Martinka 1972
Western tanager	Bennett 1991
Chipping sparrow	Bennett 1991
American robin	Bennett 1991, Nicholls et al. 1984
Hermit thrush	Bennett 1991
Cassin's finch	Bennett 1991
House wren	Nichols et al. 1984
Pine siskin	Zilka 1973 (cited in Nicholls et al. 1984)
Red crossbill	Bailey et al. 1953

Appendix 3. Organisms that are known vectors of dwarf mistletoe seed

Organism	Reference
Mammals	
Porcupine	Taylor 1935
Aberti squirrel	Patton 1975
Red squirrel	Hudler et al. 1979, Ostry et al. 1983, Nicholls et al. 1984
Flying squirel	Ostry et al. 1983
Least chipmunk	Nicholls et al. 1984

Golden-mantled squirrel	Nicholls et al. 1984
Pine marten	Nicholls et al. 1984

Birds

Gray Jay	Huddler et al. 1979, Ostry et al. 1983, Nicholls et al. 1984
Mountain chickadee	Huddler et al. 1979, Zilka and Tinnin 1976, Nicholls et al. 1984
Pygmy nuthatch	Huddler et al. 1979
Gray-headed junco	Huddler et al. 1979, Ostry et al. 1983, Nicholls et al. 1984
Chipping sparrow	Huddler et al. 1979
Williamson's sapsucker	Huddler et al. 1979
Yellow warbler	Ostry et al. 1983
Palm warbler	Ostry et al. 1983
Yellow-rumped warbler	Ostry et al. 1983, Nicholls et al. 1984
Cassin's finch	Zilka and Tinnin 1976
Red crossbill	Zilka and Tinnin 1976
Stellar's Jay	Zilka and Tinnin 1976, Nicholls et al. 1984
Hermit thrush	Nicholls et al. 1984
Townsend's solitaire	Nicholls et al. 1984
American robin	Nicholls et al. 1984
Northern saw-whet owl	Nicholls et al. 1984
Three-toed woodpecker	Nicholls et al. 1984

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PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2012) **279**, 3853–3860
doi:10.1098/rspb.2012.0856
Published online 11 July 2012

Mistletoe as a keystone resource: an experimental test

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Various entities have been designated keystone resources, but few tests have been attempted and we are unaware of any experimental manipulations of purported keystone resources. Mistletoes (Loranthaceae) provide structural and nutritional resources within canopies, and their pervasive influence on diversity led to their designation as keystone resources. We quantified the effect of mistletoe on diversity with a woodland-scale experiment, comparing bird diversities before and after all mistletoe plants were removed from 17 treatment sites, with those of 11 control sites and 12 sites in which mistletoe was naturally absent. Three years after mistletoe removal, treatment woodlands lost, on average, 20.9 per cent of their total species richness, 26.5 per cent of woodland-dependent bird species and 34.8 per cent of their woodland-dependent residents, compared with moderate increases in control sites and no significant changes in mistletoe-free sites. Treatment sites lost greater proportions of birds recorded nesting in mistletoe, but changes in species recorded feeding on mistletoe did not differ from control sites. Having confirmed the status of mistletoe as a keystone resource, we suggest that nutrient enrichment via litter-fall is the main mechanism promoting species richness, driving small-scale heterogeneity in productivity and food availability for woodland animals. This explanation applies to other parasitic plants with high turnover of enriched leaves, and the community-scale influence of these plants is most apparent in low productivity systems.

Keywords: parasitic plant; removal experiment; eucalypt woodland; Loranthaceae; Santalales; facilitation

1. INTRODUCTION

The idea of an ecological keystone was first transferred from an individual species to a generalized resource derived from multiple species by Leighton & Leighton [1] (see also Terborgh [2]) in their work on palm seeds, figs and nectar as food for birds and mammals in a Bornean forest. Since then, lichens, saguaro cacti, mineral licks, water, honeydew, mistletoes, salmon, acorns and various fruiting trees *inter alia* have been proposed to represent keystone resources, either within a particular region or generally [3–5]. With one notable exception [6], there have been no manipulations to quantify the direct and indirect influence of purported keystone resources. With most resources, removal would be logistically difficult, if not impossible, and various procedural difficulties confound the design or interpretation of supplementation experiments. Although our understanding of keystone species has been informed by numerous experiments (natural and controlled; removal and addition), the lack of manipulative tests represents a major impediment to advancing our understanding of how purported keystone resources influence diversity.

Engaged in a network of interdependencies with host plants, seed dispersers, pollinators and natural enemies, mistletoes are a group of highly interactive plants that have been proposed to represent keystone resources in forested ecosystems worldwide [7]. In addition to many regular and occasional consumers of their enriched foliage, abundant fruit and nectar resources offered when little else is available [8–10], mistletoe clumps are popular nest and roost sites [11–13] and numerous studies have reported positive relationships between mistletoe occurrence and species richness [10,14]. Mistletoe occurrence and density also affect several ecosystem processes: their abundant enriched litter has pronounced positive effects on nutrient dynamics and understorey composition [15,16] and changes to infected hosts increase colonization and functional diversity of mycorrhizal communities [17,18], increasing canopy complexity and changing fire behaviour and severity [19], thereby altering successional dynamics at the stand-scale [20].

Having called for removal experiments to test the keystone status of mistletoes, a series of predictions were outlined [7], detailing the short- and medium-term effects of mistletoe removal on community composition and structure. If mistletoe represents a keystone resource, areas where mistletoe has been removed would be expected to have:

1. lower abundances of mistletoe-obligate frugivores and folivores, with local populations declining towards local extinction;
2. lower abundances of regular mistletoe foragers (folivores, frugivores and nectarivores);
3. lower abundances of species that nest in mistletoe clumps and hollows;
4. lower richness of vertebrates generally; and
5. increased sensitivity to drought and other extreme events, supporting fewer residents and displaying increased seasonal and inter-annual variability in

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2012.0856 or via http://rspb.royalsocietypublishing.org.

Received 15 April 2012
Accepted 15 June 2012

species richness, compared with control plots with typical numbers of mistletoe plants (after Watson [7]).

These predictions were provisionally tested by comparing two adjacent eucalypt woodlands, from one of which all mistletoe plants had been removed from one woodland five years prior to study [6]. Marked differences in avian species richness and incidence were detected, consistent with the predicted effects of mistletoe on resource availability, offering preliminary support for the keystone resource hypothesis. This study had an effective sample size of one and no pre-treatment data were collected, so the recorded effects may include pre-existing habitat differences and may not be representative of the influence of mistletoe more generally.

Here, we report on a large-scale experiment evaluating the influence of mistletoe on community-level diversity and designed to test these five predictions. Pre-treatment bird diversities (estimated at the woodland scale) were compared explicitly with diversities three years post-treatment, contrasting changes in woodlands where all mistletoes were removed with those in control woodlands where mistletoe numbers were unmodified. As the first experimental test of a purported keystone resource, to our knowledge this 6-year study yielded a refined understanding of the direct and indirect effects of mistletoe on diversity and community composition. More broadly, this study contributes to a growing understanding of the role of parasitic plants as facilitators, affecting occurrence patterns of other plants and dependent animals through altered nutrient dynamics.

2. METHODS

(a) *Study area and site selection*

This study was conducted in the upper Billabong Creek catchment in southeastern New South Wales, Australia [21] (for a map, see electronic supplementary material, figure S1), located at the transition between xeric plains to the west and mesic highlands to the east [22]. Elevation ranges between 220 to 889 m a.s.l., and average annual rainfall increases from approximately 550 mm in the west to 900 mm in the east of the catchment. The study period (2003–2008) coincided with a prolonged drought affecting southeastern Australia, with annual rainfall totals for the nearby Albury weather station being approximately half of the long-term annual average of 770 mm.

Rather than individual trees or stands, entire woodland remnants were used as study units, isolated 80–100 years ago as surrounding habitats were cleared for agriculture. Sites qualified for selection if: canopy cover was more than 5 per cent; fragment area was 1.5–25 ha (larger woodlands were not considered because complete mistletoe removal was deemed prohibitively difficult); vegetation was classed as either Dry Foothill Forest or Grassy Box Woodland; the woodland had ‘hard’ edges *sensu* [23] and was at least 500 m from the nearest study site. The ground layer of all woodlands was dominated by grasses (both native perennials, and native and exotic annuals) with occasional shrubs (*Acacia* spp., *Exocarpus* spp.) in low-to-very-low densities. Mistletoe plants occurred at medium-to-low densities in these woodlands—primarily *Amyema miquelii* but with occasional *Muellerina eucalyptoides*, *Am. pendula* and *Am. miraculosa* (Loranthaceae). Except for the latter species (principally epiparasitic on *Am. miquelii* in this part of its range), these species are primarily eucalypt parasites, the plants forming dense pendulous clumps at the edge of the canopy [24].

(b) *Bird surveys*

To estimate bird species richness in the 40 woodlands, inventories were compiled from eight patch-scale surveys that were conducted each season in 2003/2004 prior to treatment and again in 2007/2008, three years after treatment. Surveys were conducted using the standardized search [25,26] with sample duration set at 20 min, using a quantitative, results-based stopping rule to determine the number of samples per survey. The stopping rule applied—stop sampling once observed richness of woodland-dependent species exceeds 80 per cent of predicted richness using the Chao 2 estimator [27]—yielded surveys of between three and six samples (i.e. 60–120 min of continuous sampling), with 260 of the 320 surveys tripping the stopping rule after three samples. Sampling involved walking throughout the woodland remnant and identifying all birds seen or heard within the woodland, including species flying beneath the canopy. Sampling was conducted only during favourable weather conditions, avoiding periods of heavy rain, strong wind or intense heat.

In addition to yielding richness estimates of uniform completeness, this approach generated incidence measures for each species in each woodland remnant, expressed as the proportion of samples in which it was detected [25]. Two incidence totals were calculated for each site in both years: summed incidence of all species that regularly feed on mistletoe nectar and/or fruit using the list compiled by Reid [28], and summed incidence of all species that nest in mistletoe clumps using [12]. In addition to total richness and richness of woodland-dependent species (after Watson [6] and references therein), a third richness measure was used for analysis—resident richness: those woodland-dependent species recorded in at least two seasons for the given year (excluding transients that were detected only in a single season). Analysis was restricted to changes in richness and incidence—interactions with patch and landscape-scale factors and comparisons of the individual responses of particular species and functional groups will be explored in subsequent contributions.

(c) *Experimental design*

The woodland remnants selected for study varied considerably in management history, area and degree of isolation from other remnant vegetation, potentially confounding the effects of mistletoe on diversity patterns. To guard against this, we ensured treatment and control groups were comparable, assigned treatment (mistletoe removal) using a blind stratified random approach and compared the effects of treatment in terms of proportional rather than absolute change. To assign treatment, woodland area was plotted against percentage tree cover, yielding a scatter plot of 40 points distinguishing larger and more densely wooded remnants from smaller, more open woodlands. Points closest to one another in graphical space were paired and treatment assigned by coin toss, yielding two groups of 20 woodland fragments with similar ranges of tree density and patch area (electronic supplementary material, table S1). A series of tests confirmed that these two groups exhibited comparable mean values for woodland area, percentage of tree cover in the surrounding 1 km radius buffer (an index of habitat openness), area of tree cover in the surrounding 1 km radius buffer (a measure of land-use intensity), mistletoe abundance and species richness of woodland-dependent birds prior to treatment. Some woodlands did not contain mistletoe, so, rather than a simple binary comparison, there were three groups: control woodlands with mistletoe ($n = 11$), treatment patches with mistletoe plants removed ($n = 17$) and woodlands from which mistletoe was naturally absent ($n = 12$); hereafter, they are referred as 'control', 'treatment' and 'mistletoe-free' woodlands, respectively.

(d) *Mistletoe removal*

Mistletoe plants growing within treatment woodlands were systematically removed over a five-month period (winter and spring of 2004) by teams of volunteers using pole-mounted loppers and pruning saws. Unlike some groups of mistletoe (e.g. *Arceuthobium* spp., Viscaceae) that cause systemic infections throughout the host, these loranthaceous mistletoes can be removed by cutting proximal to the haustorium, the lack of cortical strands in these species precluding re-sprouting [24]. Hydraulic boom-lifts towed by four-wheel drive vehicles were used to access plants up to 18 m above the ground, the telescoping boom arm allowing access to most parts of the eucalypt canopies (electronic supplementary material, figure S2). Mistletoe plants and associated sections of host branches were left where they fell: beneath their former hosts. Sham removals were conducted in the control sites, driving within the woodland and removing branches from infected and non-infected trees, but leaving all mistletoe plants intact. Tree and branch selection was haphazard, determined partly by ease of access and partly to avoid any mistletoe clumps within the canopy. Comprehensive surveys conducted six months and three years after initial treatment revealed that not all mistletoe plants were removed, but less than four per cent of the original number of mistletoe plants remained or recolonized, which were subsequently removed in follow-up treatment in the summer of 2006/2007.

(e) *Data manipulation and analysis*

Responses to mistletoe removal were measured in terms of net change between pre- and post-treatment inventories. In some cases, this was simply the datum for the 2003/2004 subtracted from the equivalent datum for 2007/2008. To make these values more meaningful, many of these differences were expressed as proportions of the original (pre-treatment) value. The only mistletoe-obligate frugivore detected was the mistletoebird *Dicaeum hirundinaceum*, so prediction 1 was tested by comparing mistletoebird incidence before and after treatment. Predictions 2 and 3 were tested using summed incidence of mistletoe-feeding and mistletoe-nesting species (respectively), comparing control and treatment woodlands in terms of the difference in the net change of summed incidence. Tests were conducted on the actual values, while plots correspond to proportions of total incidence (pre-treatment) to place the differences in biological context. Prediction 4 was tested by comparing the change in species richness in control versus treatment woodlands, expressed as a proportion of the pre-treatment value (i.e. proportional change). For prediction 5, the study period coincided with a prolonged drought, with many species responding by leaving the study area completely or only occupying some habitats seasonally. The change in numbers of residents between the two years was expressed as a proportion of the initial value (i.e. the proportion decreasing as the number of transient species increased). Except for prediction 1, which entailed a paired t-test applied to the 17 treatment woodlands, all treatment effects were tested using Mann–Whitney–Wilcoxon tests (one-tailed) comparing mean values for the 17 treatment sites (with mistletoe plants removed) with the 11 control sites (with mistletoe left intact), with exact probabilities of less than 0.05 deemed significant (using SPSS v. 17.0). Tests were conducted using all species ('total species') and the subset of species considered to depend on woodland as their primary habitat ('woodland species'; excluding most raptors, aerial foragers, open country and exotic species, after Watson [6]). Non-parametric tests were used, as sample sizes were uneven and the data were generally heteroscedastic, and one-tailed tests were appropriate as all comparisons were testing explicitly directional predictions [7]. In addition to comparing treatment and control sites, values for mistletoe-free woodlands are presented to contextualize the changes associated with experimental treatment and represent background variation between sites and years not associated with experimental manipulation.

3. RESULTS

Mistletoe exhibited a highly irregular distribution across the 40 sites, being entirely absent from 12 sites and occurring in remaining sites at densities ranging from less than one per hectare to almost 200 per hectare. A total of 5493 mistletoe plants were removed: the great majority (5169; 94%) during the initial removal phase in mid-2004 and an additional 324 plants in follow-up removals in summer 2006/2007, most of which were immature plants.

Of the 75 woodland-dependent bird species recorded in the two years combined, 12 species were recorded only during pre-treatment surveys and two species were recorded only during post-treatment surveys—i.e. there was a net loss of 10 species, or 14 per cent of the pre-treatment diversity of woodland-dependent species across all 40 sites. Turnover in the other 41 species was more symmetrical, with seven species recorded only pre-treatment (2003/2004) and eight species recorded only post-treatment (2007/2008)—i.e. a net gain of one species (or 3% of the pre-treatment total). Additional detail on bird richness and mistletoe occurrence is summarized in the electronic supplementary material.

(a) *Prediction 1: specialist frugivores*

A significant difference in mistletoebird *D. hirundinaceum* incidence was detected in the 17 treatment sites ($t = 1.825$, $p = 0.043$, one-tailed), reflecting declines in the treatment woodlands following mistletoe removal—incidence decreased in two sites and the species became locally extinct in a further four. By contrast, mistletoebird incidence increased in five of the 11 control woodlands, decreased in three others and they were not recorded in the remaining three.

(b) *Prediction 2: mistletoe foragers*

No significant differences were detected between treatment and control sites in terms of net change in summed incidence of all 31 mistletoe foragers ($p = 0.132$, one-tailed), or for the 24 woodland-dependent mistletoe foragers ($p = 0.373$, one-tailed) for ranked data (figure 1*a*) [28,12]. There were decreases across all sites, with treatment sites losing an average of 8.7 per cent of summed incidence for

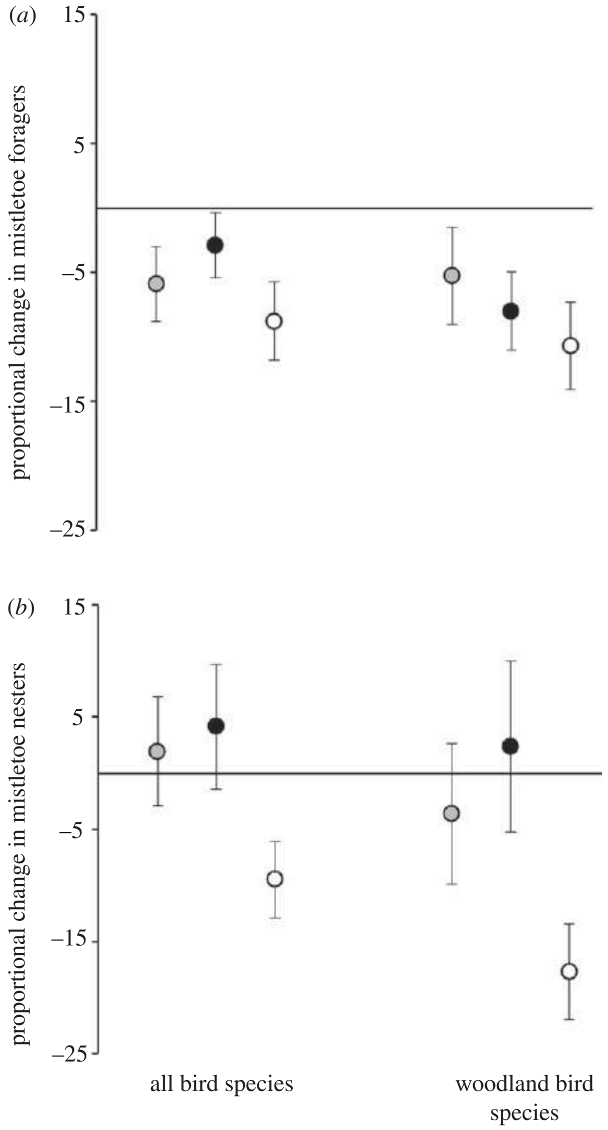

Figure 1. Proportional change in summed incidence of bird species between the two years (2003/2004 and 2007/2008) were compared using Mann–Whitney–Wilcoxon comparison of means (one-tailed), for the 12 mistletoe-free sites (grey), 11 control sites (black) and 17 treatment sites (white). (*a*) Summary of changes for those species that regularly forage on mistletoe nectar and/or fruit (31 species, of which 24 are woodland-dependent; after Reid [28]). No significant differences were detected, and prediction 2 was not supported. (*b*) Summary of changes for those species that have been recorded nesting in mistletoe clumps (67 species, of which 48 are woodland-dependent; after Cooney *et al.* [12]). Significant differences between means for treatment and control sites were detected ($p = 0.008$); treatment sites lost a greater proportion of mistletoe nesters than control sites, supporting prediction 3.

total species and 10.6 per cent of woodland-dependent species (figure 1*a*), and control sites losing 2.9 per cent and 8 per cent, respectively. Note that these recorded losses were less than changes in summed incidence across all species in the treatment woodlands between years (decreases of 15.4% and 24.7%, respectively).

(c) *Prediction 3: mistletoe nesters*

Clear differences in summed incidence of the 67 mistletoe nesters were detected between treatment and control woodlands ($p = 0.016$, one-tailed), equating to a mean loss of approximately 9.4 per cent of total incidence (s.e. = 3.4) in treatment woodlands, becoming more marked if just the 48 woodland-dependent species were considered ($p = 0.008$, one-tailed; mean loss of 17.6% of total incidence, s.e. = 4.26). Although significantly greater than decreases in control woodlands (figure 1*b*), these changes were less than change in incidence across all species in the treatment sites (decreases of 15.4% for all species; 24.7% for woodland-dependents).

(d) *Prediction 4: species richness*

Total species richness decreased markedly in the treatment woodlands after experimental removal of mistletoe—a significant difference compared with control woodlands ($p = 0.004$), reflecting mean losses of 20.9 per cent of their original richness (s.e. = 4.04). This pattern was more marked for those species dependent on woodlands as their principal habitat ($p = 0.002$, one-tailed; compared with control sites), equating to mean losses of 26.5 per cent (s.e. = 4.58) of their original woodland-dependent species richness (figure 2*a*). This change compares with a mean decrease in total richness of 10.3% (s.e. = 6.04) in mistletoe-free woodlands and an increase of 4.7 per cent (s.e. = 8.38) in the control woodlands (for total species richness); with woodland-dependent species richness decreasing by an average of 6.5 per cent in mistletoe-free woodlands (s.e. = 9.63), while control woodlands gained an average of 10.2 per cent of their pre-treatment richness (s.e. = 12.68).

(e) *Prediction 5: sensitivity to drought*

For total species, clear-cut differences between control and treatment were detected ($p = 0.008$): treatment sites lost a mean proportion of 29.5 per cent (s.e. = 9.25) of their initial residents, while control sites exhibited an increase in the proportion of residents of 1.73 per cent (s.e. = 7.73). Differences in woodland-dependent species were greater ($p = 0.002$); control woodlands increased their proportion of residents (14.5%; s.e. = 12.34) while the proportion of residents in treatment woodlands decreased by 34.8 per cent (s.e. = 10.3), transient species becoming more dominant (figure 2*b*).

4. DISCUSSION

The influence of mistletoe on diversity was evaluated directly with a woodland-scale removal experiment, and the hypothesized status of these hemiparasites as keystone resources was strongly supported. Removing mistletoe plants from entire woodlands resulted in average losses of more than a quarter of the woodland-dependent bird species, with the number of resident species decreasing by more than a third. Over the same period, control woodlands with variable mistletoe densities exhibited moderate increases in woodland-dependent species richness, while no marked changes to richness or incidence were detected in naturally mistletoe-free sites. Rather than affecting just those species that feed on mistletoe or nest preferentially in mistletoe clumps, these changes were apparent across the community, being more pronounced for woodland-dependent species and residents. The magnitude of these changes within three years of

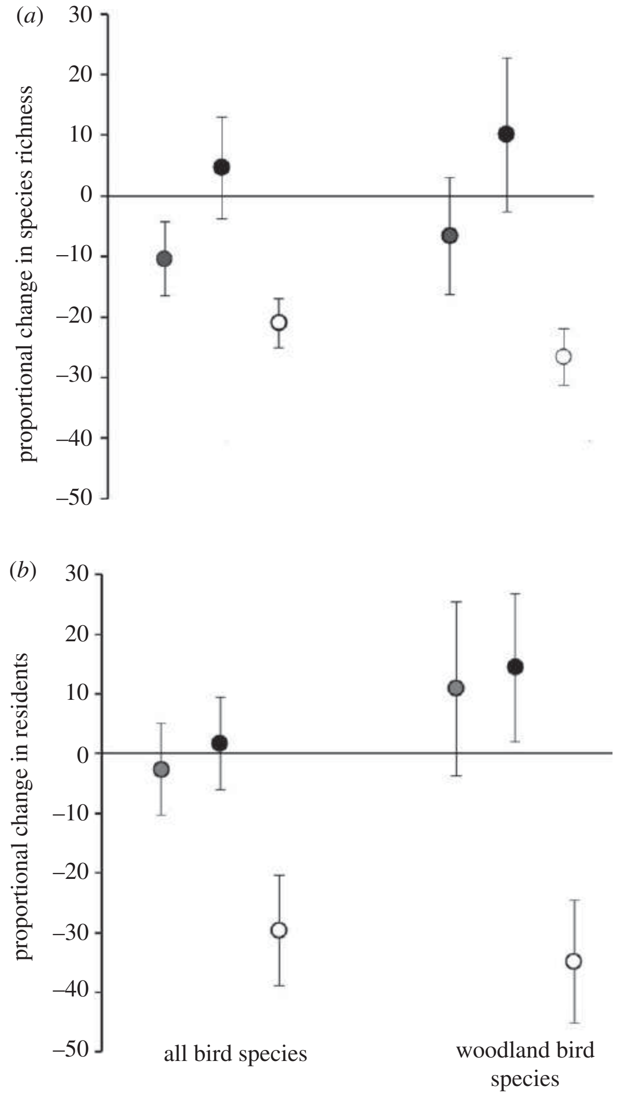

Figure 2. (*a*) Proportional change in species richness between 2003/2004 and 2007/2008 was compared using Mann–Whitney–Wilcoxon comparison of means (one-tailed), for the 12 mistletoe-free sites (grey), 11 control sites (black) and 17 treatment sites (white). Treatment sites lost significantly more species than control sites, in terms of both total species ($p = 0.004$) and woodland-dependent species ($p = 0.002$), lending support to prediction 4. (*b*) The effect of mistletoe removal on sensitivity to drought was tested by comparing the proportional change in residents after mistletoe removal. Treatment sites lost significantly more residents than control sites ($p = 0.008$ for total residents; $p = 0.002$ for woodland-dependent residents), providing support for prediction 5.

mistletoe removal provides clear evidence that mistletoes directly modify resource availability in woodlands and forests, consistent with previous descriptive work relating mistletoe density to community-level diversity in a range of other ecosystems [10,14].

Two aspects of this study probably underestimate the measured influence of mistletoe, so reported effect sizes should be regarded as conservative. The study period coincided with the final years of a prolonged drought affecting southern Australia, so the pre-treatment inventories yielded lower species richness estimates than anticipated. Rather than supporting comparable bird diversities in the two years, the 11 control woodlands gained an average of 10.2 per cent woodland-dependent species because numbers of drought-sensitive species rebounded in 2007. So the mean-recorded loss of 26.5 per cent woodland-dependent species in the treatment remnants may actually reflect net losses closer to 36.7 per cent species richness once the confounding effects of regional climatic conditions are removed, comparable to the 34.8 per cent mean-recorded loss of woodland-dependent residents. Second, mistletoe densities within the study sites were low compared with other habitats in the region, the hemiparasites being completely absent from 12 of the 40 woodlands. The same mistletoe species are two to five times more abundant in adjacent riparian and floodplain woodlands and nearby box-ironbark forests, probably having more pronounced effects on diversity and community composition.

(**a**) ***Mistletoe as a direct nutritional resource***

One of the main elements of the evidence base assembled to justify designation of mistletoe as a keystone resource [7] was dietary information for terrestrial vertebrates, with the popularity of mistletoe fruit, nectar and foliage deemed instrumental in explaining observed relationships with species richness. Although mistletoe specialists declined following mistletoe removal (in support of prediction 1), regular mistletoe foragers did not show significant reductions in occurrence or abundance following mistletoe removal (figure 2*a*). While it is likely that more of the bird species recorded in this study occasionally consume mistletoe fruit or nectar, Reid's [28] list corresponds closely with our own observations of nectarivory and frugivory, both within the study region and across southern Australia, and this negative result is considered robust.

We suggest that regular consumers of mistletoe fruit and nectar represent only a small component of the suite of species influenced by mistletoe occurrence in this system, and that direct nutritional effects comprise a relatively minor component of the community-level influence of mistletoe in general. Eucalypt forests are remarkable for their lack of fleshy fruited plants, and frugivorous species are only a minor component of the associated avifauna. Thus, changes in mistletoe diversity and abundance probably have more pronounced effects on frugivore occurrence in other systems, explaining temporal and spatial variation in frugivores numbers [8,29]. In terms of nectar, although 13 of the 75 recorded woodland-dependent species feed on mistletoe flowers and an additional seven visit mistletoe flowers opportunistically [28], none depends on mistletoes as their primary food source. Rather, eucalypts represent the dominant nectar-bearing plant in this region—the canopy-dominant sclerophyllous trees exhibiting mass flowering events that are highly variable through space and time, driving large-scale movements as nectarivores track peak flowering across large distances [30]. Hence, the direct influence of mistletoe fruit and nectar availability on community-scale diversity may not be as consistently great as predicted, and the influence of more abundant fruit and nectar-bearing plants in the canopy or understorey is probably far greater in most systems [31,32].

(**b**) ***Structural attributes***

In addition to nutritional resources, mistletoes provide dense evergreen structures within forest canopies that are widely used by birds and mammals for nesting and roosting, and these structural attributes formed the second main justification for designating mistletoes as keystone resources. Accordingly, those species that use mistletoe for nest sites were expected to decrease in abundance following mistletoe removal (prediction 3). Although treatment sites displayed significant reductions in these species in terms of summed incidence, recorded changes were less than those exhibited across all woodland-dependent species—i.e. mistletoe-nesting species were no more likely to undergo declines following mistletoe removal than any other woodland species. This conclusion is supported by the relatively small number of nests found during mistletoe removal—fewer than one per cent of the plants removed had nests associated with them. So, although widely used as nesting and roosting sites, and preferentially selected by some species, we found no evidence that mistletoes were limiting as a nesting substrate, nor that woodlands with mistletoe can support greater abundances of mistletoe-nesting species.

Previous research has evaluated mistletoe nesting in more depth, and suggested that microclimatic factors may be important in explaining the widespread practice. Compared with nests elsewhere in the canopy, nests within mistletoe foliage experienced reduced fluctuation in both temperature and humidity, with the ambient climate ameliorated by the semi-succulent foliage of the hemiparasite [13]. The lack of signal detected here may reflect the temperate climate of the study region, and mistletoe is likely to have more pronounced effects in areas with more extreme climates. Indeed, research on wildlife use of dwarf mistletoe brooms in Arizona found evidence that mistletoes may be a limiting resource [33]. The influence of mistletoe on canopy structure may be better considered in terms of reproductive success rather than in terms of species richness, increasing the seasonal extent and geographical breadth within which successful fledging and recruitment can be achieved.

(c) *Facilitation via litter-fall and nutrient concentration*

Rather than direct nutritional supplementation or increased structural complexity in infected host canopies, we propose that the marked influence of mistletoe on diversity is mediated primarily via the abundant enriched litter shed by these hemiparasites, increasing productivity and promoting coexistence through bottom-up trophic dynamics of woodland and forest food webs. Previous work on the contribution of mistletoes to litter-fall and nutrient dynamics within the study area estimated that individual *Amyema miquelii* plants contributed an average of 544 g of leaf litter annually, with 0.81 ± 0.08 g of mistletoe litter produced per gram of mistletoe leaf biomass in the canopy [15]. The variation in mistletoe occurrence noted at the patch scale was even more pronounced within infected patches: mistletoe plants aggregated in discrete 'infection centres' and concentrated around the perimeter of remnants. Hence, rather than incremental changes in litter-fall across woodlands, mistletoe occurrence increases heterogeneity in litter-fall, effectively doubling or tripling total litter-fall in heavily infected stands. The effects of these qualitative changes in litter-fall are magnified by the enriched status of mistletoe litter compared with host litter, leading to marked increases in nutrient inputs [16] and pronounced spatial heterogeneity in nutrient returns.

In addition to affecting overall productivity and composition of understorey plant communities [15], these changes to the litter layer directly affect the litter-dwelling arthropods that form the principal food source for many woodland-dependent fauna. Previous work on the habitat preferences, dietary composition and foraging ecology of birds in eucalypt woodlands has consistently identified litter depth as a critical factor [34 and references therein], with deeper and more extensive litter beds considered to contain higher abundances of preferred prey [35]. Thus, we suggest that quantitative changes to litter-fall associated with mistletoe occurrence, plus qualitative changes in the chemical composition and associated rate of decomposition of resultant litter, result in fundamental changes to litter-dwelling arthropod communities, increasing and prolonging availability of prey for insectivores.

Rather than supplanting direct nutritional and structural factors, the facilitation explanation incorporates these pathways, with nutrient contributions by foraging and nesting animals adding to the inputs provided directly by mistletoes. Unlike litter-fall that represents reallocation of nutrients from the host to the litter-layer beneath the host, these animal-derived nutrients are drawn from a much larger pool, extending beyond the infected host and stand [36]. Similar mechanisms have been postulated to explain high concentrations of animal-derived elements near hollow trees, rock outcrops and copses of trees surrounded by grassland, summarized by Watson [37]. Rather than simply increased productivity, we suggest it is the heterogeneity of nutrient availability driven by the highly aggregated distribution of mistletoes that underpins their pervasive effects on diversity, boosting species richness by promoting species coexistence.

(d) *Effects of parasitic plants on diversity*

Rather than being unique to this system, nutrient enrichment is an attribute of parasitic plants generally, and numerous studies (of other mistletoes and various root parasites) have reported findings consistent with facilitation via enriched litter-fall. These findings involve a range of vegetation types, from alpine tundra [38] and arctic shrubland [39] to coniferous forests [40]. In addition to direct effects of hemiparasite litter on decomposition and nutrient availability, these studies demonstrate various indirect effects of parasitic plants, including the boosting of species richness by preferentially parasitizing competitively dominant species [41,42]. Parallel research on dwarf mistletoes (Arceuthobium: Viscaceae) has detected increased colonization of infected *Pinus edulis* by ectomycorrhizae [17] and increased functional diversity of fungal communities beneath infected *Pinus contorta* [18], suggesting that the fundamental shifts in soil microbial communities detected by Bardgett *et al.* [43] in grasslands experimentally infected with *Rhinanthus minor* may apply to parasitic plants more generally.

All sampling was carried out under Scientific Research Permit S10921 issued by the Department of Environment and Climate Change (Parks and Wildlife Division) and the authority of Charles Sturt University Animal Care and Ethics Committee approval 05/054.

This research was supported by the Australian Research Council (DP034259), the Winnifred Violet Scott Trust and Charles Sturt University. We are indebted to the 18 landowners in the upper Billabong Creek catchment for granting access to their properties, supporting our research and sharing their insights about woodland dynamics. This work would not have been possible without our dedicated band of assistants: chief mistletoe removalist David Webb, Hugh McGregor, Scott Hartvigsen and teams from Australian Trust for Conservation Volunteers and Greencorps. We are grateful to two anonymous referees for their considered input and constructive comments.

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Dwarf Mistletoes

Ecology and Management in the Rocky Mountain Region

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1. INTRODUCTION

The genus *Arceuthobium* (Santalales: Viscaceae) is a group of small plants that are exclusively parasitic on conifers and can strongly influence forest structure and dynamics. There are about 42 species, mostly in North and Central America, where they occur only on members of the family Pinaceae. Eight species occur in Eurasia and Africa, where some are also parasitic on junipers (family Cupressaceae). *Arceuthobium* species tend to be fairly host-specific.

Five species occur in the Rocky Mountain Region (Table 1). Most of our abundant tree species (piñon, lodgepole and ponderosa pines, and Douglas-fir) are commonly infected in at least parts of their ranges. Common conifer species that are not, or only rarely, hosts of mistletoes in the Region include all spruces and true firs.

Table 1. Dwarf mistletoes and their hosts in the Rocky Mountain Region (Hawksworth & Wiens 1996, Mathiasen *et al.* 2005).

	Hosts [a]	
Arceuthobium species	Principal	Other
A. americanum	Lodgepole pine	Secondary: ponderosa pine Occasional: whitebark and limber pines; Rare: Engelmann and blue spruces, bristlecone pine
A. cyanocarpum	Limber, whitebark and bristlecone pines	Rare: ponderosa and lodgepole pines
A. divaricatum	Piñon	
A. douglasii	Douglas-fir	Rare: subalpine fir, blue and Engelmann spruces
A. vaginatum subsp. *cryptopodum*	Ponderosa pine	Occasional: bristlecone pine, lodgepole pine; Rare: limber and southwestern white pines, blue spruce

[a] Hosts are in the following categories:
Principal: More than 90% infection when close to heavily infected trees.
Secondary: Frequently attacked (50–90% infection) when close to heavily infected principal hosts.
Occasional: Occasionally attacked (5–50% infection) when close to heavily infected principal hosts.
Rare: Rarely attacked (≤ 5% infection), even when close to heavily infected principal hosts.

2. LIFE CYCLE

Let’s begin with a dwarf mistletoe seed clinging to the bark of a young twig. After germination, the young radicle contacts the host bark and forms a disk-like holdfast that enlarges and grips the bark tightly. From it, a wedge develops and penetrates the bark. Penetration continues to the cambium and stops. From this penetration peg, cortical strands begin to grow in the bark toward the shoot tip, away from the shoot tip, and around the circumference.

As the cortical strands extend through the bark, they periodically send additional pegs radially to the cambium like the first penetration peg. These each form a meristem that is continuous with the host cambium. Whenever the cambium grows, adding wood and phloem, the mistletoe meristems grow as well, producing tissue in the newly formed wood and keeping up with growth so it is not torn apart. As the years go by, these “sinkers” are embedded radially in the wood and in fact are integrated into the wood rays. They do not actively penetrate existing wood, instead they cleverly incorporate themselves into the wood as it grows. Together, the cortical strands and sinkers are called the endophytic system and provide anchorage and absorption of nutrients and water for the dwarf mistletoe.

Infection generally occurs in host shoots that are one to five years old. That is because such shoots are most likely to have needles that intercept flying seeds, but also because the bark is thin enough to be penetrated before the germinating seed depletes its resources.

There are two types of infections by dwarf mistletoes:

– **Systemic infection**: The endophytic system grows to the tip of the shoot and may even invade the bud. It keeps pace with shoot growth and may invade all branches subsequently produced from it. Dwarf mistletoe shoots may be produced anywhere along the systemically infected branch system or at annual bud scars. In our area, systemic infections are produced by lodgepole pine dwarf mistletoe and by Douglas-fir dwarf mistletoe.

– **Local infection**: The endophytic system does not advance far towards the shoot tip. Mistletoe shoots are produced only near the original site of infection. This is typical of southwestern, limber pine and piñon dwarf mistletoes. Lodgepole pine dwarf mistletoe may occasionally produce local infections, especially in the early stages of disease development.

About 3–5 years after infection, after the endophytic system is developed, the mistletoe plant produces shoots. Shoots are generally less than 8 in (20 cm) tall. The smallest species in our area is Douglas-fir dwarf mistletoe, with shoots only 0.8 in (2 cm) tall and 0.04 in (1 mm) in diameter, and the largest is southwestern dwarf mistletoe, typically 4 in (10 cm) tall and 0.12 in (3 mm) diameter. Shoots are yellow to olive green or orange to reddish brown. They have small, scale-like leaves in pairs at each node. The leaf bases tend to fuse together during development, forming a small cup around the node. Plants are dioecious (only one gender in a given plant); male and female plants may differ in color and/or form. Shoots are segmented at the nodes. Shoots typically live for 5 to 7 years and may produce several crops of flowers before they die and dehisce. The plant stays alive inside the host, however, and typically produces new shoots repeatedly for many years.

Time of flowering varies among the species. The species in Region 2 that occur on the most economically important hosts (*A. americanum*, *A. vaginatum* ssp. *cryptopodum*, and *A. douglasii*) flower in spring or early summer (Table 2). The other two species flower in late summer or fall. Seed is typically dispersed in late summer or fall of the year after flowering. The time from flowering (pollination) to fruit maturation thus varies from about 12 to 17 months in our species.

Table 2. Phenology of flowering and seed dispersal in the *Arceuthobium* species of the Rocky Mountain Region (Hawksworth & Wiens 1996).

	Flowering	Seed dispersal
A. americanum	early April – early June	mid-May – late Sept.
A. cyanocarpum	mid-July – early Sept.	mid-Aug. – late Sept.
A. divaricatum	early Aug. – late Sept.	early Sept. – late Oct.
A. douglasii	May	late Aug. – late Sept.
A. vaginatum ssp. *cryptopodum*	mid-May – June	late July – early Aug.

Both wind and insects are likely involved in pollination. Insect pollinators may include a variety of flies, thrips, bees, and ants (Stevens & Hawksworth 1984).

The mature fruit contains a single seed that is explosively discharged by one of the most effective hydrostatic mechanisms among flowering plants. During maturation, the fruit pedicel bends so that the seed is discharged at about 30 degrees above the horizontal (Hawksworth 1961b, data for southwestern dwarf mistletoe), an angle that maximizes lateral distance for targets within 35 vertical feet below the source, and also allows the possibility of climbing. The initial velocity of the seed is about 27 m sec^{-1} (60 mph). Maximum dispersal distance is about 52 ft, but most seeds fall within 33 ft. The seed is coated with a mucilaginous substance (viscin), so it adheres to needles that it strikes. It remains on the needle until rain wets the viscin, whereupon the lubricated seed slides down the needle and, if the needle is upright, makes contact with the bark and needle base. Seeds that fall from downward-pointing needles may be intercepted by lower branches. Seeds germinate in spring or early summer of the year following dispersal, except for *A. vaginatum* ssp. *cryptopodum*, whose seeds germinate in August or September immediately after dispersal.

The entire life cycle, from infection to fruit maturation and dispersal, takes 6 years or more for lodgepole pine dwarf mistletoe and 7 or 8 years for southwestern dwarf mistletoe.

2.1 Vectors of dwarf mistletoes

Nicholls *et al.* (1984) provided a detailed review of the literature on vectoring of dwarf mistletoe seeds by animals. A more recent summary was provided by Hawksworth & Geils (1996).

Although dwarf mistletoe seed is primarily dispersed by explosive discharge of the sticky seed from fruits, numerous birds and mammals have been implicated as potential vectors that could have a role in occasional long-distance dispersal. The primary candidates are passerine birds and squirrels. Direct proof and quantitative measurement of effective vectoring (i.e., resulting in establishment of a new infection center) would be difficult or impossible to obtain. Evidence generally consists of capturing animals with attached seeds of dwarf mistletoe and the existence of isolated, “satellite” infection centers. Satellite centers could result from animal vectoring or from survival of small, residual infected trees from a previous stand or larger residuals that subsequently died or were removed.

Successful establishment of new infection centers by vectoring almost certainly occurs, but its frequency and ecological importance are unclear. Dispersal over very long distance (beyond the common distance for pollen dispersal, which is unknown) is unlikely to result in successful establishment because dwarf mistletoes are dioecious, so both male and female plants are required for seed production. Although vectoring may be important in considering biogeography and dispersal over a time scale of centuries and millennia, it is generally considered to be relatively unimportant to the epidemiology of the disease from a management perspective.

An apparent exception is limber pine dwarf mistletoe, *Arceuthobium cyanocarpum* on limber pine, *Pinus flexilis*, in the Rocky Mountains. Infections often occur in isolated trees or in the tops of otherwise uninfected trees, and birds are therefore thought to be important in dispersal in this case (Hawksworth & Geils 1996, citing unpublished 1968 data of Urban).

Red squirrels and flying squirrels have been trapped in infested stands of *Picea mariana* in Minnesota with seeds of *Arceuthobium pusillum* stuck to their fur (Hudler *et al.* 1974, Ostry *et al.* 1983). In *Pinus ponderosa* heavily infested with *A. campylopodum* in Oregon, up to 50% of squirrels carried one or more seeds (Lemons 1978). Squirrels up to 150 m away from infected trees were found with seeds. However, Lemons doubted they were important for establishment of new and distant infection centers because squirrels groom seeds from their fur soon after they become attached.

In lodgepole pine in Colorado, seeds of *Arceuthobium americanum* were found occasionally on least chipmunk, golden-mantled ground squirrel, red squirrel and American marten (Nicholls *et al.* 1989, Nicholls *et al.* 1986). Although chipmunks and ground squirrels carried seeds more frequently than the others, they were thought to be unlikely vectors because they spend most of their time near the ground. Red squirrels may carry seeds to appropriate infection courts more often because they reside in tree crowns, but they have a small home range and are thus unlikely to result in long-distance dispersal.

Birds are more likely than mammals to result in long-distance dispersal because many frequent tree crowns and may travel over relatively large areas. When isolated infections occur in the tops of tall, otherwise uninfected trees, vectoring by birds is a likely explanation. Numerous species have been trapped with seeds stuck to their feathers or other surfaces (Hawksworth & Geils 1996, Nicholls *et al.* 1984). For *A. americanum* in lodgepole pine, during peak time for seed dispersal, 22% of captured birds had seeds (Nicholls *et al.* 1984); over all time periods 6.3% carried seeds (Nicholls *et al.* 1986). The most important bird species were gray jay, mountain chickadee, Steller's jay (Figure 1), gray-headed junco, and Audubon's warbler. In Colorado ponderosa pine forests, *A. vaginatum* ssp. *cryptopodum* was found on 4% of 411 birds, including pygmy nuthatch, mountain chickadee, gray-headed junco, chipping sparrow, and Williamson's sapsucker (Hudler *et al.* 1979).

In two studies, birds were observed to deposit seeds from their external surfaces onto susceptible hosts. Birds with artificially acquired seeds, caged with potted black spruce, deposited several seeds on spruce foliage during preening (Ostry *et al.* 1983). In ponderosa pine stands in Colorado, chickadees with naturally acquired seeds transferred seeds to pine needles in five instances (Hudler *et al.* 1979).

Figure 1. Frank Hawksworth (1926-1993), a foremost authority on dwarf mistletoes, and a Steller's jay, a foremost potential vector of lodgepole pine dwarf mistletoe. Photo courtesy of Tom Nicholls.

3. DWARF MISTLETOES OF THE ROCKY MOUNTAIN REGION

3.1 Lodgepole pine dwarf mistletoe – *A. americanum*

Lodgepole pine dwarf mistletoe (sometimes called American dwarf mistletoe) is the most widely distributed, one of the most damaging, and the best studied dwarf mistletoes in North America. Shoots are yellowish to olive green, 2–3.5 in (5–9 cm) long (maximum 12 in) and up to 0.04–0.12 in (1–3 mm) diameter, with verticillate branching (in whorls). The distribution generally follows the distribution of its principal host, lodgepole pine, in the Rocky Mountain Region (Figure 2).

Arceuthobium americanum infects systemically, sometimes causing large witches' brooms with elongated, pendulous branches.

An interesting feature of this species, potentially useful in management, is that the upper elevational limit is usually 185–200 m (about 600–650 feet) below the upper elevational limit of lodgepole pine for a given latitude (Figure 3*)*. Experiments have shown that the mistletoe can survive at higher elevations, but it cannot reproduce because the fruit is killed by early autumn frosts before it can fully mature (Hawksworth & Wiens 1996).

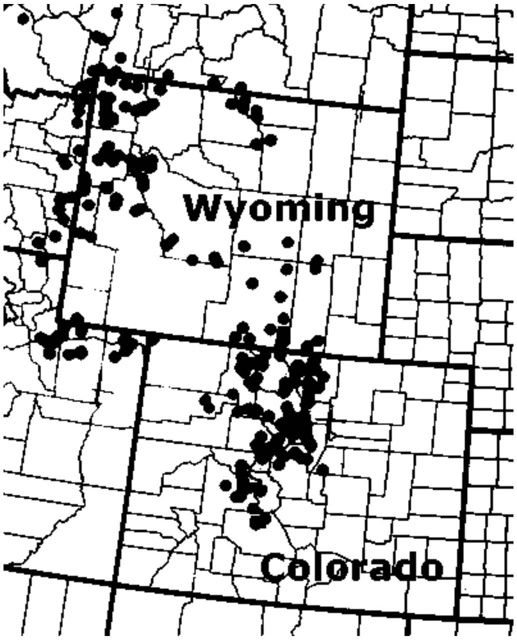


Figure 2. Distribution of American dwarf mistletoe, *A. americanum,* in the Rocky Mountain Region (from Hawksworth & Wiens 1996).

As noted in *Table 1*, ponderosa pine is considered a secondary host of this species. However, *A. americanum* can sustain itself and even be aggressive in pure stands of Rocky Mountain ponderosa pine in northern Colorado and southern Wyoming, sometimes a mile or more away from infected lodgepole pine (Hawksworth & Wiens 1996). This generally occurs in areas outside the range of ponderosa pine's usual parasite, southwestern dwarf mistletoe.

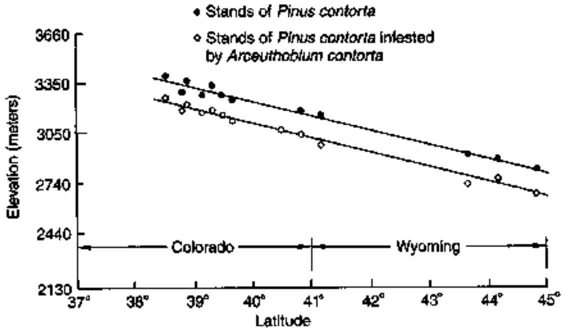


Figure 3. Upper elevation limits of American dwarf mistletoe and stands dominated by its host, lodgepole pine, in Colorado and Wyoming (Hawksworth 1956, Hawksworth & Wiens 1996).

Spread rate in even-aged stands can be about 1.7 ft per year in open stands and 1.2 ft per year in dense stands (Hawksworth & Johnson 1989).

Intensification (increase in number of infections over time) occurs most quickly in stands 15–60 years old in Colorado. During that time dwarf mistletoe rating (DMR) increased one class in 14 years (Hawksworth & Johnson 1989).

A Forest Insect and Disease Leaflet is available for this disease (Hawksworth & Dooling 1984).

3.2 Limber pine dwarf mistletoe – *A. cyanocarpum*

All of the high-elevation white pines in the Rocky Mountain Region, including limber, whitebark, and Rocky Mountain bristlecone pine, are primary hosts of limber pine dwarf mistletoe (see *Table 1* for definitions of host categories). The only endemic white pine that is not a host in nature is southwestern white pine. Shoots are yellow green, 1.2–2.8 in (3–7 cm) long and up to 0.08 in (2 mm) diameter. Branching is flabellate (fan-shaped) and shoots are densely clustered. It is generally distributed along the Continental Divide in our area, but also occurs in other mountain ranges (Taylor & Mathiasen 1999).

Arceuthobium cyanocarpum causes small, tightly clustered witches' brooms. It causes extensive mortality of limber pine in many parts of the Rocky Mountains and can also cause mortality in other hosts when severe. It is the most important native disease of high-elevation white pines in the West; only white pine blister rust is more damaging. The potential for damage from white pine blister rust must be considered while planning any management in white pine stands.

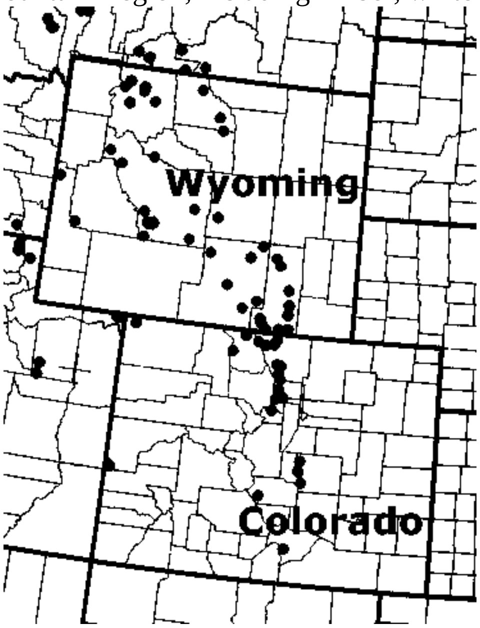


Figure 4. Distribution of limber pine dwarf mistletoe, *A. cyanocarpum,* in the Rocky Mountain Region (from Hawksworth & Wiens 1996).

Some animals depend on seeds of white pines at certain times of year. For instance, limber pine seeds can be an important part of the diet of black and grizzly bears (McCutcheon 1996), Clark's nutcracker (Tomback & Kramer 1980), and red squirrels (Hutchins & Lanner 1982). Whitebark pine seeds may play an even more critical role in the diet of grizzly bears (Baskin 1998, Mattson & Reinhart 1994). The large reduction in seed production in severely infested stands may have a consequent impact on populations of these animals.

Lateral spread in single-storied stands is estimated to be 1.5–2 ft per year. A Forest Insect and Disease Leaflet is available for this disease (Taylor & Mathiasen 1999).

3.3 Piñon dwarf mistletoe – *A. divaricatum*

Piñon dwarf mistletoe infects only piñons. Shoots are olive green to brown, about 3–5 in (8–13 cm) long and up to 0.16 in (4 mm) diameter. Shoots often have a long, thin and spreading appearance. Branching is flabellate (fan-shaped). In our area *A. divaricatum* occurs only in Colorado west of the Continental Divide (Figure 5).

This dwarf mistletoe may not result in well-developed witches' brooms, and those that do develop are usually small. However, growth loss and mortality can be high when infection is severe (DMR 5 or 6).

Southwestern dwarf mistletoe greatly affects seed production of ponderosa pine (see 4.2, Forest dynamics), but mistletoe effects on piñon are unknown. This may be a particularly important effect in piñon because the nuts are collected for food by humans in many areas and are used by wildlife, as well as being necessary for reproduction.

A Forest Insect and Disease Leaflet is available for piñon dwarf mistletoe (Mathiasen *et al.* 2002).

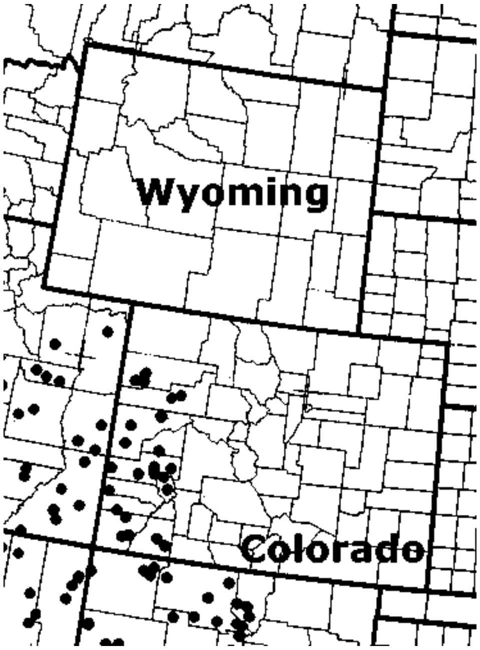


Figure 5. Distribution of piñon dwarf mistletoe, *A. divaricatum*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996).

Another mistletoe also occurs in the piñon-juniper cover type, *Phoradendron juniperinum* on junipers (Geils *et al.* 2002). Although it is practically leafless, it is a true (American) mistletoe rather than a dwarf mistletoe. In the Rocky Mountain Region it occurs only in western Colorado. A Forest Insect and Disease Leaflet is available for *Phoradendron* spp. on conifers (Hawksworth & Scharpf 1981).

3.4 Douglas-fir dwarf mistletoe – *A. douglasii*

Douglas-fir dwarf mistletoe has the smallest shoots of all mistletoes in our area, but it can cause formation of the largest witches' brooms. It primarily infects its namesake, although several true firs and spruces are occasional or rare hosts in some circumstances (see *Table 1* for host categories). Shoots are olive green, average 0.8 in (2 cm) long (maximum 3 in or 8 cm) and 0.04–0.06 in (1–1.5 mm) diameter, with flabellate branching. The pathogen occurs throughout the range of Douglas-fir in the central and southern mountains of Colorado, but it is absent from northern Colorado (except for the extreme northwest) as well as the portion of Wyoming in the Rocky Mountain Region (Figure 6).

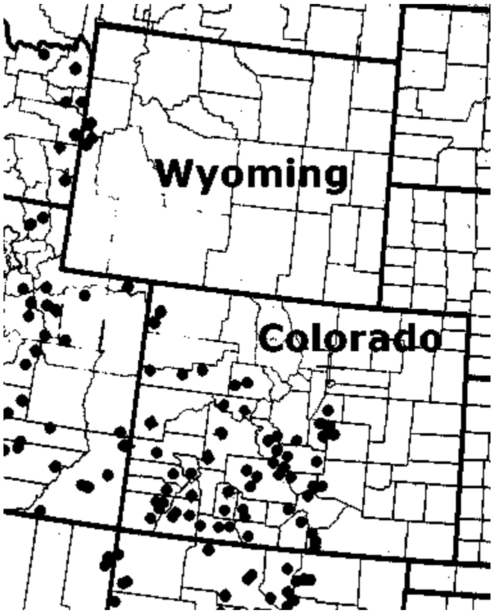


Figure 6. Distribution of Douglas-fir dwarf mistletoe, *A. douglasii,* in the Rocky Mountain Region (from Hawksworth & Wiens 1996)

Arceuthobium douglasii infects systemically. Mistletoe shoots may be spread along young host branches or be aggregated at the annual bud scar zones. Because shoots are so small, they are normally detectable only in branches close to the ground, and witches' brooms are used for detection and rating. Witches' brooms become noticeable about 10 years after infection and develop best in direct sunlight (Hadfield *et al.* 2000). They occur mostly in the lower half of tree crowns. They can weigh hundreds of pounds, can break off the tree, and are considered hazards in developed sites.

Where it occurs in the Region, dwarf mistletoe is generally the most important disease of Douglas-fir. It has reportedly increased in abundance since the late 1800s (Hadfield *et al.* 2000). At least in the northern Idaho and western Montana, Douglas-fir stands have become more widespread due to fire suppression, a history of selective harvesting that removed pines and encouraged shade-tolerant and less valuable species, and white pine blister rust, which largely eliminated western white pine.

Data on growth effects from western Montana indicate that light, medium and severe infections caused decreases in basal area growth rate of 14, 41 and 69%, respectively (Hadfield *et al.* 2000). Effects on height growth were similar.

Horizontal spread in single-storied stands is estimated at 1.5–2 ft per year. Upward spread in crowns is about 4–6 in (10–15 cm) per year. A Forest Insect and Disease Leaflet is available for this disease (Hadfield *et al.* 2000).

3.5 Southwestern dwarf mistletoe – *A. vaginatum* ssp. *cryptopodum*

Southwestern dwarf mistletoe primarily infects the Rocky Mountain variety of ponderosa pine in the four-corner states (Colorado, Utah, Arizona and New Mexico, with a small distribution in west Texas) and is distinct from western dwarf mistletoe (*A. campylopodum*), which infects the Pacific coast variety of ponderosa pine from southern California to northern Washington and western Idaho. Within the Rocky Mountain Region, southwestern dwarf mistletoe is confined to southern Colorado on the Western Slope and extends into northern Colorado on the Front Range (Figure 7). Damage is usually greater in the Front Range than in southwestern Colorado (Hawksworth & Wiens 1996). No dwarf mistletoe occurs in the Black Hills National Forest, where ponderosa pine is most productive in the Region.

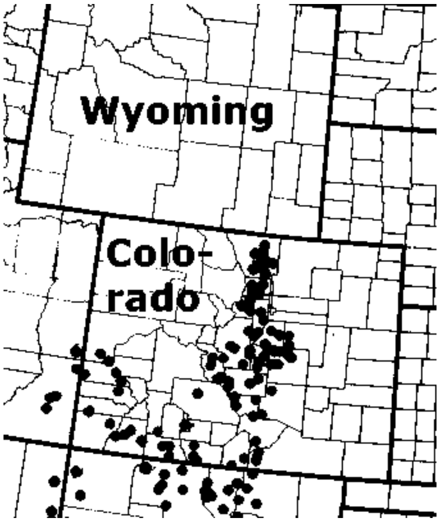


Figure 7. Distribution of Southwestern dwarf mistletoe, *A.vaginatum* subspecies *cryptopodum*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996)

Both witches' brooms and swellings are common symptoms. Development of witches' brooms can be weak, but large and robust brooms with thick, distorted branches are common in older infestations. Shoots vary in color from orange to reddish brown to almost black. Shoots are the largest of our dwarf mistletoes, approximately 4 in (10 cm) long (maximum 11 in or 27 cm) with a basal diameter of 0.08–0.4 in (2–10 mm). The species is unusual among dwarf mistletoes in temperate areas in that seed germination occurs immediately after dispersal in the fall, rather than the following year. This unusual life cycle trait and the robust size of this dwarf mistletoe reflect the fact that this is the extreme northern distribution of a tropical/subtropical species (B. Geils, pers. comm.).

Mortality due to southwestern dwarf mistletoe was quantified in a 32-year study at Grand Canyon National Park (Hawksworth & Geils 1990). Ninety percent of uninfected or lightly infected (DMR 0–1 at the start) trees survived the entire study period. Of heavily infected trees (DMR 6), only 5% over 9″ DBH survived, and none survived in the 4–9″ size class. Intermediate infection levels were associated with intermediate mortality levels. Infection intensified during the study, so that most trees that died were in DMR class 6 by the time of death. Based on the data, the authors estimated the half-life of trees (time in which half the trees are expected to die) by DMR class (Table 3).

Table 3. Expected half-life (time in years for half the trees to die) of ponderosa pine infected with Southwestern dwarf mistletoe at Grand Canyon National Park (Hawksworth & Geils 1990).

	Half-life	
Initial DMR	4-9″ DBH	>9″ DBH
0-1	ND [a]	ND [a]
2-3	30	57
4-5	17	25
6	7	10

[a] No decrease in longevity detected; half-life too long to estimate

Estimates of spread rate in single-storied stands vary. Recent estimates clock it as one of the faster dwarf mistletoes at 2–3 ft per year (Beatty & Mathiasen 2003). An earlier estimate is about 1.3 ft per year in open stands and 0.9 ft per year in dense stands (Hawksworth 1961b, calculated from slopes in his Fig. 32). Spread from overstory to understory is faster in ponderosa than in lodgepole pine.

Two Forest Insect and Disease Leaflets are available for this disease (Beatty & Mathiasen 2003, Lightle & Weiss 1974).

4. IMPACTS OF DWARF MISTLETOES ON TREES AND FORESTS

4.1 Tree growth and longevity

Dwarf mistletoes can have large impacts on trees when infection is severe. Effects have traditionally been quantified as loss of timber productivity. The total annual loss (reduced growth increment and mortality) caused by dwarf mistletoes in the United States was estimated at 418,000,000 cubic feet or 3,000,000,000 board feet (Drummond 1982). At $472 per thousand board feet (average ponderosa pine sawlog price in western Montana, Anonymous 2004b), that loss is more than $1.4 billion per year. Growth in height and diameter is decreased, so that immature lodgepole pine trees infected at an early age have only 23% of the cubic-foot volume of healthy trees after 70 years (based on stands up to 147 years old, Hawksworth & Hinds 1964). When mortality is included, merchantable volume is only 12.4% of that of healthy stands (Figure 8). In severely infested stands, all economic value of wood products from the stand is often lost.

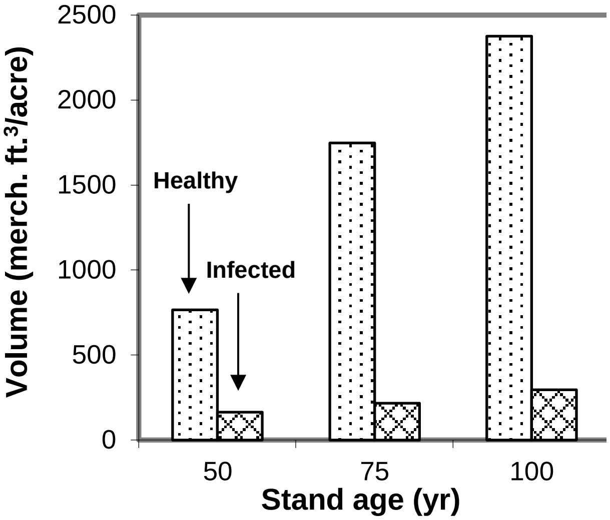


Figure 8. Effect of infection of lodgepole pine by dwarf mistletoe at an early age on volume (which integrates effects on height growth, diameter growth, and mortality). Data from Hawksworth & Hinds (1964).

Dwarf mistletoes typically increase mortality rates when DMR is > 4. Certain dwarf mistletoes are considered to be especially lethal (Hawksworth & Wiens 1996), and four of the five in the Rocky Mountain Region have that distinction (Table 4). Mortality due to dwarf mistletoe is difficult to quantify because tree growth is less in infested than in uninfested stands, so a lower proportion of the mortality is due to competition. Therefore, mortality due to dwarf mistletoe is underestimated when subtracting mortality in uninfested stands from that in infested stands.

Table 4. Dwarf mistletoe-host combinations in Colorado and Wyoming that have particularly high mortality rates (Hawksworth & Wiens 1996).

Pathogen	Host
A. americanum	lodgepole pine
A. cyanocarpum	limber and whitebark pines
A. douglasii	Douglas-fir
A. vaginatum	ponderosa pine

Using averages from multiple studies, the increase in 10-year mortality rates caused by dwarf mistletoes has been quantified (Table 5). However, mortality is affected by many variables. Mortality due to dwarf mistletoe is greater on dry than on wet sites (Baranyay & Safranyik 1970) and also during or following a drought (Geils & Hawksworth 2002). When heavily infected, large trees survive longer than small trees. Heavily infected (DMR 6) ponderosa pines > 9 inches dbh have an expected half-life of 10 years; smaller trees have a half-life expectancy of only 7 years (Table 3). Even large, mature ponderosa pines can be killed by dwarf mistletoes (Roth 2001).

In lodgepole pine stands infested for 80 years, 15% of the standing basal area was killed by dwarf mistletoe (determined by subtracting standing mortality in similar but uninfested stands, Hawksworth & Hinds 1964). However, most of the snags in that study were quite small.

Mechanisms of tree damage are related in part to allocation of resources. The biomass of the mistletoe plant itself may be a minor drain to the tree (although the endophytic systems of systemically infecting mistletoes can be much larger than the shoots); disruption of tree physiology may be a bigger effect. High hormone levels in the mistletoe (primarily cytokinins and indole-acetic acid) cause photosynthate and other nutrients to be shunted to infected branches (Livingston *et al.* 1984). Although host tissues near the infection may receive much of this bounty, the tree is damaged because nutrients do not go to the growing top and roots where they are needed most. Witches' brooms develop luxuriantly while the upper crown thins and dies. It is not uncommon to observe that infected branches are the last part of the crown to die.

Table 5. Increase in 10-year mortality rate in stands infested with *Arceuthobium* sp., relative to uninfested stands.

		Additional ten-year mortality due to disease (% of trees) by stand DMR					
		DMR					
Pathogen	Host	1	2	3	4	5	6
A. abietinum	white fir	1[a]	3	6	10	15	21
A. americanum	lodgepole pine	2	4	5	6	7	8
A. douglasii	Douglas-fir	1	2	4	9	15	23
A. vaginatum	ponderosa pine	1	4	8	15	23	34

[a] The percent of trees dying per decade was estimated for each stand. The value for uninfested control stands was subtracted from the corresponding infested stands, and the average of those values from multiple stands and studies is reported here. From Hawksworth *et al.* (1996, 1992).

An additional mechanism of damage relates to water relations. Dwarf mistletoes are typically less efficient at water use and transpire at a rate several times that of their host, with even greater differential under conditions of water stress (Hawksworth & Wiens 1996). During a drought, this additional water demand may result in decreased growth or even death of other parts of the tree.

Dwarf mistletoes frequently increase susceptibility to attack by bark beetles (Hawksworth & Wiens 1996, Stevens & Hawksworth 1984). In Colorado, dwarf mistletoe increases susceptibility of ponderosa pine to mountain pine beetle (MPB, *Dendroctonus ponderosae*) and western pine beetle, *D. brevicomis* (Frye & Landis 1975, Fuller 1983, Johnson *et al.* 1976, McCambridge *et al.* 1982, Ziegler 1978). Ponderosa pine may also have increased susceptibility to attack by *Ips* spp. when infected by dwarf mistletoe. Recent evidence from a 2002 outbreak in in Arizona indicated that severely infected trees of intermediate crown class are at greatest risk during outbreaks and are selectively killed by *Ips* spp. (Kenaley 2004). Ponderosa pines killed by *Ips* spp. had significantly higher dwarf mistletoe ratings than paired live trees, and the authors suggested that severely infested stands have greater probability of attack (Kenaley *et al.* 2006).

A similar effect is seen in piñon. In an outbreak of *Ips confusus* on piñon in Arizona, regression analysis showed that dwarf mistletoe infection and tree diameter were good predictors of individual tree attack by the beetle (Negron & Wilson 2003). Beetle-infested trees and plots had significantly more dwarf mistletoe than did uninfested trees and plots. This supports earlier observations that dwarf mistletoe predisposes piñon to attack by ips (Wilson & Tkacz 1992).

In the case of *D. pseudotsugae* and Douglas-fir, dwarf mistletoe may have little effect on bark beetle susceptibility (Furniss *et al.* 1981). However, such predisposition has been suggested for northern Idaho (Weir 1916a).

Lodgepole pine dwarf mistletoe apparently *decreases* susceptibility of lodgepole pine to MPB (McGregor 1978, Roe & Amman 1970, Ziegler 1978). However, data from the Shoshone National Forest, Wyoming, and Sawtooth N.F., Idaho, showed no significant difference in DMR or number of brooms between attacked and unattacked trees, though the high incidence of mistletoe may have clouded the results (Rasmussen 1987). Hawksworth & Johnson (1989) suggested that also in Colorado dwarf mistletoe has little or no effect on MPB susceptibility in lodgepole pine. Decreased susceptibility, where it occurs, is probably due to smaller diameter and thinner phloem caused by dwarf mistletoe (Roe & Amman 1970). However, stem infections, which often have thicker bark than the rest of the tree, may be selectively attacked by MPB (McGregor 1978).

4.2 Forest dynamics

Dwarf mistletoes are closely related to the fire regime in many of our forest types. Fire has been the most important single factor governing the distribution and abundance of dwarf mistletoes (Alexander & Hawksworth 1975). Because they are obligate parasites, dwarf mistletoes die when trees are killed by fire. In most cases, trees recolonize the site much more quickly than does the dwarf mistletoe. Even scorching of lower branches from a surface fire can substantially reduce the abundance of dwarf mistletoe in a surviving overstory (Conklin & Armstrong 2001, Koonce & Roth 1980).

Although a stand-destroying fire removes dwarf mistletoe over a large area, infected trees that survive the fire can reinfest a portion of the stand, explaining in large part the continued survival of dwarf mistletoe in ecosystems with infrequent, stand-replacing fire regimes.

Because dwarf mistletoe is often eradicated locally or at least reduced by fire, it may seem strange that dwarf mistletoes would increase the likelihood of such a fire. But they do. Infected trees often have large witches' brooms in the lower crown, persisting after the lower branches of healthy trees become shaded and die. These brooms, full of resin and dense accumulations of live and dead needles, act as fuel ladders that increase the opportunity for a surface fire to torch or become a crown fire. Numerous observers have noted selective torching of infected trees during a surface fire. In general, infested stands have greater total fuel loading than uninfested stands (Hawksworth & Wiens 1996, Hoffman *et al.* 2007, Koonce & Roth 1985).

Dwarf mistletoe abundance therefore increases the likelihood of severe fire, and can be viewed as contributing to the feedback loop that regulates the frequency and severity of fire. When such fires occur, dwarf mistletoe abundance decreases. This was demonstrated in a study in lodgepole pine: the current abundance of dwarf mistletoe was inversely related to fire frequency during the period from the late 1800's to the 1980's (Zimmerman & Laven 1984). The feedback loop can thus be viewed from the other side: fire regulates the abundance and distribution of dwarf mistletoe on the landscape.

Other effects of dwarf mistletoes on stand dynamics are less well studied, but logically predictable and easy to observe. Because dwarf mistletoes selectively reduce growth and increase mortality of their hosts in mixed stands, they can increase the likelihood and rate of succession when infecting seral species, or maintain early seral species when infecting late seral or climax species (Hagle *et al.* 2000). For example, growth reduction and mortality of lodgepole pine caused by *A. americanum* can be spectacular, encouraging succession to Engelmann spruce and subalpine fir, which are largely immune to indigenous mistletoes in our Region. On the other hand, the role of dwarf mistletoes in facilitating crown fires can have just the opposite effect. When fire destroys a mixed stand of mature lodgepole pine with invading spruce and fir, lodgepole pine readily recolonizes the site in pure stands, due in large part to its serotinous cones. Thus, dwarf mistletoes can either hasten succession or reset it, enhancing the persistence of seral forest types.

The latter effect may explain the conundrum hinted at earlier: what possible advantage could there be for dwarf mistletoes to enhance the likelihood of severe fire? Although dwarf mistletoe contributes to its local demise in the immediate future, over the longer term it may help to perpetuate its seral host, increasing opportunities for infection in the future.

Dwarf mistletoe infection also reduces the number and viability of seeds produced by ponderosa pine (Hawksworth & Wiens 1996) and presumably other hosts. Seed production was not affected by light infection, but moderate infection reduced it to 42% of healthy trees (by weight); severe infection reduced it to 29% of healthy trees (Korstian & Long 1922). When viability is considered, the effect is somewhat greater. Consequences on forest regeneration are considered in management but have not been explicitly studied.

5. IMPACTS OF DWARF MISTLETOES ON ANIMALS

Birds and mammals may be influenced, directly or indirectly, positively or negatively, by dwarf mistletoes. Among the features and effects of dwarf mistletoe that may influence animals are:

- Shoots of the dwarf mistletoe plant, which may be used as a food source.
- Witches' brooms, which may be used by some animals for nesting, denning, hiding, caching, or foraging.
- Decrease in number and size of seeds produced by the host tree, which may affect animals that use the seeds for food.
- An increase in mortality of host trees, which may influence animals through a change in the dynamics or size of snags.
- Through growth inhibition and mortality of the host species, the vegetation type may gradually change, influencing animals in various ways.

5.1 Diversity and abundance of vertebrates

5.1.1 Dwarf mistletoes as a food source for vertebrates

Numerous birds and mammals have been reported to feed on dwarf mistletoe shoots and/or fruits, though in most cases it is not a significant part of their diet. They may also feed on bark of tree shoots that are swollen and otherwise modified by dwarf mistletoe. A recent list of 21 species recorded as feeding on dwarf mistletoes was provided by Shaw *et al.* (2004). Birds that feed on dwarf mistletoes usually use it as a small part of their diet except for the euphonia in the Dominican Republic and the gray silky-flycatcher in Mexico (Hawksworth & Geils 1996). Among dwarf mistletoe herbivores in the United States are blue grouse, for which Douglas-fir dwarf mistletoe forms 2-8% of the diet in eastern Arizona, and Abert's squirrel, which feeds occasionally on dwarf mistletoe shoots and grazes on infected bark of ponderosa pine. Red squirrel in lodgepole pine forests often feed on pine shoots 6-13 mm in diameter; a preference for mistletoe-infected shoots has been observed (Hawksworth & Geils 1996). Bark of mistletoe cankers on various hosts is frequently gnawed, mostly by squirrels. In ponderosa pine forests of Colorado and the southwest, there are indications that dwarf mistletoe shoots may make up to 25% of the diet of porcupines at certain times of year, although individual porcupines apparently vary in this regard (Hawksworth & Geils 1996). In general, feeding by animals on dwarf mistletoes primarily occurs during winter when other food sources are unavailable. Dependence by any vertebrate has not been reported.

Urness (1969) conducted nutritional analyses of Southwestern dwarf mistletoe (*A. vaginatum* ssp. *cryptopodum*) in comparison with five species of true mistletoes in the genus *Phoradendron*, which are more heavily used for food by wildlife. The dwarf mistletoe had much higher levels of acid-detergent fiber (inversely related to digestibility) than all the *Phoradendron* spp. Crude protein was among the lowest levels of the species tested. The dwarf mistletoe had moderate levels of phosphorus but low levels of calcium. When exposed to rumen contents of deer, digestion of the dwarf mistletoe was lower than that of all the true mistletoes and comparable to that of available shrubs.

5.1.2 Ponderosa pine and southwestern dwarf mistletoe

Perhaps the most widely cited work on effects of dwarf mistletoe on wildlife diversity is a paper by Bennetts *et al.* (1996) on bird diversity. Eight ponderosa pine stands with varying levels of southwestern dwarf mistletoe (*Arceuthobium vaginatum* ssp. *campylopodum*) in two Front Range locations in Colorado were studied. Average dwarf mistletoe ratings (see 7.2, Bennetts *et al.* used a nonstandard approach of a mean of cell means within the stand, rather than a mean of all individual trees) were about 0.0, 0.6, 2.1 and 3.6 for the Cheesman Reservoir location and 0.0, 2.5, 2.5 and 4.6 for the Florissant location.

Although the abstract reports that abundances of 24 of 28 bird species were positively correlated with dwarf mistletoe, this proportion misrepresents the actual results. The number 24 in the abstract includes those for which the positive relationship was not significant at any tested level of α, and the number 28 excludes those with insufficient observations to estimate slope. As noted by a subsequent researcher, “Bennetts *et al.*’s (1996) study is frequently misinterpreted because regression coefficients for insignificant equations are reported. . . . Conclusions from [the] study can be somewhat misleading” (Parker 2001).

The abundance of 4 species was positively correlated with DMR and had a slope significantly different from 0 at $\alpha = 0.05$. When α was relaxed to 0.10, 5 additional bird species had a positive correlation and slope significantly different from 0. The remainder either had insufficient detections to estimate slope (19 species), had positive slopes that did not differ significantly from 0 (16 or 21 species, depending on α), or had negative correlation (4 species, slopes were not significantly different from 0). Thus, in contrast with the abstract, only 4 of 47 species detected on the plots were significantly associated with dwarf mistletoe using usually accepted statistical criteria.

DMR was positively correlated with the number of bird species detected per stand. The trend was apparent overall as well as within each location. DMR was not associated with species evenness.

Snag abundance was correlated with DMR, and the authors suggested that dwarf mistletoe caused an increase in mortality in the study areas. Since many of the bird species may have been favored by snags because of increased foraging or cavity-nesting opportunities they presented, it is not clear to what extent the positive associations of bird abundance with DMR is an effect of snags vs. a direct effect of dwarf mistletoe shoots and witches’ brooms.

The authors opine that all dwarf mistletoe control should be abandoned except where timber production is the sole management goal (Bennetts *et al.* 1996). On public lands, no areas have exclusive management goals, so this is a recommendation to completely abandon dwarf mistletoe management on public lands.

The question was revisited more recently (Parker 2001). In 19 stands in northern Arizona, with DMR ranging from 0 to 3.7, the abundance of four species was positively and significantly correlated with measures of dwarf mistletoe, five species were negatively and significantly correlated, and seven were unrelated. The total number of species observed was not given (>25), but 16 species were abundant enough to be analyzed in detail. The number of species observed was not correlated with DMR.

As in the previous study (Bennetts *et al.* 1996), snag abundance was positively correlated with dwarf mistletoe severity (Parker 2001). Three of the four species that were positively correlated with dwarf mistletoe were cavity-nesting birds.

Garnett *et al.* (2004) compared wildlife use of broomed vs. nonbroomed trees in 12 stands in northern Arizona. All study stands had DMR ≥ 1. Broomed trees were used significantly more than nonbroomed trees for wildlife activities (mean over all sites was 25% use of broomed trees and 2% use of nonbroomed trees), including foraging/caching, nesting, and roosting/resting. Animals observed in brooms included Abert’s squirrel, porcupine, and passerine birds. Of 226 brooms examined, 23% had evidence of wildlife use, 75% of which was Abert’s squirrel. Of the 39 brooms with Abert’s squirrel evidence, 8 were nesting and 31 were caching/foraging. Only 10 of the 226 brooms were used by birds, 2 for nesting and 8 for roosting/resting.

5.1.2.1 Abert’s squirrel

Abert’s squirrel (Figure 9; also known as tassel-eared squirrel) is endemic to the Southern Rockies, the Colorado Plateau, and the northern Sierra Madre Mountains of Mexico. In the United States, it occurs primarily in Colorado, New Mexico, Arizona, and in a small part of Utah, but the distribution has expanded into southern Wyoming in recent decades (Keith 2003). Although many local subspecies have been named, they do not conform to phylogenetic variation in mitochondrial DNA (Lamb *et al.* 1997).

Although it is often stated that Abert’s squirrel depends on ponderosa pine for food, cover and nest sites, the squirrel was introduced to and established successful populations in mixed-conifer and spruce-fir forests with little to no ponderosa pine in the Pinaleño Mountains of Arizona (Edelman & Koprowski 2005). The populations used similar food items as in ponderosa pine forests (see below), but the conifers used most frequently were Douglas-fir and southwestern white pine. Cavity nests were more common in this introduced population (10% of nests found) than in native populations, and large aspen with stem decay were favored sites for cavity nests (Edelman & Koprowski 2006). Abert’s squirrel has been noted in many other habitats aside from ponderosa pine forests (see references in Edelman & Koprowski 2005).

Large nests are typically built in pine trees, especially on crotches against the bole (Burt & Grossenheider 1976, Keith 2003). Nests are constructed of fine twigs, usually 2-10 cm in length. Nests are 30 to 100 cm (1.0 to 3.3 feet) in diameter (Keith 2003). Witches’ brooms may be incorporated into or support Abert’s squirrel nests (Anonymous 2003). Of 226 brooms examined in northern Arizona, 8 were used by Abert’s squirrel for nesting and 31 for caching/foraging (Garnett *et al.* 2004). Brooms

Figure 9. Abert’s squirrel, *Sciurus aberti*. Photo from Keith (2003).

that were used for caching and foraging tended to have more branches and be on taller trees than unused brooms, leading to the recommendation that ponderosa pines >18 m tall having brooms with >7 branches be retained for squirrel use (Garnett *et al.* 2006). Too few nests were found in brooms for statistical analysis. No information was given on nesting or caching/foraging outside of brooms. Of 40 nests identified at a site in Colorado, 10 were built in witches' brooms (Farentinos 1972a), but in this case brooms were rare and all large brooms were occupied.

The diet of Abert's squirrel is varied. Preferred foods are seeds of ponderosa pine and mushrooms. Mushrooms (especially hypogeous fungi such as truffles) are an important food in late summer and early fall and "provide an important source of moisture in the diet of these squirrels, for in many areas where they live they must derive most of their water from their food" (Hoffmeister 1986). Squirrels also feed on the cambium and phloem of young shoots, needles, terminals, and flowers of ponderosa pine (Burt & Grossenheider 1976, Hoffmeister 1986). Bark grazing on larger branches, though not a major form of feeding, is confined to mistletoe-infected branches (Allred & Gaud 1994). Acorns of Gambel oak, insects, carrion, and occasionally pieces of shrub and grasses may also be consumed. There is evidence that shoots of dwarf mistletoe may also be a minor food source (Keith 2003).

An important effect of dwarf mistletoe infection is reduced seed production (see 4.2, Forest dynamics). Since Abert's squirrel sometimes depends on ponderosa pine seed as a food source, and indeed the populations of the squirrel vary notably with the pine cone crop (Farentinos 1972b), it is likely that moderate to heavy dwarf mistletoe infestations decrease food availability for squirrel populations and may negatively impact carrying capacity. However, these effects on the squirrel have apparently not been studied.

It is not clear that dwarf mistletoe is important to the squirrel, and no work has shown an effect of mistletoe on Abert's squirrel population size, positive or negative. In a 62-page assessment of the status of the squirrel in the Rocky Mountain Region by an authority on Abert's squirrel, no dependence or association with dwarf mistletoe was mentioned other than minor feeding on mistletoe shoots (Keith 2003).

The Natural Heritage Program gives Abert's squirrel a rating of "demonstrably secure" globally and in Colorado (Anonymous 2004c). It is not on the Rocky Mountain Region sensitive species list nor any federal or state list of threatened or endangered species. Populations in Colorado are considered secure and several southwestern states, including Colorado, Arizona and New Mexico, classify it as a game animal and administer a hunting season for Abert's squirrel (Anonymous 2004d). The squirrel has expanded its range in Colorado and crossed the border into southern Wyoming in the latter part of the 20th century (Keith 2003).

However, it is a management indicator species (MIS) in several National Forests of Colorado. A number of projects, such as the Missionary Ridge Fire Salvage, have been stopped by appellants or litigants, who have pointed out that population data are missing for the squirrel and other MIS (Draper 2004).

5.1.3 Lodgepole pine and lodgepole pine dwarf mistletoe

Witches' brooms caused by *Arceuthobium americanum* in lodgepole pine are often used as nest sites by red squirrel and American marten (Hawksworth & Geils 1996). The animals are not dependent on the presence of brooms as nesting habitat, but it is not clear to what extent brooms are preferred or enhance survival or reproductive success. Apparently no studies have tested the effect of dwarf mistletoe intensity on wildlife diversity in lodgepole pine.

Although an emphasis is placed on witches' brooms as nesting sites of arboreal squirrels by some workers, the consensus seems to be that populations of northern flying squirrel and other squirrels are limited more often by food abundance rather than nesting and hiding sites (Ransome *et al.* 2004, Ransome & Sullivan 2004, Waters & Zabel 1995). Arboreal squirrels like northern flying squirrel often use witches' brooms when they are available, but they successfully use constructed nests and cavities in the absence of brooms (see literature cited in Ransome & Sullivan 2004). Although they did not study the role of dwarf mistletoe, Ransome *et al.* (2004) found that young lodgepole pine (29-39 yr old) thinned 12 years earlier had populations of northern flying squirrel and red squirrel at levels recorded in old-growth forests over three years of measurements. Diversity of small ground mammals in a related study was also found to be similar in young, thinned and old-growth lodgepole pine stands (Sullivan *et al.* 2005).

5.1.4 Douglas-fir and *Arceuthobium douglasii*

A variety of owls and accipiters have been reported to nest in the large, dense witches' brooms often caused by Douglas-fir dwarf mistletoe (Hawksworth & Geils 1996). Some of these raptors apparently prefer brooms as nesting sites. However, in a study designed to assess the role of brooms as wildlife habitat in Douglas-fir (Parks *et al.* 1999a, discussed in detail below), only two avian nests were found, both in nonbroomed trees.

Porcupines in northeastern Oregon often use brooms in Douglas-fir for shelter (Smith 1982). Flying squirrels and red squirrels also may use the brooms for cover, caching and nesting (Hawksworth & Geils 1996, Shaw *et al.* 2004).

Parks *et al.* (1999a) inspected 117 trees with witches' brooms and 42 nonbroomed trees for evidence of wildlife use in northeastern Oregon. Evidence of mammalian nesting and resting was found only in broomed trees (18%). Evidence of mammalian foraging was found in 51% of broomed trees and 29% of nonbroomed trees. On the other hand, evidence of foraging was found on the ground beneath 36% of broomed and >62% of nonbroomed trees. Few avian nests were found (2), and they were only in nonbroomed trees.

Although the results suggest that brooming may influence certain kinds of wildlife use, no statistical analysis was provided that compared wildlife use of broomed vs. nonbroomed trees. A sampling issue also makes it difficult to draw conclusions: half (22) of the nonbroomed trees were in uninfested stands where there was no comparable sample of broomed trees, suggesting that stand differences were not controlled and may not have been comparable between broomed and nonbroomed trees. No comparison of use of nonbroomed trees in infested vs. uninfested stands was provided.

More recently, Bull *et al.* (2004) reported a study on the effects of dwarf mistletoe treatment on red squirrel and northern flying squirrel. Two treatments were tested: (1) thin from below, selectively removing broomed trees, but leaving untreated, infested islands up to 0.5 ha in size – one island occurred in about every 3.7 ha; (2) removing all trees with brooms >25 cm diameter. Squirrels were live-trapped one or two years before treatment and again both one and two years after treatment. Trapped squirrels were anesthetized, and received ear tags and radio collars in all but the last year of the study.

In general, red squirrel trapping went up after the treatment, and northern flying squirrel trapping decreased (Bull *et al.* 2004). However, it is difficult to interpret the results and support the conclusions of the authors for the following reasons:

a) There were no untreated control stands. Trapping was only done for one year before treatment vs. two years after treatment, and the data were variable, so it is not clear that the data would be consistent in the absence of treatment. Other studies have shown that populations of northern flying squirrel may vary significantly from year to year in the absence of treatment (Carey 1995, Ransome & Sullivan 2003).

b) No statistical analysis of these data was presented, although other results in the study were thoroughly analyzed. I analyzed data provided by the author (Table 6). The island treatment had no significant effect on flying squirrel numbers at all, but it increased numbers of red squirrel significantly the first year (not the second year or overall). The total removal treatment had no significant effect on flying squirrel in either year, but when both years are combined the decrease was marginally significant. Total removal caused highly significant increase in red squirrel in both years and overall. These results do not support some of the conclusions presented in the paper (Bull *et al.* 2004), which stated that both treatments negatively affected northern flying squirrel numbers, and de-emphasized the increase in red squirrel numbers in discussing management implications of the study.

c) The potentially negative effect of trapping, anesthesia and radio collars on flying squirrel survival was not discussed. This potential makes an untreated control all the more important.

d) Each treatment was done in only two stands, and the variability between stands was not reported or analyzed.

Table 6. Statistical analysis of abundance of red squirrels and northern flying squirrels (percent of trap/nights with squirrels) before and after two treatments for dwarf mistletoe control in northeastern Oregon. Raw data for analysis provided by E. Bull (personal communication) based on the study by Bull et al. (2004).

Treatment	Red squirrel			Northern flying squirrel		
	Percent	P[a]		Percent	P[a]	
Island						
Pretreatment	1.40			0.21		
Posttreatment 2001	2.75	0.011	} ns	0.25	ns	} ns
Posttreatment 2002	1.28	ns		0.07	ns	
Total removal						
Pretreatment	0.69			0.64		
Posttreatment 2001	1.53	0.022	} <0.001	0.29	ns	} 0.04
Posttreatment 2002	3.14	<0.001		0.21	ns	

[a] Comparison of counts of positive and negative trap/nights between pretreatment and posttreatment measurement years and with posttreatment years combined, by chi-square analysis. ns = not significant at $\alpha = 0.05$

Hedwall *et al.* (2006) compared the use of different types of witches' brooms in Douglas-fir by red squirrels. They found that brooms resulting from infections within 1 m of the stem and those on the stem itself had more evidence of nesting, caching and foraging than brooms farther out on branches. Unbroomed trees were examined but apparently had little evidence of use (Hedwall, personal communication). Evidence of use is more likely to be caught and retained in brooms, particularly large, dense ones with platforms, than in unbroomed branches, and it is difficult to separate this difference from differences in actual use by animals.

5.1.5 Five-needle pines and *Arceuthobium cyanocarpum*

Some animals depend on seeds of white pines at certain times of year. For instance, limber pine seeds can be an important part of the diet of black and grizzly bears (McCutcheon 1996), Clark's nutcracker (Tomback & Kramer 1980), and red squirrels (Hutchins & Lanner 1982). In whitebark pine areas, seeds of that species may play an even more critical role in the diet of grizzly bears (Baskin 1998, Mattson & Reinhart 1994). The large reduction in seed production in stands severely infested by *A. cyanocarpum* may have a consequent impact on populations of these animals.

5.2 Effect of mistletoe-caused snags on vertebrates

The effect of dwarf mistletoes on mortality, resulting in snags, is discussed in section 4.1, Tree growth and longevity. Snags may also be created during management projects by girdling or burning to reduce dwarf mistletoe incidence while providing wildlife habitat (Parks *et al.* 1999b).

Snags and, in a broader view, coarse woody debris contribute to wildlife habitat in a variety of ways (Bull *et al.* 1997). Snags and downed logs provide sites for nesting, roosting, denning, foraging, resting and hiding for a variety of wildlife species. The diversity of organisms for which there is less active concern, such as fungi and insects, can also be associated with coarse woody debris (Bader *et al.* 1995, Nilsson & Baranowski 1997, Rydin *et al.* 1997). Decaying wood is an important site for nitrogen fixation, a reservoir for soil moisture and nutrients, and is a favored habitat for mycorrhizal roots, especially on dry sites (Harvey *et al.* 1987, Jurgensen *et al.* 1989). Managers have been encouraged over the past decade to increase coarse woody debris, including snags, in managed forests (Hagan & Grove 1999).

The literature cited in the previous section (4.1, Tree growth and longevity) indicates that, in the short term, mistletoe-infested stands often have more snags than otherwise comparable, uninfested stands. In the long term, however, snag habitat may be more abundant and of higher quality in the absence of dwarf mistletoe because of effects on snag size and potential for occurrence of internal decay.

Since trees grow faster and survive longer without dwarf mistletoe, they are larger when they do die. Larger snags remain standing for a longer period and provide higher quality wildlife habitat. Subsequently, as coarse woody debris, this larger material also provides more habitat for a wider variety of wildlife species (Bull *et al.* 1997).

Trees that survive longer are more likely to develop internal stem decay (“heart rot”) which develops only in living trees over a long period and greatly enhances nesting and denning opportunities in living trees (Figure 10), as well as in the resulting snags and coarse woody debris (Parks & Shaw 1996). For instance, primary cavity nesters often detect and select living trees with internal decay for excavation (Conner *et al.* 1976, Hooper *et al.* 1991), and that habitat feature persists after tree death. Large diameter greatly enhances the value of hollow trees, snags and logs to a variety of wildlife, including primary cavity nesters, secondary cavity nesters, American marten, bears, etc. (Bull *et al.* 1997, Fan *et al.* 2003).

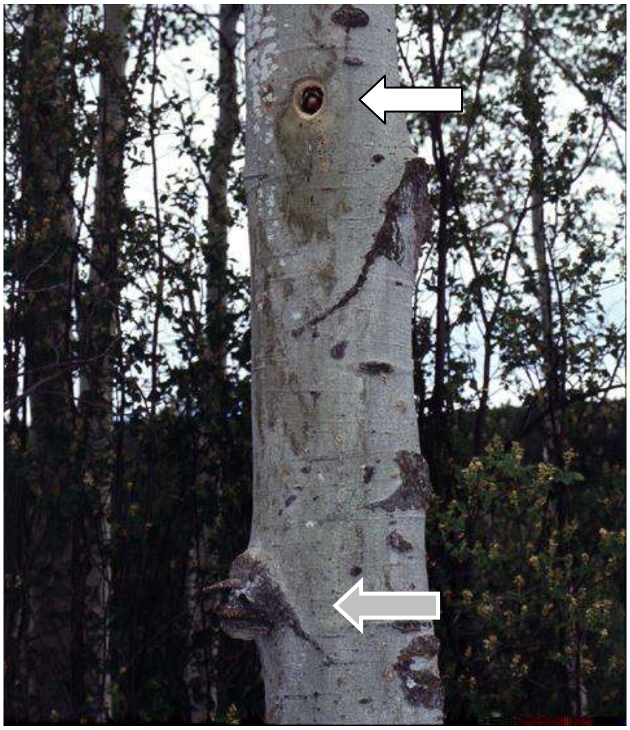


Figure 10. Woodpecker in cavity (white arrow) in quaking aspen (*Populus tremuloides*) with conk of the stem-decay fungus, *Phellinus tremulae,* about a meter below (gray arrow).

5.3 Effects of dwarf mistletoes on insects

Several insects are known to feed on dwarf mistletoes (Stevens & Hawksworth 1984). The best known are two species of *Mitoura*, the hairstreak butterflies (Lepidoptera: Lycaenidae), whose larvae are obligate dwarf mistletoe herbivores and the adults of which are prized by butterfly collectors. *Mitoura johnsonii*, a candidate for listing as a threatened species in Washington state (http://wdfw.wa.gov/hab/phsinvrt.htm) but not federally, is found on several species of *Arceuthobium*, but most commonly on *A. tsugense* (hemlock dwarf mistletoe). *Mitoura* (*Callophrys*) *spinetorum*, the thicket hairstreak (Figure 11), occurs from southern British Columbia to central Mexico on *Arceuthobium* spp. It is relatively common and has no federal listing status. The Natural Heritage Program lists it as “demonstrably secure” globally and in Colorado (Anonymous 2004c). It is not clear if these butterflies have a significant impact on dwarf mistletoe populations.

Other lepidopterans that feed on dwarf mistletoes and are said to be more damaging than the *Mitoura* spp. are *Dasypyga alternosquamella* (Pyralidae, the snout moths) and *Filatima natalis* (Gelechidae, the twirler moths) (Hawksworth & Geils 1996). The larvae of both species mine large shoots and consume small shoots. These insects destroyed complete crops of dwarf mistletoe shoots in local areas, but, because plants are not killed when the shoots are consumed, it is not known how much or how often they affect population increase of the mistletoe. Spittlebugs are often seen on dwarf mistletoe in the Southwest, especially *Clastoptera distincta*.

Figure 11. Thicket hairstreak butterfly, *Mitoura spinetorum* (male). The larvae are obligate dwarf mistletoe herbivores. Photo from (Anonymous 2004a).

5.4 Dwarf mistletoes and animals: Conclusions

Clearly many wildlife species make use of dwarf mistletoes, associated witches’ brooms, and affected forests. In most cases this use appears to be incidental. A wide variety of animals has been observed feeding on dwarf mistletoe shoots, but it is a small part of their diet. There is little or no evidence that the success or abundance of animals is affected by the presence of witches’ brooms, and no indication that any mammal or bird in the United States depends on dwarf mistletoe.

In one study, the number of bird species and abundance of certain species were positively correlated with mistletoe abundance (Bennetts *et al.* 1996); in another study bird diversity was not correlated with mistletoe and abundance of other species was inversely correlated with DMR (Parker 2001).

Evidence suggests that the most likely effect on animals, particularly birds, is indirect. By decreasing the longevity of trees, dwarf mistletoes tend to increase the number of snags in young to middle-aged stands. Snags are important to many animals, particularly those that nest in cavities in dead trees. Evidence suggests that larger snags are the best habitat overall, because they are suitable for the largest number of species and persist for a long time (Bull *et al.* 1997). Because every tree that lives will eventually die, it must be considered that the small snags made available now due to dwarf mistletoe means there will be fewer large snags at a later time. Trees that are infected but not killed by dwarf mistletoe will be smaller than uninfected trees due to the growth effects. From a management perspective, one must weigh the potential advantages and disadvantages of small snags early in stand development vs. large snags later.

Research regarding wildlife and dwarf mistletoe must be evaluated carefully, as some statistical analyses, data and conclusions selectively emphasize certain findings. There are a number of complexities in the relationships between dwarf mistletoe and species abundance, diversity and richness, such that a simple trend with increasing mistletoe may not be expected:

1. Competitive interactions among wildlife species may cause populations of some to decrease as others increase.
2. Nest predators such as Steller's jay and Abert's squirrel (Craig 1998) may nest in witches' brooms, although their abundance is not always correlated with DMR (Parker 2001). Reproductive success of some songbirds could then be lower where predator nest sites are common.
3. Similarly, severe dwarf mistletoe infestation and associated mortality can create a competitive advantage for other plant species. As plant species diversity increases, wildlife diversity may increase. Again, this is not a unique feature of mistletoe-infested stands.
4. Effects of dwarf mistletoe on a given species likely have an optimum level of mistletoe for such an effect. For instance, if a species benefits from a certain level of dwarf mistletoe, there may be no further benefit or even a net detriment above that level as the stand eventually deteriorates because of disease severity.
5. Because dwarf mistletoes increase tree mortality, they often increase snag density. Because this is not a unique feature of mistletoe-infested stands, a strict correlation of abundance or richness with DMR may be confounded if other causes of mortality are present.
6. Viewed over the long term, dwarf mistletoe infestation may reduce the value of snags and coarse woody debris as wildlife habitat because the snags are smaller (due to both reduced growth rate and early mortality) and are less likely to have internal stem decay (heart rot).

6. FACTORS AFFECTING DWARF MISTLETOES

6.1 Fire

Fire is the most important factor affecting the distribution and abundance of dwarf mistletoes in most forest types of the western United States. The mutual interaction of dwarf mistletoes and fire is described in detail in section 4.2, Forest dynamics.

Fire that kills infected trees reduces the population of dwarf mistletoe, at least in the short term. Large, continuous, stand-replacing fires substantially reduce dwarf mistletoe populations across the landscape over long periods and may eliminate local populations and result in new stands that are disease-free to maturity. Patchy burns also reduce dwarf mistletoe populations, but scattered, infected residuals may provide inoculum for early infection of new regeneration (Alexander & Hawksworth 1975).

6.2 Stand structure and composition

Size structure. Size structure of forest stands has a strong effect on the rate of mistletoe spread. This relationship has been well documented (literature summarized by Parmeter 1978). Because of the nature of seed dispersal, trees under an infected overstory are more likely to be hit by seeds than are trees in a single-storied stand (*Figure 12*). Because of their trajectory, seeds from an infested overstory are also dispersed a greater distance before they strike the understory than is the case between trees of equal size, so spread rate is greater in two-storied or multi-storied stands. Trees in the understory can be infected anywhere in the crown, whereas trees in single-storied stands are most likely to be infected in the lower crown where the infection has less effect and can spread less effectively. Finally, trees infected at a young age suffer much greater damage than trees infected when they are old.

Very small and young trees are unlikely to be infected. This is not because of resistance, but because they have been exposed to inoculum for a relatively short time and because they present a small target for randomly dispersed seeds to strike. Generally, trees less than 1 m tall or less than 10 years old (whichever comes first) are unlikely to be infected (Wicker 1967, Wicker & Shaw 1967).

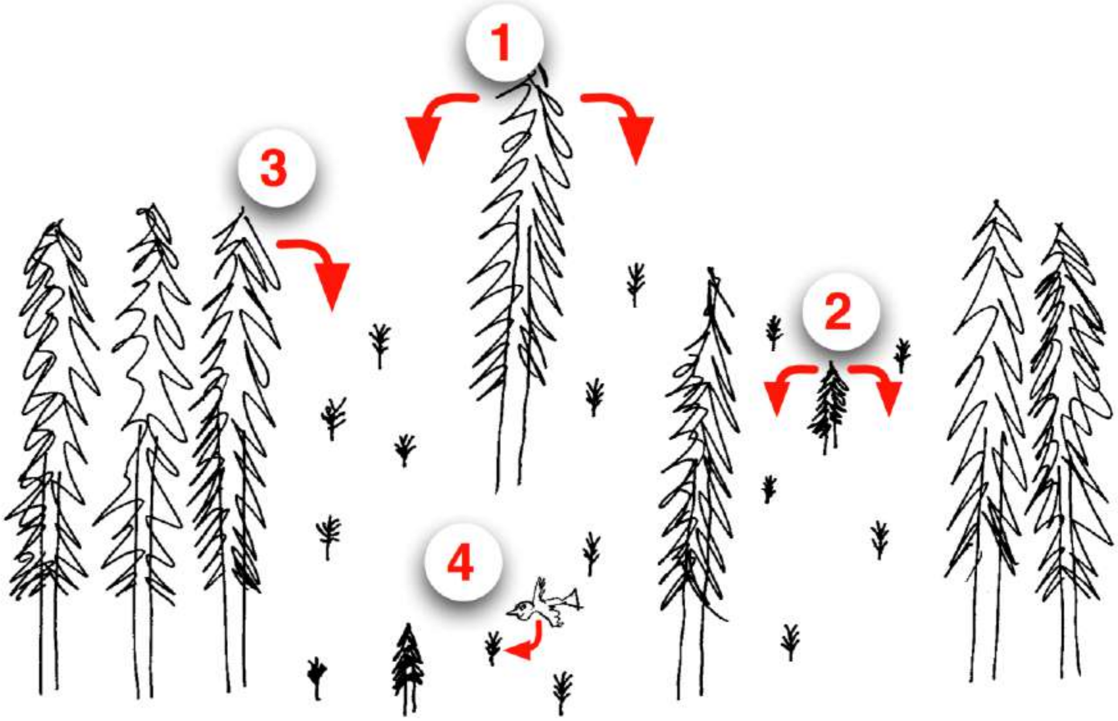


Figure 12. Sources of dwarf mistletoe infection for a young stand, in order of importance. In the scenario used for illustration, a shelterwood has been established in a larger infested area, but a similar pattern could be established by mixed-severity wildfire. Sources of infection are: 1) residual overstory trees after seedling establishment; 2) pre-existing (advanced) regeneration that is infected; 3) spread from infected trees at the border of the treated area, and; 4) vectoring of seed by wildlife. The first is critically important, the last is usually considered unimportant from a disease management perspective.

Density. Tree density can have a strong influence on spread rate (distance through the stand over time) at the extremes of density. Obviously, spacing beyond the maximum dispersal distance (about 52 ft) will result in little or no spread (Figure 13). As density increases, more seeds will successfully make the jump and spread rate increases. However, as density increases further, seeds are intercepted before they get very far, so spread rate decreases again (Hawksworth 1961b). As a practical matter, within the range of densities usually found in forests, mistletoes spread more rapidly in open than in dense stands, i.e., most stands are to the left of the apex in Fig. 9 (Hawksworth & Johnson 1989, Parmeter 1978).

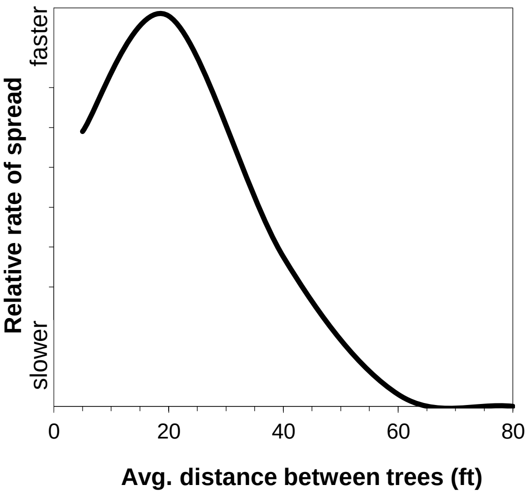


Figure 13. Hypothetical rate of dwarf mistletoe spread in relation to stand density for ponderosa pine 30-40 years old in the Southwest (from Hawksworth 1961b). The curve would be shifted to left for younger stands and to the right for older stands.

Spatial arrangement of trees can affect dwarf mistletoe spread as does density. Particularly important is the consideration that host-free areas greater than 27 m wide provide an effective barrier to spread of the disease. This can include meadows or other forest openings, streams, roads, etc.

Composition. Composition of stands also affects dwarf mistletoes. In a mixed stand containing hosts and nonhosts, with the nonhosts large and abundant enough to intercept flying seeds, the spread rate of dwarf mistletoe between host trees is likely slower than in pure stands of hosts (Parmeter 1978). Also, it seems safe to predict that the frequency of infection should be less in mixed stands because a portion of the trees cannot be infected. However, these relationships have not been quantified.

6.3 Historic practices

In presettlement forests, it is generally considered that dwarf mistletoes tended to be patchily distributed (Kipfmueller & Baker 1998). Some early management practices tended to increase the abundance and distribution of dwarf mistletoes. Thinning commonly practiced in ponderosa pine of the Southwest (“improvement selection”) may have prevented mortality due to mistletoe, but also contributed to its spread and intensification (Conklin 2000, Hawksworth 1961b, Heidmann 1968, Heidmann 1983). Selectively harvesting the most valuable trees (high-grading) concentrated the mistletoe in the overstory while creating opportunities for reproduction, establishing ideal conditions for dwarf mistletoe spread and intensification. Similarly, incomplete clearcuts left unmerchantable, infected trees that led to heavy infection of the regeneration. Excessive grazing, road building, and direct fire suppression have decreased fire frequency, enhancing multi-story, dense stands that are more susceptible to dwarf mistletoes in some forest types, while at the same time removing the single most important natural control of dwarf mistletoes.

These factors contributed to an increase in the distribution and abundance of dwarf mistletoes in many forests of the western United States (Shaw *et al.* 2004, see also section 4.2, Forest dynamics). In ponderosa pine forests of the Southwest, for instance, it is widely acknowledged that past overgrazing, fire suppression and logging practices have resulted in increased distribution and severity of southwestern dwarf mistletoe (Pollock & Suckling 1995). Surveys conducted in the 1950s and 1980s indicate an increase in the distribution of southwestern dwarf mistletoe on National Forests of Arizona and New Mexico from 30% to 38% of the ponderosa pine type, a 27% increase (Maffei & Beatty 1988). Similar surveys conducted with consistent methods over a 41-year period on the Bighorn National Forest indicate continuing increase in incidence of lodgepole pine dwarf mistletoe from 31% in 1958 to 36% in 1978 and a conservative estimate of 44% in 1999 (Harris 2003), an increase of 42% in only 41 years. Forest changes since European settlement east of the Cascades in Washington and Oregon are associated with increased distribution and severity of dwarf mistletoes in Douglas-fir and true fir forests (Hessburg *et al.* 1994). Because of changes in fire frequency, a similar increase in western dwarf mistletoe is inferred for ponderosa pine forests in that region. Douglas-fir dwarf mistletoe has increased in the Inland West where historic practices have made the host more widespread and continuous (Hadfield *et al.* 2000).

Veblen *et al.* (2000) hypothesized that logging and changes in fire regime have increased mistletoe infection over large areas in lodgepole pine of the Pike and San Isabel National Forests, Colorado. Dwarf mistletoe infection in lodgepole pine increased with time since the last fire in several studies, and a general increase in dwarf mistletoe intensity and distribution over time was anticipated due to changes in fire return interval (Kipfmueller & Baker 1998, Zimmerman & Laven 1984). In lodgepole pine forests of eastern Oregon and Washington, although dwarf mistletoe was undoubtedly severe in some presettlement forests, it is now more widely distributed and carrying over between stands now partially replaced by mountain pine beetle rather than more completely replaced by fire (Hessburg *et al.* 1994). In lodgepole pine of western Montana and northern Idaho, the increase in dwarf mistletoe, together with fire exclusion and increasing mountain pine beetle vulnerability, have created a huge potential for fires, likened by Monnig & Byler (1992) to "holding water behind a leaky dam. We can either draw the water down gradually or we can wait for the dam to break." An exception is the Targhee National Forest in Idaho, where incidence of dwarf mistletoes declined in both lodgepole pine and Douglas-fir between 1978 and 1996 (Smith & Hoffman 1998). In that case, widespread bark beetle outbreaks and threat of wildfire led to a huge effort at salvage, regeneration and seedling protection that shifted forest structure from mostly mature, heavily infested stands to younger, lightly infested stands.

6.4 Host vigor and site

The chief attributes of host vigor that influence dwarf mistletoes are crown density and rate of height growth. Vigorous trees tend to have larger, denser crowns with more foliage and longer needles. All else being equal, these trees should intercept more seeds and therefore be more liable to infection than trees growing poorly (Parmeter 1978). The rate of infection would therefore increase with host vigor, assuming constant inoculum.

Dwarf mistletoe plants on vigorous trees also grow better. It is a common misconception that all parasites grow better on weak hosts than on vigorous hosts. Cortical strands invade vigorous tissue more quickly, shoots are larger and more fruit is produced on vigorous hosts (Parmeter 1978). This is a common, if unwanted, side effect of thinning.

The rate of height growth may have an opposite effect, giving vigorous trees an advantage over the mistletoe. Infection of only the lower crown usually has little effect on tree growth or survival (unless a large broom develops). Severe damage is usually associated with infections in the middle and upper crown. In the absence of seed sources from above, a tree infected in the lower crown is in a race with the dwarf mistletoe. If the tree can grow in height faster than the mistletoe can climb, the tree will be in little danger from that infection and may even outgrow it as lower branches die (Parmeter 1978, Scharpf 1978, Scharpf & Parmeter 1976). However, if the mistletoe climbs the crown faster than the crown grows, infection becomes severe.

Vigorous trees, with faster height growth, may thus prevent the infection from becoming severe by staying ahead of it. The denser crown of a vigorous tree provides an added advantage because it slows the vertical spread of the mistletoe. Whether these advantages of vigor outweigh the disadvantages discussed above probably depends on other factors, such as stand structure, location of infected trees, etc. Rates of vertical spread have been estimated or measured for various mistletoe-host combinations, and range from 3 inches to several feet per year (Parmeter 1978). Estimates for our area have apparently not been made.

Perhaps because of slow height growth, southwestern dwarf mistletoe in Colorado was most severe on the driest ponderosa pine sites, typically the *Pinus ponderosa*/ *Muhlenbergia montana* habitat type (Merrill *et al.* 1987). The wetter *P. ponderosa*/*Quercus gambelii* habitat type had the lowest severity.

Dwarf mistletoes are often more abundant on ridgetops than on slopes and least common on bottom sites. This pattern is often observed with southwestern and lodgepole pine dwarf mistletoes, but Douglas-fir dwarf mistletoe had only a weak relationship to topographic position (Hawksworth & Wiens 1996, Merrill *et al.* 1987). Steep slopes often have lower incidence of dwarf mistletoe than gentle slopes. These relationships may be due to differences in fuel accumulation and fire behavior, but they may also be due to differences in host vigor in different topographic positions.

6.5 Diseases and herbivores of dwarf mistletoes

A number of fungi parasitize and kill dwarf mistletoe shoots, or kill host tissues colonized by the endophytic system, indirectly killing the mistletoe. It is not known how much these diseases impact dwarf mistletoe populations, nor do we have systems for effectively encouraging the activity of these organisms as biological control agents. Tests of inundative biological control of lodgepole pine dwarf mistletoe using *Colletotrichum gloeosporioides* were unsuccessful (Ramsfield *et al.* 2005). Similar tests of *Neonectria neomacrospora* (anamorph *Cylindrocarpon cylindroides*) against hemlock dwarf mistletoe on Vancouver Island had partial success, particularly when swellings were wounded prior to inoculation (Rietman *et al.* 2005). Two diseases are described here.

One of the most specialized diseases of dwarf mistletoes is caused by *Caliciopsis arceuthobii* synonym *Wallrothiella arceuthobii*). The spores of this fungus germinate on and grow into the stigma of the female flowers in the spring, like a pollen grain. However, the fungus takes control of fruit development, replacing most of the fruit with its own black reproductive structure and preventing viable seed from being produced. The following spring, spores are released to initiate a new cycle of infection. This pathogen infects *A. americanum* and *A. douglasii* in our area (Hawksworth & Wiens 1996). Cases have been observed where the fungus killed up to 90% of the fruits of *A. douglasii*. In a four-year study, fruit production in *A. americanum* was reduced an average of 58% by natural infection (Ramsfield *et al.* 2009).

A rust fungus, *Peridermium bethelii*, infects lodgepole pine branches where they are already infected by *A. americanum* (Hawksworth & Wiens 1996). It occurs in Colorado and Wyoming in forests where *A. americanum* occurs, especially in forests where comandra blister rust also occurs (B. Geils, personal communication). The rust fungus apparently infects both the tree bark and the mistletoe's cortical strands. Infected branches die, killing the mistletoe as well. Generally the rust is not abundant enough to have a substantial impact on mistletoe populations.

Herbivory may also potentially reduce populations of dwarf mistletoes, but no impact by herbivory has been demonstrated or suggested. Herbivory of dwarf mistletoes by by vertebrates is discussed in section 5.1.1, Dwarf mistletoes as a food source for vertebrates, and that by insects is discussed in section 5.3, Effects of dwarf mistletoes on insects.

7. DETECTION AND EVALUATION

7.1 Symptoms and signs

Although dwarf mistletoes are easier to detect and diagnose than many other types of tree diseases, there are substantial limitations to detection. Latent infections (too young to have shoots or to cause witches' brooms are a major factor, but older infections in a large tree can also be difficult to detect.

Swellings. Swelling, the first symptom of infection, is due to an increase in the size and number of cells (hypertrophy and hyperplasia). It is more common and persistent with local infections than with systemic infections (see section 2, Life cycle). Swelling at the site of infection usually precedes shoot production and is fusiform (tapered gradually at the ends). On pines, swellings may also be caused by rusts. However, rust swellings are either distinctly spherical (western gall rust) or the rust causes cankers soon after swelling.

Witches' brooms. Infection by dwarf mistletoes typically leads to profuse, dense branching, forming a mass called a witches' broom. Branches are often distorted. Witches' brooms may be a side effect of the elevated cytokinin levels in the mistletoe plant, which serve to direct allocation of nutrients to infected branches.

It is important to distinguish witches' brooms caused by dwarf mistletoe from other abnormal branching. Old ponderosa pine in the Southwest may develop a broom-like branching habit that is not due to dwarf mistletoe (B. Geils, pers. comm.). Elytroderma needlecast, caused by *Elytroderma deformans*, also causes witches' brooms in ponderosa pine, but it is generally restricted to wet sites; one-year-old needles turn red in spring; black, elongate fungal fruiting bodies occur on diseased needles; and brooms are generally small. Lodgepole pine may develop "stimulation brooms" as a physiological response to canopy opening or age (Hawksworth 1961a). Several features can help in distinguishing them from mistletoe brooms (Table 7).

Table 7. Features distinguishing dwarf mistletoe brooms from stimulation brooms in lodgepole pine (Hawksworth 1961a).

	Dwarf mistletoe brooms	Stimulation brooms
Dwarf mistletoe shoots and basal cups	Yes	No
Location	Any height or distance from bole	Usually < 30 ft high, at or near bole
Crown class of tree	Any	Suppressed or intermediate trees, or whose tops are dead or broken
Branches	Many branches, tips usually point upward	Fewer branches, tips may point upward or sidways
Dead brooms	Can usually be found on other trees in vicinity, sometimes on trees with living brooms	None

Other crown effects. The upper crown eventually begins to thin in trees with many infections or with one or more large brooms in the lower crown. This symptom may progress to branch die-back and then death of the top of the tree. Because resources are preferentially allocated to infected branches, they are often the last part of the crown to die.

Cankers. Cankers (death of cambium and bark due to disease) are usually seen on main stems, but may also be common on branches in limber pine. Although infection of young shoots often causes swelling, older tissues often die when infected for a long period.

Mistletoe shoots. Shoots were described in section 2, Life cycle, and in the description of each species. In systemic infections (Douglas-fir and lodgepole pine dwarf mistletoes) shoots may be aggregated at the points where the annual bud scars occur. Although shoots are often useful for detecting infection, several factors must be considered:

a) There is a latent period, typically 2–5 years, between infection and shoot production.

b) Shoots of some species (e.g., Douglas-fir dwarf mistletoe) are very small and difficult to see in a mature tree, even with binoculars.

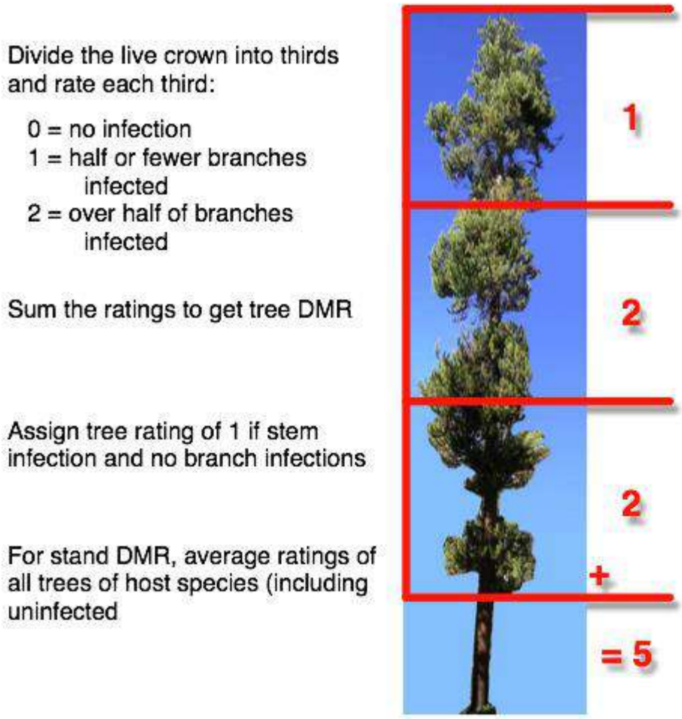
c) Shoots are relatively short-lived, 5–7 years. Although new shoots are typically produced, it is not unusual for established infections to have no shoots because of drought or other factors. Although this hinders detection, the mistletoe plant survives well without shoots.

It has been estimated that we may detect only 2/3 of infections in a stand visually (Hawksworth *et al.* 1977, Knutson & Tinnin 1980, Merrill *et al.* 1988). Put another way, there may be 50% more infections than we can see in a stand. A major reason for this is latent infections. The "half-again" rule, developed from studies in lodgepole pine, states that the proportion of trees infected about 5 years after sanitation will be about half the amount removed in the first operation (Hawksworth 1978, probably does not apply at very high infection levels).

Basal cups. When a shoot dies and falls off, it leaves behind on the bark surface a small basal cup. Suspected infections without shoots can often be confirmed by seeing these cups.

7.2 Dwarf Mistletoe Rating (DMR)

Although many systems have been used to rate levels of infection of dwarf mistletoe, one system is now used almost universally: Hawksworth's 6-class system (Hawksworth 1977). Since this system has been used for many years, many disease parameters and management recommendations are provided in terms of DMR. Actually a 7-class system since it ranges from 0 (uninfected) to 6, it is based on rating each third of the crown on a scale from 0–2, then summing for the tree rating (Figure 14). Binoculars should be used to enhance detection. A common mistake is to stand too close to the tree, which can obscure symptoms and signs as well as cause perspective errors in dividing the crown into thirds.



Divide the live crown into thirds and rate each third:

0 = no infection
1 = half or fewer branches infected
2 = over half of branches infected

Sum the ratings to get tree DMR

Assign tree rating of 1 if stem infection and no branch infections

For stand DMR, average ratings of all trees of host species (including uninfected

Figure 14. The system for rating dwarf mistletoe infection. For this purpose, a branch is considered a primary branch with all subsidiary branches.

In a comparison of ratings of standing Douglas-fir trees with those after felling, ratings were accurate about 75% of the time (Geils & Mathiasen 1990). Rating was very reliable for trees up to 6 m tall but less so for taller trees. Heavily infected trees tended to be underrated because of failure to detect infected branches in the upper crown. Lightly infected trees tended to be overrated because of a tendency to lower the boundary between the lower and middle third. These rating errors tended to cancel each other out, although overall there was a slight underestimate.

Although initially a "1" was assigned to any third that has no branch infections but does have stem infection (Hawksworth 1977), in more recent applications stem infections are only considered if there are no branch infections at all, in which case the tree is scored "1" (Hawksworth & Wiens 1996).

Several stand parameters can be estimated from rating a sample of trees (Hawksworth *et al.* 2002). (When variable-radius plots are used for sampling, they must be expanded to an area basis

(Arvanitis 2002) before calculating stand parameters.) The basic data are incidence (percentage of host trees infected) and severity or DMI (average DMR among infected trees only). The overall stand DMR integrates incidence and severity. Stand DMR is the average rating of all trees in the population (usually of the principal host species), including the uninfected trees. These parameters are related as follows:

$$\text{DMR} = \text{DMI} \times (\text{incidence expressed as a proportion})$$

7.3 Surveys

Surveys for dwarf mistletoe vary in their intent and extent. Here we will focus on surveys designed to provide information for planning specific projects. The objective is primarily to get information on the severity and distribution of the disease, but also to relate it to stand attributes including density, basal area, size structure, etc. A suitable extent for surveys of this kind ranges from a single stand up to perhaps several thousand acres.

Survey design. The considerations in designing a sampling scheme are the same as those in cruise design. Numerous sampling procedures have been recommended and used successfully (Brown 1975, Hawksworth & Johnson 1989, Johnson & Hawksworth 1978, Muir & Moody 2002, Walters 1978, Walters & Brown 1973), and it is not essential that a particular one be used. The following considerations are important in designing a survey:

a) Sampling must be either random or systematic, i.e., no bias may influence the selection of sample points.

b) The sample must be large enough to reasonably represent the total project area under consideration, given the variability within the area.

c) Sample intensity should be consistent. If certain stands or groups of stands are sampled more heavily than others, the data must be summarized only by stand or group, as overall summaries will be invalid.

A sampling scheme modeled after the common stand examinations (Anonymous 2005c) is an efficient one and uses standard mensuration techniques. In it, a variable-radius (prism) plot is used to sample large trees (e.g., ≥5″ DBH) and a fixed-radius plot centered at the same point is used for smaller trees. A prism with an appropriate basal area factor (BAF) should be chosen that gives about 4–8 sample trees at each point. The fixed plot size can be adjusted similarly to give a suitable sample. In the fixed plots, trees can be recorded by DBH class, as is done in stand exams, or by height class.

Sampling intensity should be at least one point per 10 acres. With a systematic sample (the easiest and probably the most useful), this equates to a sample grid of 660 x 660 ft, or 10 x 10 chains. In small, variable, or high-value areas, such as developed recreation sites, a smaller sample grid should be considered (Table 8), although of course the decision is subject to time and funds available. It is not important that the points be located precisely, only that they be located without bias (this may not be true if the same survey is to be used for cruising). To make navigation easy, we typically preload the sample points in a pocket GPS unit. When we get close enough that the point starts to wander, we stop and put the plot there. A proximity alarm setting in the GPS could also be used to place the points without bias.

Table 8. Minimum sampling intensity suggested for various survey sizes by Walters (1978).

Area to survey	Grid of sample points	Pts. per 10 acres
< 200 acres	4 x 4 chains (264 ft)	6.25
200-800 acres	8 x 8 chains (528 ft)	1.56
> 800 acres	10 x 10 chains (660 ft)	1.00

In traveling between sample points, it is important that the crew look for and sketch-map the location and approximate intensity of dwarf mistletoe. This information, together with the sample data, allows preparation of an accurate map of mistletoe location and severity that can be useful in planning treatments, tailoring them to specific locations, and conducting environmental analysis.

A mistletoe survey can be integrated with surveys for other purposes, and modified accordingly. Types of surveys that a mistletoe survey can be combined with include:

a) Stand examination

b) Timber sale reconnaissance

c) K-V planning survey

d) Cruise (timber sale volume estimation)

Data analysis. If using mistletoe data from a stand exam, or putting special survey data through the computer program for analyzing stand exams, the data should be interpreted with caution. We have found that some mistletoe data are calculated incorrectly in the printouts, and the user's guide does not make clear how the calculations are done. We suggest calculating the mistletoe data manually in Excel to be sure of the results.

Calculations based on fixed-size plots are straightforward. For variable-radius plots, DMR cannot be calculated by simply averaging the sample trees. Each sample tree must be expanded to trees per acre (TPA) that it represents ($TPA = BAF/(0.005454*DBH^2)/\text{number of plots}$), and the DMR multiplied by that number before averaging (Arvanitis 2002).

8. MANAGEMENT

The information on the effects of dwarf mistletoes in the preceding sections can be used to determine what levels of dwarf mistletoe are compatible with the multiple objectives that drive decisions in managing a stand. This section assumes that such a determination has been made, and that one of the objectives is reducing the impact of dwarf mistletoe by reducing its distribution and/or severity. This could be the case under a variety of management emphases, including timber production, range, wildlife, recreation, etc.

Several features of dwarf mistletoes should make them particularly amenable to management:

1. **Dwarf mistletoes are obligate parasites**. They cannot survive without a living host. Once the branch or tree dies or is cut, the parasite dies.
2. **Dispersal distance is limited and spread is slow**. Explosive seed dispersal is only up to about 60 ft from a tall, isolated tree. In single-storied stands, spread is usually about 2 ft per year. This creates possibilities for protecting trees by distance from infected trees.
3. **The life cycle is long**. From dispersal to production of a new generation of mature fruit typically takes 6–8 years. Disease intensification (multiplication of infections and increase in severity within trees) and spread (horizontal movement of infection front) are therefore fairly slow.
4. **Dwarf mistletoes tend to be host specific**. Mixed stands and changes in composition therefore can create a disadvantage for the mistletoes.
5. **They are relatively easy to detect**. Unlike most pathogens, dwarf mistletoes are entirely above ground, partly exposed on the surface of the host, visible without a microscope, and usually cause distinctive symptoms.
6. **Impact low until infection severe**. Hosts are minimally affected by dwarf mistletoe during the first 30-40 years of infection.

If control of dwarf mistletoe were the only, or even the primary, consideration in forest management, it would be a relatively simple matter. The biology of this group of diseases is understood better than any other. In fact, development of effective management approaches was one of the first success stories of forest pathology in North America (Meinecke 1914, Weir 1916b). Today, however, despite the huge increase of knowledge in the interim (Hawksworth & Wiens 1996), management of dwarf mistletoes is more complex and challenging than it seemed back then. The challenges making mistletoe management more difficult include:

1. **Historical practices**. Fire suppression and other past practices have tended to increase the abundance and distribution of dwarf mistletoes (see sections 4.2, Forest dynamics and 6.3, Historic practices).
2. **Integrating disease management with modern silviculture**. Because of advances in silvicultural understanding, tailored to management of particular forest types and conditions, approaches that might be ideal for disease control are sometimes unacceptable silviculturally. Management approaches must also be consistent with management of other potential diseases and insect pests.
3. **Social issues**. Opposition to approaches that may be silviculturally and ecologically appropriate in some cases, such as even-aged management systems, have made disease management more difficult. In addition, the value of dwarf mistletoes to wildlife is often cited in opposition to disease management projects.
4. **Severity over time**. Because dwarf mistletoe spreads and intensifies slowly by human standards, it can be difficult to appreciate its effects on stand growth and development within the time scale of a forest. Attention is often given to issues that cause more abrubt change, even though they may involve less damage over the long term.
5. **Management over time**. It may not be feasible to accomplish dwarf mistletoe management goals in one project. In some cases, multiple entries may be required to achieve success consistent with other goals.

8.1 Management options

Management decisions can be complex, and this guide cannot anticipate all circumstances. Managers are strongly encouraged to consult with forest health specialists while assessing stands to be managed, well before prescriptions are developed. The information here should be regarded as guidelines only, and should not be translated into management plans without thorough evaluation.

8.1.1 Models

In cases where management decisions are unclear, stand growth models that incorporate dwarf mistletoe may be of use. Although they may not predict outcomes with perfect accuracy, they incorporate more considerations into their predictions, and with more quantification, than can be accomplished with the usual process of assessment and expert judgment.

The Forest Vegetation Simulator (FVS, Anonymous 2005b), which incorporates the Dwarf Mistletoe Impact Model (DMIM, Anonymous 2005a) is the system generally used and supported in USDA Forest Service. The bases of DMIM and its use are well documented (Hawksworth *et al.* 1995). An example of its use with animated stand imagery is available online (Worrall & Geils 2006).

8.1.2 Widely applicable management strategies

Management approaches that have broad applicability for many species and at various stages of development:

1. **Find borders without inoculum**. Regardless of stage of stand development or the management approach, treated areas should be bordered as much as possible by areas that will not be sources of inoculum. This includes nonsusceptible or uninfested stands, roads, forest openings, etc.
2. **Size matters**. To avoid reinfestation of treated areas that have infested stands on the border, treated areas must be large enough that spread into them from the borders is insignificant, or at least acceptable, during the life of the stand. The proportion of a treated area exposed to inoculum from an infested border or infested after 50 years decreases as the treated area becomes larger (Figure 15). In this situation, 20 acres is considered a minimum and 40 acres is recommended. At 40 acres (assuming a circular area with infested border), 13% of the area is exposed to direct inoculum at the maximum distance, and roughly 31% is infected after 50 years. As patches increase in size beyond this point, the advantage of increasing size becomes less. Irregularly shaped or long, narrow patches must be larger to have a similar area protected.

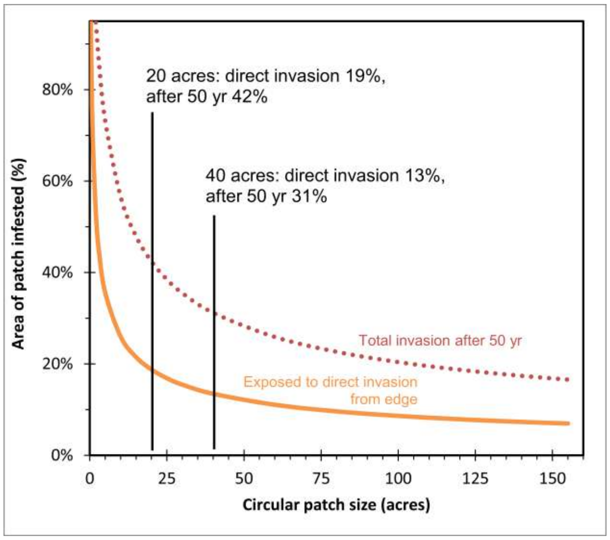


Figure 15. Proportion of a circular, treated area exposed to direct inoculum of dwarf mistletoe from the edge at the at the maximum dispersal distance (16 m or 52 ft), used because plants in tall trees are showering seed on regeneration. Also shown is the additional effect of lateral spread for 50 years, assuming lateral spread rate for a single-storied stand of 0.5 m (1.5 ft) per year. This spread rate is the average estimated for lodgepole pine dwarf mistletoe (Hawksworth & Dooling 1984) and is a conservative estimate for our other species (Beatty & Mathiasen 2003, Hadfield *et al.* 2000, Mathiasen *et al.* 2002, Taylor & Mathiasen 1999). Note that any shape other than a circle would lead to more rapid invasion.

3. **Favor nonhosts**. Whether planting, spacing, thinning, selecting seed trees, etc., encourage and favor tree species that are not hosts of the mistletoe in the stand.
4. **A grace period for seedlings**. Because of their small size as targets and their short exposure to inoculum, seedlings generally can be considered safe from infection until they are 10 years old or 3 feet tall, whichever comes first (Wicker 1967, Wicker & Shaw 1967). This gives some time before infected overstories must be treated. Infection of smaller or younger trees does occur, but it is generally rare.
5. **Sanitation**. Sanitation, removal or killing of infected trees to protect other trees, is important in many kinds of stands at various developmental stages. "Sanitation cutting" (or simply sanitation) has been distinguished from "sanitation thinning" (Hawksworth 1978). Sanitation cutting is the attempted removal of all visibly infected trees, though it usually is combined with thinning goals also. In sanitation thinning, the emphasis is on spacing, and only the most severely diseased trees may be removed, which may have little impact on reducing dwarf mistletoe.
6. **Prescribed stand-replacing fire**. As discussed earlier (section 4.2, Forest dynamics), wildfire has been a major determinant of dwarf mistletoe distribution and severity. Both even-aged and uneven-aged, infested stands can be treated with prescribed, stand-replacing fire to establish a

new stand in the absence of inoculum. Because lodgepole pine generally regenerates well after fire, consistent with its natural disturbance regime, this can be an effective, economical and ecologically beneficial means of stand replacement (Zimmerman *et al.* 1990). Fire can be used in heavily infested stands that have little economic value, or after merchantable trees are harvested. Muraro (1978) provides operational details for its use in interior British Columbia. In merchantable, infested stands, limbing is done prior to forwarding to ensure a fuel bed for the sanitizing fire. After about four weeks, the slash provides good fire coverage with a minimum of ignition effort. In any case, stands must be inspected following the fire and any infected residuals felled.

7. **Prescribed fire – low or mixed severity**. Prescribed fire may decrease severity and distribution of dwarf mistletoe without replacing the stand. Infected trees may be selectively killed because of brooms and fuel accumulation around infected trees. Also, fire may be directed at them by manipulating the location of ground fuels or selecting ignition points (Muir & Geils 2002). Lower branches of surviving trees are often killed by scorching, reducing mistletoe severity (Conklin & Armstrong 2001). In some stands of lodgepole pine, where ponderosa or Douglas-fir seed sources exist, a series of low-severity fires may encourage replacement of infested lodgepole pine by the more fire-resistant species (Muir & Geils 2002).
8. **Pruning**. Pruning may have two objectives. Pruning of large brooms, which are generally in the lower crown, can allow trees to recover vigor and substantially prolong their life. It is not likely to affect spread and intensification of the disease in the stand. Broom pruning can be used when it is important to maintain large tree cover, more aggressive silvicultural techniques are less acceptable, and the tree value justifies the cost. It is most often used in developed recreation sites, which often meet these criteria. Another objective of pruning is sanitation (i.e., sanitation pruning). Again, this is only feasible in high-value sites, but male infections can be ignored for this purpose if they can be identified as such. In lodgepole pine, candidate trees should have the following features (Hawksworth & Johnson 1989):
    a) Infected only in the lower half of the crown
    b) DMR ≤ 3
    c) No infections on parts of the bole < 5″ diameter.
    d) Infections on branches from bole < 5″ diameter are > 4″ from the bole.

    Pruning branches with infections near the main stem may not be successful because the endophytic system may already have entered the stem. The following rules of thumb can be used. For lodgepole pine dwarf mistletoe, stem infection is likely if shoots are < 4″ from the main stem. For southwestern dwarf mistletoe on ponderosa pine, stem infection is likely if shoots are < 6″ from the main stem on branches up to 1″, and the distance should be increased 2″ for every additional 1″ in diameter. Pruned stands should be retreated in 3-5 years to remove latent infections and those that were missed.

8.1.3 Recently regenerated stands (≤ 15 yrs old)

Stands that have been recently regenerated, whether by wildfire, prescribed fire, harvest, or other disturbance, provide the best opportunities to reduce dwarf mistletoe impacts through the life of the new stand. It is the only situation in which a mistletoe-free result (only over the area treated, and until it can spread in again from the edges) is highly likely. Options to consider at this point include:

1. **Kill infected residuals**. If regeneration will include susceptible species, remove or kill any residual overstory trees (at *least* those with any evidence of infection) within 10 yr after establishment of regeneration or before regeneration is 3 ft tall, whichever comes first. *This is*

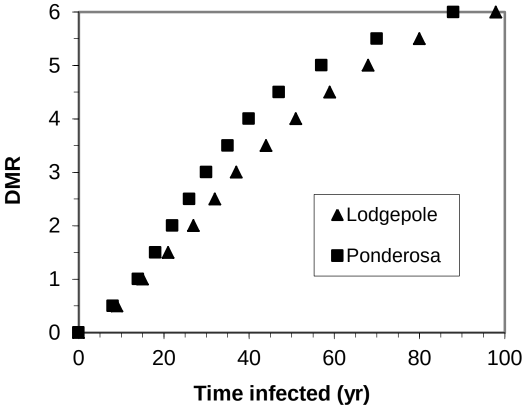


Figure 16. Approximate relationship between time since initial infection by dwarf mistletoe and stand DMR for some even-aged stands of lodgepole pine and ponderosa pine in the southern Rocky Mountains. Data from Hawksworth & Myers (1973).

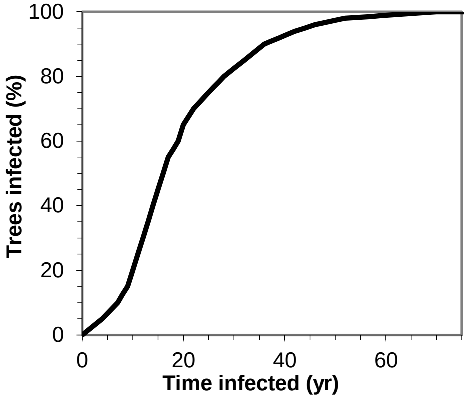


Figure 17. Approximate relationship between time since initial infection by dwarf mistletoe and incidence of infection for some even-aged stands of lodgepole pine and ponderosa pine in the southern Rocky Mountains. Data from Hawksworth & Myers (1973).

extremely important, as failure to do so can make the difference between the ideal mistletoe treatment and a worst-case scenario. It is better to do nothing than to start a shelterwood or seed-tree system and then fail to remove infected residuals on time. Because infections can be difficult to detect, and may be stimulated by the recent opening, it is best to fell or otherwise kill all trees from the previous stand, whether they appear infected or not, if consistent with other management goals. If not, the stand should be revisited within 5–10 years to remove infected residuals and sanitize the regeneration as needed. Snags can be created and/or left if desired, and of course any nonsusceptible tree species can be left. If a decision is made to retain infected trees over a developing understory, consideration should be given to pruning, occasional understory sanitation, and removing the overstory trees at a later time.

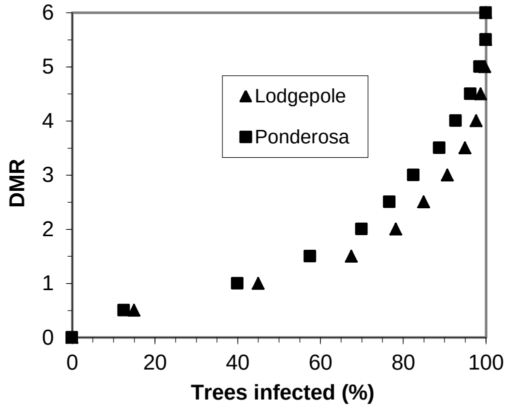


Figure 18. Approximate relationship between incidence of dwarf mistletoe and stand DMR for some even-aged stands of lodgepole pine and ponderosa pine in the southern Rocky Mountains. Data from Hawksworth & Myers (1973).

2. **Sanitize regeneration**. If there has been any opportunity for spread from residuals or from the edge, regeneration must be carefully inspected and infected trees killed. Again, because of latent infections, this should be repeated in 5–10 years.
3. **Make a “donut”**. The “donut” is created by felling all infected trees in the bordering stands 20 m (1 chain) back from the edge of the regenerated patch. With lodgepole pine, it is best to fell all trees in the 20-m zone because it regenerates well and may have infections that are difficult to detect. This prevents direct infection of the original regenerated patch from the edge. Even after dwarf mistletoe spreads through the border zone, it is less likely to spread into the original patch because the trees in the donut hole will be taller. This approach is essential if the regenerated patch is both: a) less than 20 acres or larger but irregularly shaped, and b) bordered by residual infested stands. It is optional with larger patches and completely unnecessary if there are no infected trees near the border.

8.1.4 Sapling stands

The relationships between time since infection, percent of trees infected, and stand DMR have been quantified for even-aged stands (Figure 16, Figure 17 and Figure 18). These relationships are useful in assessing stand condition and estimating parameters when one of them is known. They may have some general predictive value also. However, the basis of these data is not precisely documented, and some stands may not follow the pattern portrayed in the data.

Many stands of saplings can be sanitized like recently regenerated stands. However, because the incidence of infection can be higher and density lower, occasionally the ratio between the two will be so high that insufficient trees would be left after all infected trees are removed. This can be represented as curves for each target density, showing increasing permissible incidence of infection as initial density increases (Figure 19). Stands to the right of the curve may be successfully sanitized without falling below the minimum density.

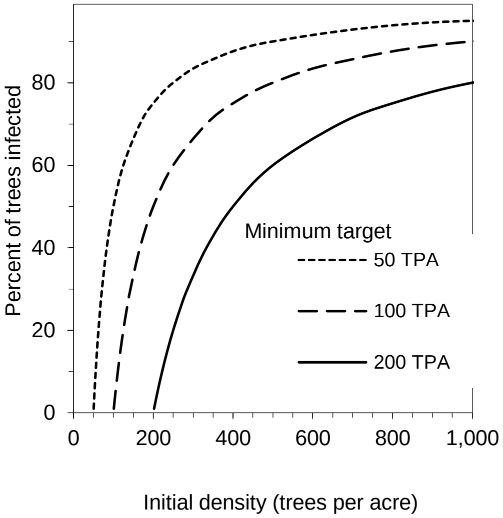


Figure 19. Guide for sanitation of young stands based on initial density, minimum target density, and percent infection. If initial density and percent infection coincide to the right of the curve representing minimum target density, strict sanitation should be feasible while leaving adequate stocking. Patchiness may alter this relationship.

Highest priority for sanitation should be given to younger stands with relatively low infection levels. Also, the better the site, the more worthwhile and effective thinning is likely to be. Action in these situations will have the greatest impact with the least cost. In general, guidelines for sapling stands can be characterized as follows:

1. **Sanitation**. Remove all trees with symptoms or signs of dwarf mistletoe if feasible, and schedule a followup treatment in about 5–7 years (some suggest 3-5 years). Strict sanitation cutting in lodgepole pine and ponderosa pine is traditionally attempted only in stands younger than 30 or 40 years (Hawksworth 1978). This is because incidence of infection in older stands is often so high that removal of all infected trees would create unacceptably large openings or low density and depress yields (Hawksworth 1978). Stands infested for 30 years can have 80% infection (Figure 17). However, the incidence of infection and minimum acceptable density is a better guide for decision-making than stand age. In lodgepole pine, strict sanitation may not be feasible with infection greater than about 40%, approximately equivalent to DMR about 0.5 (Hawksworth & Johnson 1989) or 1.0 (Figure 18). Heavily infected trees that must be left may not respond to release, and residual dwarf mistletoe will produce more seed and spread faster through the more open stand. The acceptability of such openings and possible benefits of heterogeneous stand structure to wildlife must be considered. Growth models with mistletoe modules, such as FVS, may be helpful in making such a decision. If further management is warranted, incorporate sanitation into regular thinnings. Recommendations in the literature vary slightly (Hawksworth & Johnson 1989, Muir & Geils 2002), but a good general guide for prioritizing leave trees in stands greater than 2″ (5 cm) DBH is (see also Table 9):
    a) Dominants and codominants uninfected.
    b) Dominants and codominants with infections confined to lower third of the crown (DMR ≤2)
    c) Intermediates apparently uninfected.

   d) Dominants and codominants with infection in less than half the branches in the lower two-thirds of the crown (DMR ≤3)

2. **Regeneration**. In heavily infested sapling stands on good sites in timber emphasis areas, consideration should be given to regeneration of the stand.
3. **No action**. When sapling stands are heavily infested and regeneration is not feasible, it may be best to devote the stand to wildlife and invest management efforts elsewhere, where they will provide more benefit in reducing mistletoe severity.

Table 9. Guidelines for leave trees in sanitation thinning of ponderosa pine in the Southwest (Conklin 2000). These guidelines are recommended here for single-story stands only. DMR in this table refers to that of individual trees, not stands.

DBH class	Maximum allowable DMR
0-4″	0
4-6″	1
6-9″	1 or 2
> 9″	2 or 3

8.1.5 Mature stands (even-aged)

In stands of larger trees (more than about 7 or 8″ DBH), average stand DMR may be a more important measure than percent of trees infected. There is less opportunity to select trees for future development of the stand, less concern for protecting uninfected trees, little chance of strict sanitation, and more concern for overall condition. On the other hand, there may be timber sale opportunities that can make management and stand improvement more feasible.

One consideration that becomes more important in mature stands is mortality and growth loss of moderately to heavily infected trees. Because of their shortened expected lifespan (Table 3, Table 5), as well as their limited growth, trees with DMR of 3 or more should be considered for harvest if intermediate cuts are feasible.

1. **Sanitation thinning**. Where regeneration is not anticipated in the near future, and stand DMR is less than 3, sanitation thinning may improve the condition, growth and longevity of the stand (Hawksworth & Johnson 1989). In more heavily infested stands, if a regeneration cut is not an option, selective harvesting of the most heavily infected trees can salvage them before they die. However, if this is likely to stimulate abundant regeneration, doing nothing may be the best option in that situation. Little growth response can be anticipated in heavily infected trees, and stimulating regeneration under those circumstances may lead to a worse infestation in the future. In ponderosa pine in the southwest, guidelines have been suggested for maximum allowable DMR in leave trees (Table 9).
2. **Regeneration by even-aged reproduction method or fire**. Where silviculturally appropriate, even-aged management, especially at the stage of regeneration, offers the best opportunity to establish a mistletoe-free stand. This can be accomplished by clearcut, seed-tree, or shelterwood methods. If using shelterwood or seed-tree reproduction methods, select residual trees that are mistletoe free or only lightly infected (tree DMR ≤ 2). This will contribute to higher seed production, better survival, and reduced infection of any pre-existing regeneration. For ponderosa pine in the Southwest, 20–40 ft^2/acre (5–9 m^2/ha) of uninfected seed trees are recommended; this should be doubled for infected seed trees (Heidmann 1983). See other important considerations (patch size, border guidelines, favoring nonhosts, removing residuals, etc.) in sections 8.1.2, Widely applicable management strategies and 8.1.3, Recently regenerated stands. Most important is that, *if infected residuals are used as seed/shelter trees, they* must *be removed before regeneration is 10 yr old or 3 ft tall, whichever comes first.*

8.1.6 Uneven-aged stands

As noted previously, uneven-aged stands with infected overstory trees are ideal for maximizing spread and intensification of dwarf mistletoes. Management of such stands in an uneven-aged system is problematic. Infected understory trees have the problem of the mistletoe, but its effects are compounded by their slower growth from being in the understory. Worse, inoculum continues to rain down on them from above during their most vulnerable years. Such trees have little chance of outgrowing the mistletoe and within-tree intensification is virtually assured. Because they are infected when young, the impacts are great.

The possibility of uneven-aged management has been considered primarily for ponderosa pine, and that is the focus of this section. If severity is low to moderate (stand DMR ≤ 2) there may be a chance of maintaining some uneven-aged conditions while reducing severity and, most importantly, preventing severe infection of the understory. However, it would most likely require aggressive treatment, frequent entries and, in some patches, more or less complete removal of the overstory. When overstory trees are infected, strict adherence to uneven-aged systems is probably not compatible with reducing impact from dwarf mistletoe. Options include:

1. **Convert to single-story stand**. Overall conversion to even-aged management is the surest way to reduce severity and improve long-term productivity.
2. **Adapt management to mistletoe conditions**. If overall conversion to even-aged management is not desired, the next best approach is to be flexible. Where mistletoe is present, the overstory can be removed (moderate to high severity) or sanitized (low to moderate severity) and the understory sanitized. In mistletoe-free patches, uneven-aged conditions could be maintained. Marking rules must be oriented toward aggressive removal of infected trees, or the mistletoe will bounce back quickly and may even be stimulated to faster spread and intensification by the opening of the stand. Because some infected overstory trees and latent infections in the understory will be missed, monitoring and retreatment on a frequent basis may be required. Nonsusceptible tree species can be favored in any size class.

THE FORT VALLEY STUDY

A study of dwarf mistletoe management was initiated in a previously unmanaged area at Fort Valley Experimental Forest, near Flagstaff, Arizona, in 1951 and followed for 27 years (Heidmann 1968, Heidmann 1983, Herman 1961). The forest was not explicitly described as uneven-aged, but the description shows this (Heidmann 1968). DMR and incidence of infection were not reported. The primary measure used was percentage of the area stocked by infected and uninfected trees, and some data were given in terms of infected volume. The three treatments and their results were:

Light Improvement Selection (LIS): This treatment was the standard silvicultural practice in previously unmanaged stands in 1951. Generally, sanitation was limited to measures that did not reduce stocking below that recommended for uninfected areas. The first cut harvested merchantable trees that were dying or expected to die within 20 years. This removed 30-40% of the total board-foot volume. Subsequent stand improvement was limited to that possible from K-V funds, and including release and pruning of trees in lightly or uninfected groups, favoring uninfected trees. Severely infected groups were left alone.

LIS was a complete failure. The initial treatment actually increased the proportion of area stocked by infected trees. After 13 years, the infected volume was 44% of total volume, compared to 40% before treatment began.

Limited Control (LC): This treatment was intended to reduce infection to a level that did not impact timber production, to the extent it could be financed and accomplished by contemporary allotments and regulations. Unlike LIS, sustained yield was relegated to secondary importance until reasonable control of dwarf mistletoe could be obtained. See Heidmann (1968) for detailed marking guidelines.

LC was also deemed a failure. Although it reduced infected volume from 44% at the beginning to 23% after 13 years, infection was increasing rapidly and had tripled since the initial treatment.

Complete Control (CC): This treatment reduced infection as near to 0 as possible. All uninfected trees were retained and all infected trees were cut, except that nonmerchantable, infected trees were retained in most cases if needed for stocking.

A final evaluation of the experiment concluded that complete control is the only effective approach in heavily infested, mature ponderosa pine (Heidmann 1983). After 27 years, infected stocking in the CC treatment was still well below what it was at the start. The CC treatment had the lowest proportion infected of the area stocked in 1977, and it already had higher overall stocking than the LC treatment.

3. **Push it back**. Focus on edges of infection centers, cutting most heavily there to push the edges back, decreasing the area infested.
4. **Individual tree selection**. This may be appropriate in ponderosa pine when at most 15% of trees are infected (Muir & Geils 2002). It may also be appropriate in mixed stands where nonsusceptible or resistant species can be favored (Mathiasen 1989). For individual-tree selection, recommendations are:
   a) Cut severely infected trees (DMR ≥ 5) at each entry.
   b) Retain lightly infected and healthy trees (DMR ≤ 2).
   c) Retain moderately infected trees (DMR 3 and 4) only where height growth is expected to exceed 12 in (30 cm) per year or where the next entry is scheduled within 20 years.
   d) Consider pruning infected branches or large brooms.
5. **Group selection**. Opinions differ on the potential for group selection in managing dwarf mistletoe in ponderosa pine. It may allow removal of infection centers and regeneration of disease-free patches under certain circumstances (Conklin 2000), or it may be unlikely to meet management objectives in infested stands (Edminster & Olsen 1996). In the Southwest, it may be considered when 15–25% of stems are infected (roughly corresponding to maximum stand DMR ≤0.7, Figure 18) (Muir & Geils 2002). Group size is up to 1 ha (2.5 acres). It will only be effective, and should only be considered, when the infestation is strongly aggregated in discrete patches. Individual-tree selection may be applied between the groups when light infection occurs throughout (Mathiasen 1989). A major problem is the presence of infected edges, often from latent infections, at the group boundary. Ensuring that boundaries go 30–40 ft beyond visibly infected trees should reduce the likelihood of infected edges (Conklin 2000).
6. **Do nothing**. When infection levels are high (stand DMR > 2) and there is little flexibility in diverging from strict uneven-aged management, the best alternative may be no action. Interceding under such constraints is not likely to improve matters over the long term and may make things worse.

8.2 Integrating mistletoe management with other objectives

Dwarf mistletoes are native elements of many western forests and, because of their intrinsic value in biodiversity, role in ecosystem function, and the influence they may have on other species, a balance should be sought in their management. Management objectives often include reducing the distribution and/or severity of dwarf mistletoe on part of a landscape, but eradication of *Arceuthobium* species has never been a goal.

8.2.1 Dwarf mistletoe conservation

Dwarf mistletoes are in no danger of extirpation; far from it. Indeed, in many areas it is thought that dwarf mistletoes are more widely distributed and abundant than they were before European settlement (see section 6.3, Historic practices). Still, a concern is sometimes raised that dwarf mistletoes provide valuable diversity to the forest. Although this is often justified on the basis that dwarf mistletoes enhance wildlife habitat (see section 5, Impacts of dwarf mistletoes on animals), a stronger justification may be the diversity provided by and value of the dwarf mistletoe as a species in its own right.

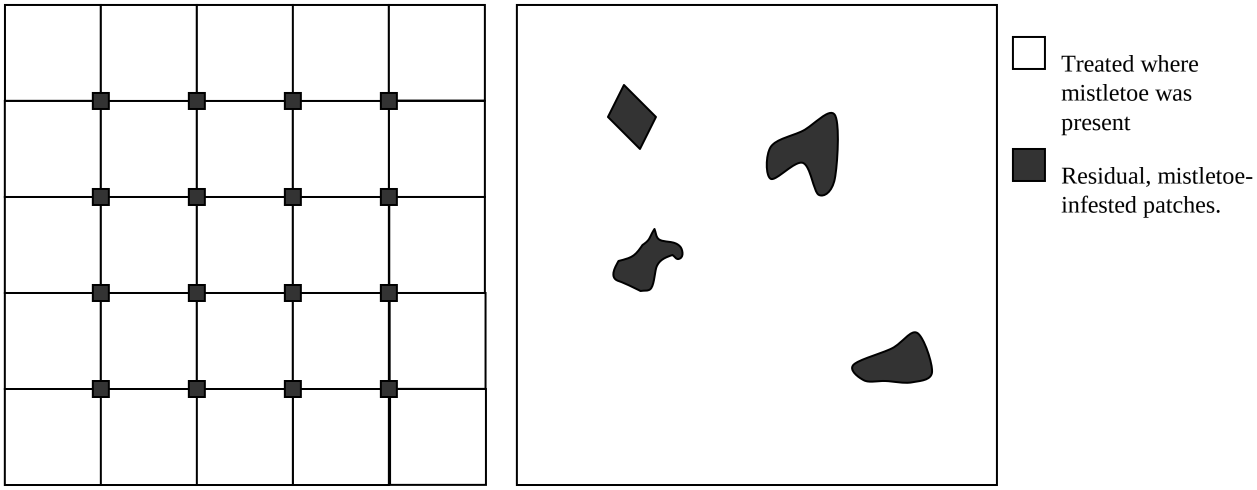
In many projects, the area proposed for treatment is surrounded by additional mistletoe-infested forest, and there is little need to be concerned about retaining dwarf mistletoe in treated units. In fact, rendering portions of the landscape more or less free of mistletoe often *increases* diversity in ways that may have important wildlife benefits.

In other projects, the area to be treated may encompass a majority of the infested forest in the immediate area. Depending on management emphases and objectives in this situation, there may be a desire to explicitly retain some mistletoe in treated units.

In this situation, what may happen is a compromise: reducing mistletoe somewhat, but leaving enough to nominally satisfy the diversity objective. However, partial treatment of mistletoe over a whole unit in this way can be a lose-lose proposition. The best-developed brooms and clusters of trees that may have the best wildlife value are removed, but enough mistletoe is left behind that the goal of improving productivity may not be met over the long term.

Rather than partially treating dwarf mistletoe uniformly over the unit, spatial segregation of dwarf mistletoe may be much more effective at achieving both objectives. Islands of heavy infestation can be left to achieve whatever diversity benefits are ascribed to them, and the remainder treated to allow trees to grow larger and live longer. An additional advantage of this approach is that it creates a patchy distribution of infection, in keeping with the natural distribution of the disease in a landscape. The only cost is the lowered productivity within the residual islands, and some expansion of the mistletoe from them over time.

Because of considerations on the size of treated areas in relation to subsequent spread from untreated areas (Figure 15), this strategy is most effective with larger treatment units. To avoid reinfestation of treated portions of the stand within a reasonable time, treated portions should be a minimum of 40 acres. Small, infested, residual patches could be left between them. In a thousand-acre treatment area, for instance, there could be a maximum of 25, 40-acre treated patches, with small (≤ 1 acre) infested patches between them (Figure 20A). However, treatment and residual patches would have to be on a perfect grid to be effective with that number. If fewer infested patches were left, they could be larger (perhaps up to 5–10 acres), and their placement and shape would be less critical and could be designed to take advantage of high mistletoe severity, patches with the biggest brooms, the most snags and other features that may be preferred by wildlife (Figure 20B).



A. 1000 acres with 25, roughly 40-acre treated areas. Small (≤ 1 ac.), mistletoe-infested patches could be left between them if desired.

B. The same area with fewer residual mistletoe-infested patches. In this approach the position, shape and size of the residual patches is more flexible. This approach would lead to less mistletoe spread, would be easier to lay out, and may be preferable for wildlife.

Figure 20. Two alternatives for leaving residual, mistletoe-infested patches in a hypothetical treated area of 1000 acres if this is desired while managing to reduce dwarf mistletoe impacts on tree growth and survival

8.2.2 Fuel reduction

In recent years, there has been an increasing need to reduce the risk of severe fire, particularly near communities and where the fire regime is substantially altered from the historic range of variability. In planning and accomplishing fuel reduction projects, it is important that dwarf mistletoe be incorporated into decision-making. Fuel reduction treatments in infested stands, if done without considering the effect on dwarf mistletoe, may increase the spread and intensification of the mistletoe. In the long run, this could lead to more heavily infested stands that actually increase the risk of severe fire.

A rapid evaluation of the mistletoe situation by a forest health specialist and a silvicultural prescription, based on forest health and fuel specialists' recommendations and information in this guide, take little additional time and are highly recommended. In addition to short-term fuel reduction, these fuel reduction projects should be an opportunity to improve forest conditions in a broader and longer sense.

8.2.3 Bark beetle prevention

Management of dwarf mistletoes and reduction of bark beetle risk are generally compatible and should be viewed as an integrated objective. Although risk factors vary slightly among the bark beetle species, stands of older, larger diameter, less vigorous trees are generally most susceptible. Dwarf mistletoe sanitation is compatible with reduction of basal area or average DBH to reduce stand susceptibility to bark beetles. Regeneration to establish new stands free of dwarf mistletoe is compatible with enhancing age diversity across the landscape to reduce landscape vulnerability to bark beetles.

In most cases, dwarf mistletoe increases susceptibility of trees to bark beetle attack (see section 4.1, Tree growth and longevity), suggesting that dwarf mistletoe management should be part of any objective to reduce stand susceptibility to bark beetles. Although lodgepole pine may be an exception to this generality, management objectives would often include low levels of both dwarf mistletoe and bark beetle mortality.

For lodgepole pine, stand susceptibility to mountain pine beetle is based on elevation, age and average stand DBH (Amman *et al.* 1977, McGregor & Cole 1985). Treatments recommended to reduce susceptibility include: a) patch cuts to regenerate stands with high susceptibility or with tree sizes conducive to beetle outbreaks, creating landscapes with low overall risk; b) partial cuts to remove individual trees in the high-risk category (>8″ DBH), and; c) favoring nonhosts. These approaches are all consistent with dwarf mistletoe management. Patch cuts would need to meet size and border guidelines for mistletoe management. Thinning may enhance resistance to bark beetle attack by increasing tree vigor (McGregor & Cole 1985), although it can also lead to thicker phloem development that can render trees more susceptible and increase brood development in attacked trees (Amman *et al.* 1977). Partial cuts, when appropriate from both mistletoe and beetle perspectives, could accomplish sanitation while reducing beetle susceptibility.

For ponderosa pine, risk of mountain pine beetle is rated based on basal area, average DBH and stand structure (Schmid & Mata 1992, Stevens *et al.* 1980). For most of Region 2, stands are rated high-risk if they are single-storied, average DBH is > 10″, and basal area is > 150 ft^2/acre, or if 2 of the 3 factors meet those criteria and the third meets the medium (2-storied, avg. DBH 6–10″, basal area 80–150). In the Black Hills, Nebraska and Samuel McKelvie National Forests, the basal area factor has a lower threshold for high risk (120 ft^2/acre). Treatments to reduce average DBH or basal area are almost always compatible with sanitation. The only potentially incompatible approach would be shifting from single-story to 2-story stands to reduce bark beetle risk; this would tend to increase the spread of dwarf mistletoe in most cases.

ACKNOWLDGEMENT

Thanks to Brian Geils, Fred Baker, Kelly Burns, Tom Nicholls and Roy Mask for review and substantial assistance in improving this document.

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Forests **2014**, *5*, 103-133; doi:10.3390/f5010103

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Review

Management for Mountain Pine Beetle Outbreak Suppression: Does Relevant Science Support Current Policy?

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Received: 4 December 2013; in revised form: 27 December 2013 / Accepted: 6 January 2014 / Published: 15 January 2014

Abstract: While the use of timber harvests is generally accepted as an effective approach to controlling bark beetles during outbreaks, in reality there has been a dearth of monitoring to assess outcomes, and failures are often not reported. Additionally, few studies have focused on how these treatments affect forest structure and function over the long term, or our forests' ability to adapt to climate change. Despite this, there is a widespread belief in the policy arena that timber harvesting is an effective and necessary tool to address beetle infestations. That belief has led to numerous proposals for, and enactment of, significant changes in federal environmental laws to encourage more timber harvests for beetle control. In this review, we use mountain pine beetle as an exemplar to critically evaluate the state of science behind the use of timber harvest treatments for bark beetle suppression during outbreaks. It is our hope that this review will stimulate research to fill important gaps and to help guide the development of policy and management firmly based in science, and thus, more likely to aid in forest conservation, reduce financial waste, and bolster public trust in public agency decision-making and practice.

Keywords: bark beetle; clearcut; climate change; climate change adaptation; daylighting; *Dendroctonus ponderosae*; forest pest management; monitoring; sanitation; thinning

1. Introduction

Insect outbreaks are increasing in size and severity on a global scale [1]. In North America alone, three massive insect outbreaks occurred within the last two decades, all involving native bark beetles in conifers [2]. Of these, the mountain pine beetle (*Dendroctonus ponderosae*) outbreak is an order of magnitude larger than any previously recorded. A variety of factors, natural and anthropogenic, converged to result in these dramatic events [2]. Each outbreak has not only had severe ecological effects, but each has also triggered human responses that, for better or for worse, have resulted in additional impacts along with massive expense [3]. Predictions are that outbreaks of bark beetles will become more frequent and severe in the future [4,5] indicating an imperative need to critically assess the efficacy and impacts of our approaches to their management.

Outbreaks of bark beetles are not new. They have been occurring for millennia and have played a major role in shaping coniferous forest ecosystems of the world. While considerable research has been conducted on controlling bark beetles, massive gaps in knowledge remain. In particular, there is a disturbing dearth of rigorous replicated empirical studies assessing the effects of various management strategies, particularly timber harvest treatments, for bark beetle outbreak suppression. Even fewer studies have focused on how such treatments meet explicit goals or affect forest structure, function and future outbreak dynamics [6]. Particularly pertinent at this time, there is a lack of information to address forest adaptation to climate change in light of increasingly “out of historic norm” behavior of bark beetles. Despite this, there is a widespread belief in the policy arena that timber harvesting is an effective and necessary tool to address beetle infestations. That belief has led to proposals for, and enactment of, significant changes in federal environmental laws to encourage more timber harvests. Our question is, does that belief have a sound grounding in current science?

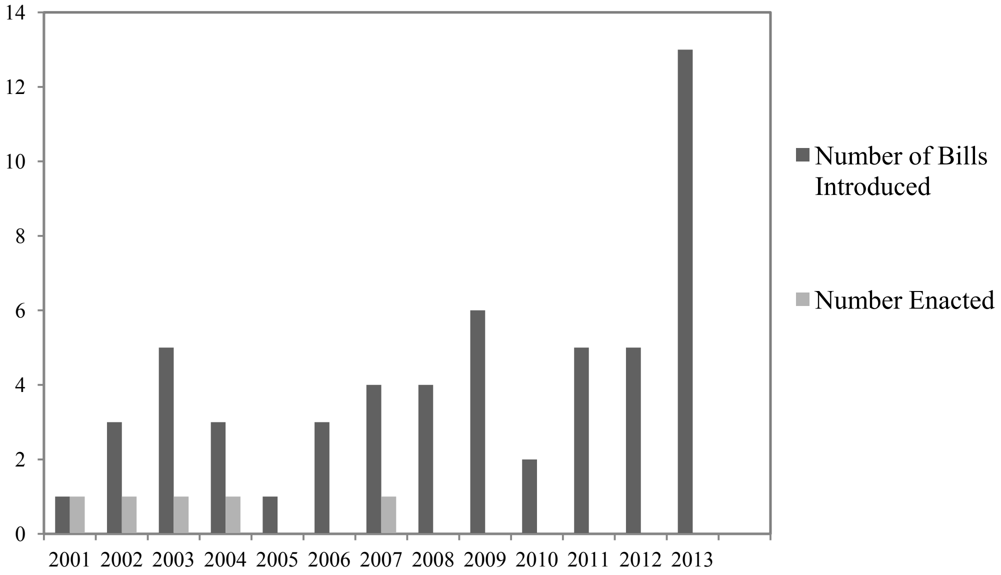
In this review, we focus on mountain pine beetle as an exemplar to critically evaluate the state of science behind the use of timber harvest treatments for bark beetle suppression during outbreaks. The mountain pine beetle was chosen because it is the most studied, most intensively managed, and most aggressive of the irruptive bark beetles. It has also responded strongly to climate change, resulting in a recent massive outbreak of unprecedented size that, in turn, has initiated numerous human responses, mostly involving implementation of timber harvests. It has also initiated many policy changes with many more currently in the pipeline.

We begin with an overview of the current policy situation. We then briefly review the biology of mountain pine beetle to form a foundation for understanding the factors that initiate and maintain outbreaks and how anthropogenic factors are contributing to current problems. We then describe the primary timber harvest treatments used to suppress bark beetle outbreaks and examine how well relevant science and ecological principles support their use. We conclude with a discussion on how well policy reflects the actual state of current science and identify where significant gaps between science and practice occur particularly in light of climate change. We also discuss the need to use advanced tools, including genetics and remote sensing, to adapt old practices to new situations-particularly in the realm of climate change adaptation. It is our hope that this review will stimulate research to fill important gaps and to help guide the development of policy and management firmly based in science, and thus, more likely to aid in forest conservation, reduce financial waste, and bolster public trust in public agency decision-making and practice.

2. The Current Policy Situation

There have been many recent proposals to streamline, reduce, or eliminate perceived legal obstacles to implementing timber harvests to address beetle epidemics on federal public lands (Figure 1). Between the 107th Congress (January 2001) and the 113th Congress (present), we found 55 bills that were introduced where at least one goal of the legislation was to increase timber harvests in order to respond to beetle infestations (Figure 1). Most of these proposals focused on the US Forest Service, which manages the majority of forests on federal public lands.

Figure 1. Number of bills involving timber sales that included bark beetle control that were introduced and/or enacted from 2001 to 10 July 2013.



Some of these proposals have been enacted. By far, the most important legal change has been the Healthy Forest Restoration Act of 2003 (HFRA). HFRA reduced the level of environmental analysis required for certain timber projects under the National Environmental Policy Act (NEPA), specifically by limiting the number of alternatives that the Forest Service was required to analyze. It also significantly restricted the ability of members of the public to challenge certain timber projects in court (by making participation in the agency's administrative process a precondition for filing suit). Further, it sought to streamline the Forest Service's internal administrative process for considering citizen challenges to certain timber projects. HFRA applies nationally to all National Forest System and Bureau of Land Management lands, and has resulted in forest treatment projects on an average of 220,000 acres of federal land per year since its enactment [7]

HFRA authorizes this streamlined process for timber projects on "Federal land on which…the existence of an epidemic of disease or insects, or the presence of such an epidemic on immediately adjacent land and the imminent risk it will spread, poses a significant threat to an ecosystem component, or forest or rangeland resource, on the Federal land or adjacent non-Federal land" [8,9].Moreover, while other types of HFRA projects in old growth forests are subject to limitations intended to protect old growth structure and large trees, timber projects to address insect epidemics can occur in old growth forests without those limitations [10,11].

HFRA also sets up a special experimental management process to develop better management methods for beetle infestations. After a long list of findings by Congress about the risks of beetle infestations in US forests, Congress authorized up to 250,000 acres of "applied silvicultural assessment and research treatments" on National Forests that would be categorically excluded from NEPA; these treatments could include timber harvesting [12,13]. HFRA section 401(b)(3) [14] requires that these applied silvicultural assessments and treatments must be peer reviewed by non-agency scientists.

HFRA is not alone. Another enacted bill created exemptions from environmental laws to allow timber harvest projects in a geographically limited area. As part of a massive supplemental appropriations act to address recovery from the September 11, 2001 terrorist attacks, Congress exempted a series of timber harvest projects in the Black Hills of South Dakota from any and all environmental laws; the law specifically stated that the projects were intended to reduce both fire risk and beetle infestations [15].

Other recent enactments create additional incentives for timber harvests intended to address beetle infestations. Congress permitted state forestry agencies to perform beetle control timber harvest projects on federal lands in Colorado and Utah under what is called "Good Neighbor Authority" [16]. These state forestry agencies must also implement "similar and complementary" services on state land adjacent to federal land in order to use the authority. Additionally, in the 2008 Farm Bill, Congress expanded subsidies for the production of "renewable biomass" energy to include timber produced from projects intended to reduce or contain disease or insect infestation [17].

There have been many more recent proposals for additional changes. Congress has considered multiple bills to expand the scope of HFRA. One proposal would require the Forest Service to implement at least one insect and disease control pilot project in at least one subwatershed in every national forest in a state that is "subject" to an insect or disease epidemic [18–24].Congress has also considered many other changes to encourage timber harvesting to control beetle infestations besides expanding HFRA. Some proposals would expand the exemptions to the Forest Service's Roadless Rule (which prohibits commercial timber projects and road construction in unroaded areas of National Forests) in order to allow more timber projects that are intended to address beetle infestations; some of these projects would be exempt from judicial review [25–27].

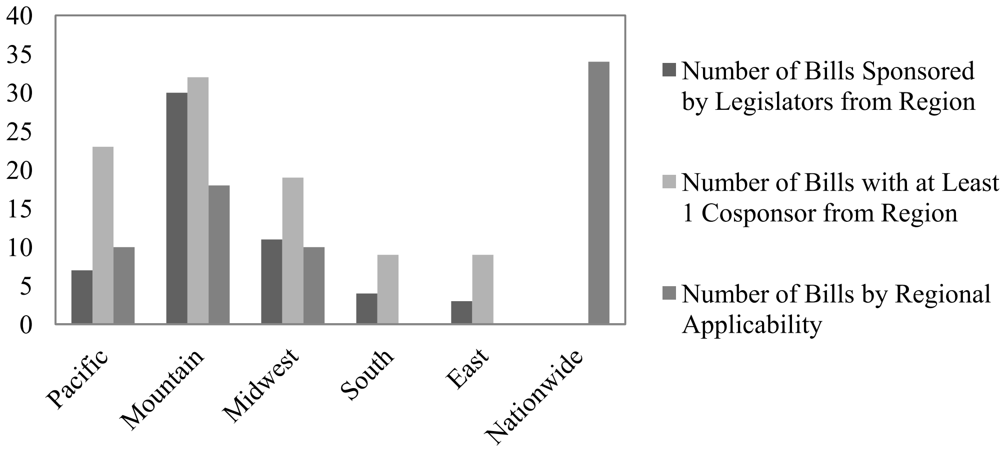
Congress has considered giving additional benefits under the Clean Air Act for "renewable biomass" produced from timber projects on federal lands, including projects intended to control beetle infestations [28,29], giving grants and other subsidies for beetle control timber projects [30], extending the Good Neighbor Authority to more states [31–33], and reducing or eliminating the fee that private timber contractors pay for timber contracts in exchange for agreements to implement restoration work, such as culvert removals, road improvements, or invasive weed removal, if the project provides insect control and other forest management benefits [26]. Finally, two bills have proposed that designation of additional federal lands as protected wilderness be paired with exemptions of beetle-related timber projects from environmental laws [34,35].

Throughout this policy debate, members of Congress and major stakeholders have regularly stated that timber harvest on federal lands is a necessary component of efforts to fight beetle infestations and control outbreaks and that additional flexibility under environmental laws is necessary for agencies to pursue these timber harvest projects [36–41].

Likewise, the U.S. Forest Service and other U.S. federal land management agencies have prescribed timber harvests as a necessary component of beetle control. For example, the Forest Service's Western Bark Beetle Strategy calls for the agency to "reduce the number of trees per acre and create more diverse stand structures to minimize extensive epidemic bark beetle areas" by using thinning and other harvest treatments [42]. While the Forest Service has applauded HFRA as "very helpful" in addressing beetle outbreaks (U.S. Forest Service, Review of the Forest Service Response: The Bark Beetle Outbreak in Northern Colorado and Southern Wyoming, September 2011), available at [43], agency leaders do not look favorably upon all legislative proposals to weaken environmental laws to facilitate timber harvest for beetle control. For example, Tom Tidwell, Chief of the Forest Service, criticized recent bipartisan legislation [25] because it would "shortchange the environmental review process, cut out public engagement and collaboration…and override roadless protections." (Testimony from House Subcommittee on Public Lands and Environmental Regulation Legislative Hearing on H.R. __, H.R. 1294, H.R. 818, H.R. 1345, H.R. __, and H.R. 1442 available at [44].

Given the geographic concentration of federal public lands in the West, most of the bills have a specific focus on western states, and were introduced or supported by westerners (Figure 2). But that is not universally the case. Two of the proposals to expand the scope of HFRA were sponsored by Representative Markey, a Democrat from Massachusetts [19,23]. Moreover, support for these bills is bipartisan, showing that the belief that timber harvest can address beetle infestations crosses the political spectrum. Of the 55 total bills, 17 were sponsored by Democrats alone, 21 sponsored by Republicans alone, and 17 had bipartisan sponsors. Markey himself has received very high ratings from the League of Conservation Voters, with a 94% lifetime score from the group.

Figure 2. Bill sponsorship, co-sponsorship, and applicability by region. (Pacific = CA, OR, W, AK, HI; mountain states = MT, ID, NV, WY, UT, CO, AZ, NM; Midwest = ND, SD, NE, KS, MN, IA, MO, WI, IL, IN, MI, OH; SOUTH = TX, OK, AR, LA, KY, TN, MS, AL, GA, FL, SC, NC, VA, WV; east = ME, NH, VT, MA, NY, RI, CT, NJ, DE, MD, PA).



The 55 bills introduced since 2001 show that many legislators, particularly those from western states, believe that timber harvests are a necessary tool to address beetle infestations. This belief has led to the enactment of laws that reduce compliance burdens under NEPA and other federal environmental laws. There are many more proposals for additional significant changes to federal environmental laws to encourage more timber harvests for beetle control. While "there is certainly a tremendous amount of social and political pressure to 'do something' about beetles," there is also growing concern by many that timber harvests for beetle control are expensive and ineffective and that long-term impacts on forests are unknown [42 citing Ann Merwin, director of policy and government affairs for the Wilderness Society]. The policy debate demonstrates the need to critically examine how well these treatments work and place policy in the context of the best available science.

3. A Mountain Pine Beetle Primer

The mountain pine beetle is native to pine forests in western North America [45]. During outbreaks, it can kill millions of trees across extensive areas. The ability to cause such widespread mortality has led it to be described as the most destructive forest pest on the continent [46]. Indeed, economic and aesthetic impacts of outbreaks can be severe. From a manager's perspective, outbreaks are often perceived as a symptom of poor "forest health", while ecologists more often view outbreaks as natural ecological processes integral to the maintenance and resilience of the forest. These differing human perceptions have led to conflicting and ambiguous management goals as well as scientific, social, and political conflict.

The mountain pine beetle is polyphagous on pines (*Pinus*) [45]. It attacks not only native pines but also exotic pines used in ornamental landscaping. Within the natural range of the beetle, only *P. jeffreyi* appears to be avoided, likely due to its unusual chemistry [45]. Pines are well defended and are not easy targets for the beetle. They produce constitutive defenses consisting of resin that can flush the tiny beetles from trees, often drowning them [47–49]. Pines also produce induced defenses in the phloem comprised of resin containing elevated concentrations of toxic monoterpenes [49,50]. Induced defenses develop in response to attack, and thus, involve a lag time of one or more days to develop and can last for a month or more even when trees are killed [51].

To contend with a defensive host, the mountain pine beetle has evolved a complex chemical communication system it uses to coordinate a mass attack on a tree [52]. A female beetle will land, begin to tunnel, and release an aggregation pheromone that attracts conspecifics of both sexes to the tree. Subsequent arrivals release additional pheromone increasing attraction to the tree [53]. If enough beetles respond, the tree can be overwhelmed in just a few days. As defenses are depleted, the beetles release an anti-aggregation pheromone which repels late arriving beetles and acts to reduce intra-specific competition among brood [53]. At this point, the tree has reached "a point of no return" [54]. It will not recover and will slowly die, although it may remain green for nine months or more due to translocation of water to needles by capillary action in the xylem.

The number of beetles needed to kill a tree varies and depends, in part, on the strength of its defenses [55]. In general, as the strength of defenses increase so does the number of beetles needed. Several factors influence the strength of tree defenses. Trees weakened by drought, disease or damage can be overwhelmed by only a few hundred beetles while very vigorous trees may require many hundreds or even thousands [56]. Genetics of the host tree also play an important role. Within a tree species, different genotypes result in differing levels of resistance and susceptibility [57,58]. Genetic differences are even more pronounced when considering differences in defenses among *Pinus* species [59,60].

The ability of tree defenses to affect mountain pine beetle success varies by whether the beetle is in endemic (non-outbreak), incipient (building) and eruptive (outbreak) phases. During the endemic phase, when beetle populations are low, host tree defenses are the major constraint in the ability of beetles to kill trees. However, tree defenses become inconsequential once the threshold to the incipient stage has been surpassed [61]. When numbers are low, beetles attack smaller diameter trees with low defenses. However, once populations rise to the incipient stage, beetles choose larger, healthier, resource-rich trees, despite their superior defenses [61]. Because larger trees have thicker phloem resources to support larval development, they support greater beetle productivity which results in positive feedback that helps fuel the expansion of the outbreak. Thus, host tree traits (primarily host defenses and diameter class) that determine which trees are killed when populations are low, may be unimportant or even have an opposing effect on beetle success when populations are high [61].

It is often reported in the press that mountain pine beetle populations are cyclical. This is not the case. The population dynamics of insects that develop cyclical outbreaks are typically dominated by *delayed* negative density dependent feedback involving regulation by natural enemies and induced resistance mechanisms [62]. This type of feedback results in predictable intervals (cycles) between outbreaks although the amplitude of population peaks can vary due to spatiotemporal variation in abiotic conditions. Bark beetle dynamics, instead, are driven by alternations of negative density dependent and positive density dependent feedbacks resulting in sporadic unpredictable population eruptions primarily driven by threshold effects and typically triggered by abiotic factors, particularly climate [61–63]. It is critical to distinguish between cyclical and eruptive population dynamics as insects exhibiting these two types of dynamics demand different management and monitoring approaches. In particular, eruptive dynamics are triggered by abiotic factors typically outside the realm of human manipulation.

Mountain pine beetle can remain in non-outbreak phase for very long periods of time, even when forests are composed of suitable age classes of host trees and in a condition often considered to be highly susceptible and “unhealthy”. Outbreaks occur *only* when multiple thresholds involving temperature, tree defenses, and brood productivity are surpassed that allow positive feedbacks to amplify across several scales [2,64]. While outbreak development is complex, the primary elements that must exist are an abundance of suitable hosts *and* a trigger [63]. Triggers for mountain pine beetle that allow population amplification and subsequent widespread outbreak initiation are warm temperatures and drought, conditions that often co-occur [65]. There can also be a substantial lag period, even several years, from the initiation of the abiotic factors that trigger an outbreak to when populations actually amplify [65,66]. However, once a threshold number of beetles is surpassed, the outbreak becomes self-perpetuating.

While forest conditions alone do not cause outbreaks, certain forest conditions can support larger and more severe outbreaks once they are initiated. Mountain pine beetle attacks only pines (except in rare instances where it “bleeds over” into spruce) [67], and typically only those larger than ca. 15 cm in diameter [68]. Therefore, forests comprised mainly of large diameter pine can be at higher risk of widespread mortality when a trigger occurs than are forests comprised of young, small diameter pine or composed of a mix of tree species including non-pines [68]. Processes that homogenize forest structure and composition such as abnormally widespread stand replacement events (e.g., fires of 1910, Yellowstone 1988) or particular types of forest management (e.g., some timber harvest practices, fire suppression) that alter forest composition and structure over large areas, can contribute substantially to the extent and severity of an outbreak once it is initiated. Processes that result in heterogeneity, such as "normative" wildfires and bark beetle outbreaks, and some land management practices (e.g., restoration treatments focused on restoring a mosaic structure of forest stands of different age classes) tend to reduce outbreak severity and extent by reducing the amount of contiguous susceptible hosts [68].

Climate acts as a trigger for mountain pine beetle outbreaks for a very good reason. Like all insects, mountain pine beetle is poikilothermic-it cannot regulate its body temperature, and thus, all its metabolic rates and vital functions are dependent upon the temperature of its environment [69]. As temperatures rise, feeding, activity, development and reproductive rates increase. Importantly, this also means that the length of the mountain pine beetle life cycle is determined by temperature [69]. Under optimal thermal conditions, development is univoltine (one year). A univoltine cycle allows synchronized emergence of brood adults in mid-late summer, supporting not only mass attacks, but also attacks at a time that allows subsequent offspring to enter winter as cold-hardened larvae [70,71]. Cold hardening is a gradual process that occurs as temperatures fall in autumn. Once larvae are cold hardy it can take temperatures as low as −40 °C to kill significant numbers [72]. However, cold air incursions in fall when beetles are not yet cold hardened or in spring when larvae have lost cold hardening in preparation for transitioning to the adult stage can result in widespread mortality. This can halt an outbreak if subsequent conditions are no longer favorable for the beetle. However, if favorable conditions return, beetle populations rebuild. Importantly, outbreaks require a univoltine life cycle combined with moderate winter temperatures [73].

In areas where temperatures are too cool to support a univoltine life cycle, a semivoltine (longer than one year) life cycle occurs [73]. A semivoltine life cycle is maladaptive for the beetle in several ways. First, adaptive seasonality is disrupted, increasing the percentage of brood that enter winter in stages vulnerable to freezing (eggs, pupae and adults). Additionally, mortality increases when beetles must pass through two winters and feed on a food source increasingly depleted in moisture, nutrients, and symbiotic fungi [74]. Warm periods support not only greater brood production and survival in areas typically suitable for the beetle, but also allow a transition from a semivoltine to a univoltine life cycle in areas otherwise too cool. This increases the spatial extent of suitable habitat and tree mortality. Thus, abnormally warm periods can vastly increase the total area suitable for the beetle and play a major contribution to the synchronicity and coalescence of outbreaks across regions [2,65].

Drought can also play an important role in outbreak initiation. Host tree defense mechanisms are compromised during drought allowing beetles to more easily attack trees [2,75]. Tree defenses are major constraints when beetles are in non-outbreak phase. However, drought-weakened trees can support population amplification until a point where stand level densities surpass a critical threshold. Once this threshold is passed, tree defenses lose their importance in regulating beetle populations [61]. Very importantly, drought stresses large numbers of trees at a regional scale. This results in large numbers of trees that are easier for the beetles to kill, further supporting outbreak intensification [65,76].

Recent studies have found that drought occurring years or even decades before the outbreak can influence outbreak initiation. Furthermore, prolonged drought stress appears to pre-condition trees to be more susceptible, an effect that can continue for years after normal precipitation has returned [58,65,77]. There also appears to be a genetic component to tree sensitivity to drought, and subsequently, susceptibility to beetles. In two studies, one conducted in whitebark pine and the other in ponderosa pine, differences in growth of surviving trees and trees killed by beetles over the last century suggest that adaptive differences to changes in climate exist. In the whitebark pine study, the trees studied were co-dominants and not significantly different in diameter age or mean growth over their lifetimes [58]. However, trees that were killed exhibited faster rates of growth in the first half of the century suggesting they were better adapted to the cooler wetter conditions of that period. The surviving trees had greater growth in the latter half of the century when conditions were warmer and drier. Millar *et al.* [58]) suggested that the beetle-caused tree mortality in the stands they studied resulted in a strong natural selection event that removed trees less fit under our current climate while leaving those more well-suited.

Likewise, Knapp *et al.* [77] found genotypes of ponderosa pine that were slow-growing in the two to three decades prior to the outbreak were much more vulnerable to beetle infestation than those that were fast-growing, again suggesting the beetle may act as a selective agent shifting genetic structures in stands over time to those most suited to prevailing climatic conditions. In lodgepole pine, trees of similar age and diameter growing intermixed in the same stand and under the same conditions exhibited different levels of sapwood moisture that were highly correlated with susceptibility to beetle attack [74] hinting at genetic differences in water efficiency. Those with lower sapwood moisture were attacked and killed by the beetle while those with higher sapwood moisture were not [74].

While mountain pine beetle has developed outbreaks for millennia, the current outbreak is far outside the historic norm [2,78]. The unprecedented size and severity of this outbreak is due to a combination of increasingly favorable climate for the beetle and forest conditions. Warming trends have supported the development of a univoltine cycle in many areas that previously were too cool and have resulted in greater beetle productivity and survival [79]. This has led to massive tree mortality, not only in areas previously favorable for the beetle, but also in areas previously suboptimal or unusable. Warmer temperatures and high population levels have also supported expansions of the beetle’s range hundreds of kilometers further north in British Columbia and eastward across Alberta [80–82]. In these new locations, the beetle is infesting naïve hosts including (in the eastern expansion) a novel species, jack pine [80,82]. These naïve hosts exhibit lower defenses to beetle attack [83] as well as similar chemical compositions to natural hosts [84] promoting establishment. Predictions are that the beetle will continue to move across the continent through the boreal forest and finally into eastern pine forests [78].

Warming has also allowed the beetle to move higher in elevation where it is devastating whitebark pine, a tree that is foundational to the western North American subalpine ecosystem and that was previously protected from the beetle by cold [73,85]. Movement into the subalpine has been supported by overall warmer temperatures and milder winters allowing the beetle to switch from a semivoltine to a univoltine life cycle while simultaneously reducing winter mortality [85–87]. The resulting mortality to whitebark pine in many areas, particularly the greater Yellowstone Ecosystem, has been so severe the tree is now proposed for listing as an endangered species [88]. The tree is already listed as an endangered species in Canada due to the combined effects of mountain pine beetle and white pine blister rust [89].

4. Mountain Pine Beetle Outbreak Suppression

Treatments used to mitigate the effects of mountain pine beetle are grouped into three broad categories. Treatments that strive to reduce or eliminate beetle populations are termed direct controls [90]. Treatments aimed at increasing tree vigor and altering stand conditions to be less favorable for beetles are called indirect controls [90,91]. Prophylactic treatments aim to protect high value individual trees or stands of trees from infestation. Salvage, while often included in beetle management programs does not actually reduce or impact beetle populations-it is the removal of dead trees for economic or other reasons and often involves removal of trees that are already ‘empty’ of beetles and thus has no impact on beetle population size. Because our focus is on how well science supports the use of timber harvests (including tree felling and destruction of trees in place) to reduce or suppress bark beetle outbreaks, we will focus primarily on direct and indirect controls concentrating on these treatments.

Direct control includes sanitation treatments such as removing single trees or small patches of trees that are infested with the insect, clearcutting (also called block harvesting) and prescribed burning of infested trees, as well as fell and burn, trap trees, debarking, and application of insecticides or toxins such as MSMA (monosodium methanearsonate). Sanitation cuts attempt to remove most or all beetles in an area by removing infested trees before the beetles developing within them can emerge and disperse [90,92]. Prescribed burns, fell and burn, debarking, and toxin applications attempt to destroy beetles in infested trees on-site. Trap trees are trees that are baited with attractant pheromone baits in an attempt to draw beetles into specific areas where they are concentrated into the baited trees which are subsequently taken to the mill or destroyed. Each of these methods relies on killing as many beetles as possible in order to lower beetle population thresholds below which they can maintain outbreak dynamics.

Indirect controls are primarily silvicultural in nature. The main treatment used for mountain pine beetle is thinning. Thinning is thought to act by reducing inter-tree competition for water, nutrients, and light, enhancing greater tree vigor, and thus defenses against the beetle [93]. Thinning treatments are also thought to reduce successful beetle attacks by altering microsite conditions by increasing temperatures on bark surfaces on bark in summer and decreasing them in winter, as well as disrupting beetle communication by increasing wind flow [94,95]. A new treatment recommended for reducing bark beetle infestation is “daylighting” which involves removing trees and shrubs from around trees that are to be protected to increase light on the tree’s stems to disrupt beetle colonization. Other silvicultural treatments include removal of beetle-suitable hosts (mature trees and old growth) and conversion of stands from species preferred by beetles (pines) to species that are not hosts or converting stands that are primarily pine to a mixed species composition [91,92]. Most of these approaches involve, completely or partially, the use of timber harvests.

4.1. Efficacy of Direct Controls

Direct control treatments are extremely expensive in time, effort and resources. They address only one aspect of an outbreak which is the amount of beetles present in a stand or area. Because they do not address the underlying conditions that support an outbreak (climate, tree condition/stress) their effects are considered a holding action until conditions shift to being less favorable for the beetle [92].

Direct control efforts must be maintained at a high level on an annual basis until the outbreak ceases [3,90,96]. It is highly controversial whether direct controls are effective in reducing tree mortality in the short-term, and if they can be effective in halting or suppressing outbreaks in the long-term.

One of the biggest problems in assessing the utility of direct controls is a general lack of monitoring or *post hoc* assessments of the outcomes of implementing these practices. Despite decades of direct control and large-scale implementation of these practices, few rigorous studies on its efficacy have been done and there remains no agreement among scientists or foresters regarding its ability to reduce beetle populations or losses of trees. Studies conducted prior to the current outbreak have variously concluded that direct treatments may merely act to delay infestation of susceptible stands [97], or that if used correctly, can be effective [98,99]. Many studies found that while some treatments slowed the rate of infestation, overall, they had little to no impact on mountain pine beetle populations [97,100–104].

The US and Canadian governments have spent hundreds of millions of dollars in direct control efforts to address the current outbreak. However, assessments of the efficacy of these efforts are nearly non-existent and only a few studies on assessments have been published. The few that have been published are reviewed here. Although much of our review addresses how well science supports US policy, we use primarily studies conducted in Canada as few studies have been published on direct control measures during the current outbreak in the US.

Nelson *et al.* [3] evaluated the efficacy of five direct control treatments in British Columbia roughly midpoint in the portion of the current outbreak as it progressed in that province. The assessment was extremely short-term and looked only at the response of beetles in the year immediately post-treatment. However, it provides one of the very few broadscale assessments ever conducted of the efficacy of direct controls during an outbreak. The treatments assessed were applications of MSMA, trap trees, fell and burn, and clearcutting. The study was split into three geographic regions to account for potential sources of variability due to location and different background levels of beetles. The northern-most region was at the margin of the beetles range (expansion zone) and possessed relatively low beetle populations, while the central and southern regions had higher beetle populations and were known to have supported high beetle populations historically. The study found that, overall, sites receiving MSMA treatments exhibited higher infestation intensities (a metric based on kernel density estimators) than randomly selected untreated sites with similar characteristics. This was particularly pronounced in the southern region. Results for trap tree treatments showed substantial variability within and among regions. A reduced infestation rate in response to treatment was observed more often than not in the northern area where beetle pressure was low. However, in the central and southern regions where beetle pressure was higher, the range of infestation intensities was similar for treated and untreated sites although a larger number of comparisons found higher infestation intensities in the treated sites. The overall conclusion was that MSMA and trap tree treatments may be effective, but not reliably, and only when beetle pressure is low and environmental conditions are not highly favorable for the beetle.

Results for fell and burn were also variable. In the northern region, intensities were lower overall in treated *vs.* untreated sites. However, in the central area, treated areas tended to have greater infestation intensities. In the southern area, no discernible effect of treatment was seen. Therefore, like with trap trees, fell and burn appeared to sometimes be effective, but only when populations of beetles were low, and became increasingly unreliable as beetle pressure increased and the infestation moved into outbreak phase.

Removal of trees in patches was studied only in the central region. No significant effect of treatment was detected. Clearcuts were assessed in the central and southern areas and were found to lead to a significant reduction in infestation intensity. In almost all cases, infestation intensities were lower in treated *vs.* untreated areas. However, this was likely due to the removal of all living trees (potential subsequent hosts) that survived the beetle as well as the infested trees. The overall conclusion of the study was that mitigation treatments are effective when populations are low to moderate and if infested trees can be kept to 2.5 or fewer per hectare. Efficacy was also recognized to be contingent upon a high level of accuracy in detecting infested trees and wide-scale and continuous implementation of treatments. However, with only one year of data, the authors could not predict how long treatments would need to be sustained to remain effective, nor what effect beetle pressure from surrounding areas might have on the subsequent fate of treated stands. No follow up study has been published to report how these treatments fared as the outbreak progressed.

Fell and burn has been a stalwart component of the direct control efforts against mountain pine beetle in Canada during the current outbreak, particularly on the advancing front as the beetle expands its range eastward. Coggins *et al.* [105] examined the efficacy of fell and burn treatments to “stabilize” such infestations (*i.e.*, prevent expansion) using field plot data from sites at the expanding edge of the mountain pine beetle infestation in 2008 in eastern British Columbia and western Alberta. The authors used multiple modeling scenarios along with ground data to demonstrate how infestations may develop with and without mitigation, and to predict how long mitigation may need to be maintained to be effective given different levels of infestation and detection accuracy. They found non-mitigated plots experienced more tree mortality due to the beetle and that infestations in these plots expanded more rapidly. The higher the expansion factor (means rate of increase, e.g., 2 would indicate a doubling of the population each year) the greater the detection accuracy that was required to maintain a static population. When a beetle population had an expansion factor of 5.1 (high), an 80% detection rate was required, whereas with a population with an expansion factor of 1.1 (very low), the minimum detection rate could be as low as 10% and still be effective. The authors also modeled how long it would take to achieve population stability given different levels of infestation. On average, across their stands, with a 70% detection accuracy rate, mitigation would take 11 years, at 80% 6 years, and at 90% 3 years. The actual mean mitigation efficiency at their sites was found to be 43%, a level at which no control could occur. They concluded that the stabilization of mountain pine beetle populations is possible, but only with a much higher detection accuracy than commonly occurs coupled with an intense level of mitigation maintained potentially over a very long timeframe.

Wulder *et al.* [96] looked at the effectiveness of sustained mitigation on slowing the beetle’s expansion in western Canada. The results were difficult to assess because of the unevenness of application of mitigation treatments (for example, in one year only 68% of sites slated for mitigation were treated) and differences in background beetle populations. However, such a situation is typical and thus may represent the reality of many on-the-ground direct control efforts. One site where little mitigation was conducted early on, did exhibit a strong increase in tree mortality due to the beetle that declined once extensive mitigation efforts were implemented. However, overall, the conclusion was that mitigation must be extensive and continuous to work and may only be effective when populations are low to moderate.

Trzcinski and Reid [104] studied the trajectory of beetle populations in treated and untreated zones in Banff National Park from 1997–2004. The Park used a combination of pheromone-baited trees and fell and burn to remove as many beetles as possible from treatment zones—they also conducted prescribed burns to reduce beetle numbers and lodgepole pine hosts. The area colonized by the beetle increased rapidly over this time period in both the untreated and treated zones. After four years of treatment, control measures did not reduce the area affected by beetles and infestations continued to expand at a similar rate in both zones. The authors estimated that between 45% and 79% of infested trees had failed to be detected in the treated areas. This equated to *only* 0.7–3.7 infested trees remaining per thousand ha yet still was sufficient to support subsequent rapid beetle population growth.

A general consensus of these studies is that suppression of a beetle outbreak would require massive sustained efforts with extremely high detection rates to succeed. It has been estimated that 97.5% of beetles in an area must be killed to merely stabilize a mountain pine beetle population [90]. Even a small increase in survival above this value can allow a substantial increase in population size. For example, if mortality drops to 95%, this would allow a population to *double* in size annually. If the goal is not just to stabilize a population, but to reduce it, mortality of beetles would need to be higher than 97.5%, a goal that is highly unlikely given the vast areas that would need to be treated on a continual basis when conditions are favorable for outbreak development. Even if 100% removal of infested trees from an area was feasible, the migration of beetles into treated stands from surrounding areas allows reestablishment and subsequent tree mortality further decreasing the potential for effective direct control.

The on-the-ground reality is that direct control efforts typically fall far below the levels needed to stabilize, let alone control, mountain pine beetle populations. In the above cited studies, rates of detection in mitigated stands ranged from 45%–79%. These situations are not unusual. Direct control treatments are laborious, extremely costly and time consuming, and require high levels of training. Logistical difficulties, including proper seasonal timing, access, inclement weather, and lack of trained personnel, increase the odds that they will not be effective. The high financial cost of such efforts coupled with a volatile market for sawtimber, pulp and pellets further complicates the use of direct controls. Importantly, outbreak development is extremely swift and the amount of mitigation required can rapidly outstrip the ability of managers to respond.

During an outbreak the number of trees killed annually is often in the millions and infestations may cover hundreds of thousands of hectares [90]. Carroll *et al.* [90] presents an example of the degree of mitigation that would be required for an outbreak that covers 300,000 hectares with a rate of increase of 2 (the population doubles in one year-a conservative rate for an outbreak). In this case, 150,000 ha of infested trees would need to be removed each year just to maintain a *static* beetle population–this would still allow tree mortality to occur for many years, potentially until most or all mature trees were killed. In reality, such a high level of detection and mitigation is impossible. Given that the goal of direct management is to reduce populations and protect trees, the effort that would be needed to actually reduce such a high beetle population would require an even more unlikely effort.

Studies in other bark beetle systems also have found that a high degree of detection accuracy and intensity of mitigation is required to reduce beetle numbers. Fahse and Heurich [106] found that control of *Ips typographus*, a less aggressive European bark beetle, requires a detection and removal level of around 80% to be effective. They concluded that direct control efforts are useless and should be dropped if survival probabilities of the beetle after treatment are above 20%–30%. This estimate is in line with those developed in studies on mountain pine beetle in North America and highlights the challenge the high reproductive capacity of bark beetles poses when conditions are favorable for outbreak development.

It is not just the difficulty of dealing with the extreme spatial extent of outbreaks and the challenge of detection and treatment that makes the efficacy of direct control measures unlikely, but also the time frame over which direct controls must be maintained. Carroll *et al.* [90] estimated that to control a population involving 10,000 infested trees with expansion factor of 2 (conservative) and with a detection and removal rate of 80% (difficult), it would take at least 10 years of annual treatment to reduce the population to a single tree. If the population was tripling or quadrupling, a more likely scenario during an outbreak, it would take 18 or 41 years, respectively. A costly, intensive detection and treatment program lasting that long, assuming sufficient trees even remained to be infested, would be unlikely [90].

Carroll *et al.* [90] emphasized three requirements for direct controls to be effective in treating *individual* infestations: infestations must be detected early, efforts must be applied quickly and intensively, and control programs must be maintained continuously until the desired population level is achieved. Because of the cost and intensity of treating individual infestations, the US Forest Service recommends that direct control measures only be applied to higher value stands [92]. However, treating individual infestations or stands during outbreaks can fail because of the regional nature of outbreaks. Outbreaks are driven by abiotic factors that affect entire regions (warm temperatures and drought). Thus, they consist of many infestations that occur synchronously across a very large area. These infestations often coalesce to form vast expanses where beetle populations are extremely high. These characteristics mean that many stand level efforts are prone to failure due to high beetle pressure and migration into treated areas by beetles from surrounding areas. Given that treating entire regions is impossible, and that many treatments are not in line with other land use objectives, direct control efforts may in some cases, not be worth their costs. The consensus of studies and retrospectives over the course of several outbreaks is that even after millions of dollars and massive efforts, suppression using direct controls has never been effectively achieved, and at best, the rate of mortality to trees was reduced only marginally [90,101,102,105]

4.2. Efficacy of Indirect Controls

Thinning is the primary indirect control measure used to manage the mountain pine beetle. It is generally considered a preemptive measure to be implemented prior to the initiation of a mountain pine beetle outbreak, although it is increasingly employed to reduce damage by the insect during outbreaks. It is often touted as a global panacea for problems with pest bark beetles. One type of thinning is even termed “beetle-proofing” [107], further reinforcing the view among managers, the public, and policy makers, that this approach is failsafe. While overall, evidence suggests that thinning can reduce mortality of trees due to mountain pine beetle, the outcome is frequently more variable than is often recognized or reported. This is particularly true when outbreak populations are involved.

So how exactly does thinning work, and how well does thinning hold up under outbreak conditions? Surprisingly, the mechanism(s) by which thinning affects beetle activity in forest stands is still not well understood. Two, non-mutually exclusive, lines of thought exist. One hypothesis is that thinning increases tree vigor, and thus tree defenses, by reducing competition among trees for light, nutrients and water [93,108]. Intuitively, this makes sense, and indeed, immediate impacts of thinning on reducing water stress have been seen [109]. Likewise, increases in growth and photosynthetic rates also have been observed post-thinning, albeit after a lag period of one or more years [107,109,110]. Increases in growth and vigor are predicted to increase the amount of energy that trees allocate to defense, leading to greater resistance to beetle attack through increased resin and monoterpene production. In fact, the initial impetus for the use of thinning to manage mountain pine beetle came from an early study that found that ponderosa pines in thinned stands produced more defensive resin [93]. However, subsequent studies have reported a variety of responses in resin production as well as growth in response to thinning. For example, Zausen *et al.* [111] found that ponderosa pines in the thinned stands exhibited lower water stress but also produced less resin. This, along with the thicker phloem (greater food resources) found in trees in thinned stands, indicates they might be not only more susceptible to attack but also a more productive resource for beetles. In contrast, McDowell *et al.* [112] found greater resin flow in thinned stands. Both studies were conducted in southwestern US ponderosa pine forests indicating that the variable responses observed were not due to major regional differences in hosts. Six and Skov [113], in a study conducted in ponderosa pine in the northern Rocky Mountains looking at effects of thinning and burning treatments, found that resin flow was highest in trees in burn treatments, intermediate in controls, and lowest in thinned treatments. Raffa and Berryman [114] tracked the fate of trees over time during an outbreak and found no significant difference between resin flow for lodgepole pines that survived attack vs those killed by the beetle.

A number of studies have noted a reduction in beetle caused-mortality of trees immediately after thinning treatments were applied and before trees had time to respond physiologically to lower stocking densities. This timing suggests that the effects of thinning may have more to do with microsite conditions than to changes in tree vigor or defense. These observations led to the second line of reasoning that thinning affects beetle activity through changes in microsite conditions.

Thinning alters temperature, light intensity and wind speed within a forest stand; factors that can have major effects on insect behavior and success. A number of studies have tried to describe how shifts in microsite conditions due to thinning may influence mountain pine beetle activity. Bartos and Amman [94] investigated how incident solar radiation, wind speed, wind direction and temperature were altered by thinning and whether changes affected beetle responses to stands. They did not conduct statistical analyses on their data; however, there was a trend for south sides of trees in thinned stands to be warmer, and ambient temperatures in thinned stands to be overall warmer during parts of the day. Incident solar radiation was higher in the thinned stand. It is not known if bark temperature affects beetle attack behavior, although higher temperatures on south sides of trees in thinned stands have been suggested to be deleterious to beetle development [94]. However, this speculation does not account for differences in local environmental conditions. For example, at cool sites, increased temperatures and insolation could ostensibly support better beetle development by increasing thermal units sufficiently to support a univoltine life cycle.

Light intensity affects the flight behavior of mountain pine beetles [115]. However, if and how different levels of light in treated and untreated stands affect beetle attack behavior is unclear. It has been hypothesized that a reduced propensity for flight in darker stands might concentrate beetles for mass attack, while beetles may be more likely to disperse in open stands [116].

The hypothesis that light has a strong effect on mountain pine beetle behavior, particularly in reducing attacks, has led to a new treatment called daylighting. This approach is currently being implemented on a broad scale by federal and western state agencies. Daylighting involves removing trees and vegetation from around trees that are targeted for retention and is believed to work by repelling beetles from the boles of trees by increasing light and solar radiation [117]. While widely recommended, the efficacy of this treatment is unknown; there are no published studies on its effects on bark beetles.

Changes in wind speed and direction due to thinning have also been suggested to alter beetle behavior by disrupting beetle communication via disruption of pheromone communication. Schmid *et al.* [118] found no statistically significant differences in horizontal and vertical wind patterns in thinned and unthinned stands. However, disruption of pheromone plumes by greater wind speeds may affect communication and thus the potential for successful attacks [95]. Ultimately, we need to look at actual population dynamics of beetles in treated and untreated stands to understand if microsite effects hold under epidemic conditions. MacQuarrie and Cooke [119] found that, under outbreak conditions, mountain pine beetle populations exhibited density-dependent dynamics and that thinning did not change the epidemic equilibrium. In this study, population growth curves did not exhibit responses that would be expected if microsite conditions played a role in beetle behavior. It is evident that more research is needed to understand how these effects ultimately influence tree mortality due to beetle attack.

While we may not have a complete understanding of how thinning works, it is clear that this practice can have a significant effect on mountain pine beetle infestations. Several studies have reported striking differences in mortality to trees caused by beetles in thinned *vs.* un-thinned forests (reviewed in [120,121]). In contrast, only a small number of studies have reported failures. However, the disparity in numbers of successes and failures must be placed within a broader context. Many studies assessing the efficacy of thinning have been conducted under non-outbreak conditions. Their results do not reflect how stands perform during an outbreak. Additionally, failures are often not reported, dismissed as a result of poor management ‘next door’ or targeted for management without evaluation. This is unfortunate because thinned stands that fail may have particular characteristics that could inform a better understanding and application of this approach.

Studies conducted during outbreaks indicate that thinning can fail to protect stands. In Colorado, thinning treatments in lodgepole pine implemented in response to the outbreak that began in the 90s often only slowed the spread. Klenner and Arsenault [122] reported high levels of mortality due to the mountain pine beetle across a wide range of stands densities in lodgepole pine in British Columbia during the same outbreak. They noted that silvicultural treatments were largely ineffective in reducing damage to the beetle. Preisler and Mitchell [123] found that once beetles invaded a thinned stand the probability of trees being killed there can be greater than in unthinned stands and that larger spacings between trees in thinned stands did not reduce the likelihood of more trees being attacked. Whitehead and Russo [107] reported on the performance of 'beetle-proofed' (stands thinned to an even spacing of about 4–5 m between mature trees) and un-thinned stands in five areas in western Canada during approximately the same time period. These treatments were successful in protecting stands when they were combined with intensive direct control measures (removal of infested trees) in the areas surrounding the thinned units, but failed if units were exposed to beetle pressure from the neighboring area—a situation most thinned stands experience during an outbreak.

Unfortunately, long-term replicated studies monitoring beetle responses to thinned forests from non-outbreak to outbreak to post-outbreak phase are virtually non-existent. One large fully-replicated long-term study was initiated in 1999 under non-outbreak conditions and continues to track beetle activity [113]. In this study, mountain pine beetle was low in all treatments in the period leading up to the outbreak, but increased in some controls and burn treatment replicates as the outbreak developed. Although more trees were killed overall in control units during the outbreak, all controls still retained a greater number of residual mature trees than did thinned stands as they entered the post-outbreak phase [124].

Two factors contribute substantially to our inability to assess how well thinning performs under outbreak conditions. One, very few thinning treatments are monitored after implementation over either the short- or the long-term. Thus, for the vast majority of stands that have been treated, we have no data on how well they perform once an outbreak of the insect initiates (or for that matter, even under non-outbreak conditions). Second, stands that become infested, thinned or otherwise, are often targeted for intensive suppressive management and are cut without assessment or data collection. This even includes studies and sites that are intended to inform management. For example, at the sites studied by Whitehead and Russo [107], infested trees were being removed from the study sites even before data collection for their study could be completed. The long-term study discussed previously [113,124] is under continual pressure to be logged to remove beetle kill even though the site lies within an experimental forest designated specifically for studies assessing the outcomes of forest management.

5. What are the Goals?

When we manage forests, we do so in an attempt to achieve one or more outcomes, preferably with minimal negative effects on non-target resources. To be effective, management must have explicit and appropriate goals as well as clear metrics for success. Ideally, management is monitored to assess how well it meets its goals, where it falls short, and whether and how it can be improved. This approach is called adaptive management and implies an iterative process through time whereby we learn from the outcomes of our actions and base future actions on improving performance [125].

Not only outcomes, but the costs of management must be factored into decision making. These include direct financial costs as well as the less tangible (at least in dollar values) effects on ecosystem services and functions. By considering the full cost of management along with benefits as verified through monitoring and evaluation, we lessen the risk of failure, financial waste, and unnecessary negative environmental impacts.

In assessing how well we meet goals when managing for mountain pine beetle, we must ask several questions. Do our management practices actually control the beetle during outbreaks? Do the outcomes justify the financial and ecological costs? And, what long-term impacts do these treatments have on forests and their ability to adapt to climate change? These questions are difficult to answer. Only limited data are available on the short-term efficacy of direct and indirect controls, and information on long-term effects is virtually nonexistent. The results of short-term assessments can be difficult to interpret. For example, often only the proportion or numbers of trees killed by beetles post-treatment are reported. This does not allow a complete evaluation of outcomes. A study may report that 75% of trees in controls are killed by the beetle, whereas only 10% are killed in thinned stands. At first glance, this appears to be a resounding success in saving trees. However, if we approach this situation from a pretreatment perspective, our interpretation of success may change. In this example, 400 mature trees existed in each plot prior to treatment. After treatment, 100 mature trees remain in the thinned plots (300 trees have been removed by thinning). Doing the math, we find that once the beetles have run their course, more residual living trees (100) actually remain in the control plot than in the thinned plot (90) and, in fact, humans have contributed more to tree mortality than have the beetles. In the case of silvicultural intervention, humans typically must expend considerable effort and expense. They also choose the trees that remain, and thus the structure and composition of the remaining forest. This may result in very different trajectories for residual forests as discussed below.

When we include pre-treatment conditions as well as post-treatment responses we can assess the management efficacy from a more informed position. For instance, in a retrospective study investigating the effects of management on spruce beetle, researchers found that post-infestation, untreated stands had more live spruce trees and greater basal areas. When comparing only residual large spruce, final densities in both stand types were similar [126]. Six [124] found higher numbers of mature living trees remained in control stands of ponderosa pine than in thinned stands post-mountain pine beetle outbreak. In a study in Canada focusing on stocking density of living lodgepole pine post-outbreak, the authors found that, even in hard hit stands, stocking density in post-outbreak unmanaged stands was sufficient to maintain desired levels of productivity [127]. Klutsch *et al.* [128] in a study conducted in lodgepole pine forests in Colorado, found greater mortality of trees due to the beetle in more densely stocked stands. However, while the density and basal area of lodgepole pine in infested plots declined 62% and 71%, respectively, the number of trees that remained and their size distribution post-outbreak indicated that lodgepole pine would remain the dominant overstory tree. In another study in Colorado, the beetle killed 60%–92% of overstory lodgepole pine. However, these stands retained residual overstory trees as well as advance regeneration. Furthermore, untreated stands were predicted to return to pre-outbreak stocking levels approximately 25 years sooner than treated stands [129]. Other studies have found similar results for both lodgepole and ponderosa pine [130–134]. These studies highlight a seldom considered impact of mountain pine beetle- that it can act as a natural thinning agent and seldom removes all mature trees during outbreaks. These effects are an important part of the ecological role that the beetle plays in western pine forests [135].

It is also important to recognize there can be significant differences in long-term forest trajectories for stands thinned by beetles *vs.* those thinned by humans. When humans thin, they select for particular size classes, often favoring the retention of larger, older trees, selecting toward one desired tree species, and often ‘thinning from below’ which removes advanced regeneration (small trees) [123,136]. Thinning prescriptions also typically call for relatively even spacing between residual trees [92,107,121]. Mountain pine beetle, on the other hand, often selects the largest trees during outbreaks (with exceptions; [121,123,131]) which can lower the mean diameter of the stand [128]. However, beetles often leave sufficient numbers of large diameter trees to maintain a dominant overstory of pine. Beetles also leave substantial amounts of advanced regeneration to replace the mature trees that arekilled [121,129]. Spacing among trees after an outbreak is uneven, resulting in a clumpy network of living trees [129]. Patches where all trees are killed are seldom extensive and add to a mosaic structure as forests recover post-outbreak. Heterogeneous stand and mosaic forest structures are more typical of natural conditions and can support greater biodiversity and resilience against fire and subsequent beetle outbreaks [137–139]. In contrast, intensive thinning treatments by humans typically favors the retention of mature pines. Over time, these pine-dominated stands grow, they are predicted to have increased susceptibility and potential for tree mortality from future mountain pine beetle outbreaks [123,136].

Very importantly, the beetle exercises selectivity in the trees it kills. While extremely high numbers may override this selectivity, evidence is accumulating that, even under outbreak conditions, beetles choose trees that have particular qualities. Beetles commonly select trees for attack that exhibit lower growth rates, defenses, and higher water stress [58,74,77]. While these factors can be influenced both locally and regionally by site conditions and climate, much of the variation in these properties within individual stands that affect bark beetle choice likely has a genetic basis. Outbreaks can result in strong natural selection against trees with phenotypes (and likely genotypes) favorable for the beetle and for those that possess unfavorable qualities [58,77]. However, when humans thin forests, trees are removed according to size, species, and density, without consideration of genetics. Thus, trees best adapted to surviving beetle outbreaks are as likely to be removed as those that are not.

When humans thin forests, they typically manage for resistance and resilience, rather than adaptation which involves genetic change. It is very important to distinguish between resistance, resilience, and adaptation, as each have different goals and operate on different temporal scales [140]. Resistance is a short-term holding action where we try to maintain an existing state. Approaches focusing on resistance often require massive interventions and increasing physical and financial investments over time. Such approaches may set forests up for future outbreaks [136] and even catastrophic failure as they surpass thresholds in a warming climate [140]. In contrast, practices that promote resilience attempt to allow forests the ability to adjust to gradual changes related to climate change and to recover after disturbance. However, like resistance, resilience is not a long-term solution. In the long term, forests must be able to adapt to change. Adaptation involves genetic change driven by natural selection. Currently, much of forest management, including bark beetle management, focuses on resistance and resilience, mainly through direct and indirect management, respectively. However, neither approach allows for true adaptation. For long term continuity of our forests, it will be imperative to begin to incorporate this aspect of management into our approaches.

We also need to reassess the ecological role of bark beetles, including the mountain pine beetle, in our forest ecosystems. As has been well demonstrated by a century of fire suppression, the dampening or suppression of natural disturbance can alter forest trajectories in undesirable ways, many of which can be irreversible. Although beetle outbreaks, like fire, can have negative impacts on timber values and aesthetics, their natural role in many forest ecosystems is seldom considered and beetle suppression is often perceived as something that must be conducted at all costs. However, as with fire, suppression of beetles over the long term may alter forests in ways that are not desirable or sustainable. While intensive management for bark beetle suppression is called for in some situations such as in the wildland urban interface, it may not be appropriate in many other areas where natural processes including natural selection are needed to maintain a dynamic and functional forest.

6. What are the Needs in Research and Monitoring?

There is clearly a need to better understand how well management programs aimed at reducing mountain pine beetle work, particularly under outbreak conditions, and what impacts these treatments have on forests in both the short and long term.

Perhaps the biggest area of need is in monitoring. Monitoring is essential to understanding whether mountain pine beetle treatments work, and in which contexts, but as noted above there has been all too little long-term monitoring of the effectiveness of various treatment efforts. This is a failing among both agencies and researchers. Agencies often do not have strong incentives to conduct long-term monitoring: Monitoring is costly; external and internal political pressures focus on short time frames; and monitoring may produce information that conflicts with agency goals or missions. It is also difficult to get strong public pressure to force agencies to conduct the necessary monitoring, particularly when the public has been led to believe that outbreaks are strictly the result of a lack of management. Even for scientists, long-term monitoring projects are not encouraged by short-term funding time frames and professional incentives or norms; monitoring is often not viewed as "real" science, and the long-time frames required for monitoring to result in significant gains in information are often longer than the time frames used for professional advancement (e.g., completion of a dissertation, tenure review) [141].

Addressing the shortage of monitoring for beetle treatments may, therefore, require far more than simply trying to provide additional funds (even assuming additional funding is politically feasible). Scientists can help by encouraging and rewarding projects that involve long-term monitoring. Agencies might try to establish units that are focused specifically on monitoring forest health, insulating monitoring projects from adverse political or bureaucratic pressure [141]. Finally, tools that might reduce the cost of monitoring significantly, such as retrospective studies and remote sensing, should be used to complement traditional monitoring and decrease its costs.

Monitoring is all the more essential if forest health management in general, and beetle treatments in particular, are truly to be guided by adaptive management. The high levels of uncertainty and dynamism associated with beetle infestations and the effectiveness of beetle treatments make adaptive management a very appealing tool to reduce uncertainty and allow us to respond to changes in global climate and forest ecosystems. But adaptive management requires monitoring to be successful [141], monitoring that is currently not occurring even as agencies conduct massive beetle treatments and propose to pursue even more.

There is also a real need to increase research on management efficacy and, in particular, how our approaches affect forest adaptation including genetic responses of trees to climate and the role in bark beetle selectivity and fitness. With a changing climate we will need to develop new approaches rather than trying to force old methods of questionable efficacy onto new conditions.

Unfortunately, most funding for research on bark beetles is very short-term, sometimes even as short as on an annual cycle, and thus cannot hope to address the complexities of beetle responses to treatments. Funding cuts to research personnel, particularly in agencies like the US Forest Service, have exacerbated this problem exactly at the time when the need for rigorous research is increasing at a rapid pace. The US Forest Service has recognized that long-term planning must include explicit goals to increase forest resilience and adaptation to disturbance, including outbreaks of the mountain pine beetle. However, with extreme cuts to budgets and personnel, they are highly constrained to meet these needs at this time. Likewise, cuts in federal funding to agencies such as United States Department of Agriculture and the National Science Foundation concurrently reduce the ability of academic researchers to address these problems.

7. Aligning Policy to Science

Our survey of the relevant literature finds that there is significant uncertainty about whether the most commonly used beetle timber harvest treatments are, indeed, effective. Yet there has been little discussion of this uncertainty in the relevant policy debates. Politicians have instead latched on to beetle timber treatments as a cure-all for beetle infestations and have pushed to weaken or eliminate environmental laws that are perceived to be obstructing these treatments. Agencies such as the US Forest Service, to their credit, have been more nuanced in their support for bills that package beetle timber harvest treatments with weakened environmental laws; they have opposed several proposals to alter environmental laws to allow more treatments, but on the other hand, the agencies have at times also aggressively pushed for the implementation of treatments.

It seems clear that the policy debates–both in the agencies and in Congress–need to be better informed by science. Researchers should be more proactive in communicating their understandings of the current science to policymakers. This does not mean that researchers need to take a position pro or con vis-à-vis beetle treatments, or even vis-à-vis specific legal proposals. In the face of uncertainty, aggressive beetle timber harvest treatments may be warranted in some instances. However, policymakers should be aware of uncertainty when they are making the relevant decisions and should also be more willing to include the voices of scientists in the development of policy.

Given the uncertainty about the effectiveness of many beetle timber harvest treatments, the high financial costs of those treatments, the impacts on other environmental resources and values, and the possibility that in the long-run those treatments may interfere with the ability of North American forests to adapt to climate change, our position is that weakening or eliminating environmental laws to allow more beetle timber harvest treatments is the wrong choice for advancing forest health in the United States. Indeed, given the uncertainty, the costs, and the possibilities of both short-term harm to other resources and long-term ineffectiveness, we believe that the current structure of thoughtful, detailed environmental review for these projects is, in general, appropriate. If agencies believe that they need to be able to react quickly to specific infestations with treatments, and that this quick reaction is incompatible with existing legal procedures, we encourage the agencies to adopt overall programmatic environmental reviews based on the principles of adaptive management. Agencies should be able to build (or tier) on these programmatic reviews to respond quickly to individual events as needed. However, the programmatic reviews should allow the agency to build in the monitoring, replication, and variance of treatments that are essential for successful adaptive management [142].

8. Conclusions

The manner in which policy makers have accepted beetle timber harvest treatments as a panacea for responding to bark beetle outbreaks in North American forests raises a number of red flags. As ecosystems and places that have economic, social, and cultural value to human communities are altered by climate change, there is a risk that people will overreact because of a need to "do something" to respond to change, and to give themselves some sense of control over broader forces that appear to be out of control. That pressure, to "do something", might also interact with the uncertainty about which choices are effective and appropriate (as with beetle timber harvest treatments) to create an opportunity for political pressures to force the adoption of particular choices that benefit specific interest groups [143]. It is perhaps no accident that the beetle treatments that have been most aggressively pushed for in the political landscape allow for logging activities that might provide revenue and jobs for the commercial timber industry. The result is that the push to "do something," uncertainty, and political pressures might lead us to act to respond to climate change before we understand the consequences of what we are doing, in the end producing more harm than good.

Our argument here is not to forgo management, but rather that management should be led by science and informed by monitoring. Both direct and indirect management for bark beetles have their place. However, to manage our forests in a way that best ensures their long-term function while wisely using limited financial resources, policy makers and the public need a clearer understanding of current science and gaps.

Acknowledgments

This paper was funded in part though the National Science Foundation Montana Institute on Ecosystems EPSCoR EPS-1101342.

Conflicts of Interest

The authors declare no conflict of interest.

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Front. Plant Sci., 23 July 2018 | https://doi.org/10.3389/fpls.2018.00993 (https://doi.org/10.3389/fpls.2018.00993)

Are Survivors Different? Genetic-Based Selection of Trees by Mountain Pine Beetle During a Climate Change-Driven Outbreak in a High-Elevation Pine Forest

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Increased mortality of forest trees, driven directly or indirectly by climate change, is occurring around the world. In western North America, whitebark pine, a high elevation keystone species, and lodgepole pine, a widespread ecologically and economically important tree, have experienced extensive mortality in recent climate-driven outbreaks of the mountain pine beetle. However, even in stands experiencing high levels of mortality, some mature trees have survived. We hypothesized that the outbreak acted as a natural selection event, removing trees most susceptible to the beetle and least adapted to warmer drier conditions. If this was the case, genetic change would be expected at loci underlying beetle resistance. Given we did not know the basis for resistance, we used inter-simple sequence repeats to compare the genetic profiles of two sets of trees, survivors (mature, living trees) and general population (trees just under the diameter preferred by the beetles and expected to approximate the genetic structure of each tree species at the site without beetle selection). This method detects high levels of polymorphism and has often been able to detect patterns associated with phenotypic traits. For both whitebark and lodgepole pine, survivors and general population trees mostly segregated independently indicating a genetic basis for survivorship. Exceptions were a few general population trees that segregated with survivors in proportions roughly reflecting the proportion of survivors versus beetle-killed trees. Our results indicate that during outbreaks, beetle choice may result in strong selection for trees with greater resistance to attack. Our findings suggest that survivorship is genetically based and, thus, heritable. Therefore, retaining survivors after outbreaks to act as primary seed sources could act to promote adaptation. Further research will be needed to characterize the actual mechanism(s) of resistance.

Introduction

The capacity of forests to adapt to rapid climate change is not known. Their ability to adapt will vary greatly depending upon tree species, amount and type of genetic variation existing within and among populations, type and degree of change required, strength and type of selection pressure, heritability of desirable traits, and the timeframe over which selection is able to act. Many long-lived sessile organisms, including trees, are unlikely to be able to track shifting conditions through migration (Kremer et al., 2012). This is especially true for those restricted to montane ecosystems where movement higher in elevation ends at the top of the mountain and poleward migration is blocked by competitors, valleys, and development (Jump and Penuelas, 2005; Aitken et al., 2008; Dullinger et al., 2012). For many tree species and forests, adaptation will need to occur in place if they are to persist into the future (Aitken et al., 2008).

Bioclimatic envelope models used to predict range expansions and contractions of forest trees treat species as clones, with all individuals exhibiting identical responses (Mimura and Aitken, 2007). While these models are useful to provide estimates of shifts in habitat suitability, they can mask the high genetic diversity and geographic differentiation of most tree species (Mimura and Aitken, 2007; Thuiller et al., 2008; Reed et al., 2011). Likewise, most management focuses primarily on increasing forest resilience through manipulating stand structure and composition while ignoring genetic diversity, natural selection, and the potential for adaptation (Churchill et al., 2013; O'Hara and Ramage, 2013; DeRose and Long, 2014).

Except for highly fragmented or relictual populations, forest trees possess moderate to high levels of standing genetic variation and often exhibit considerable local adaptation and within and among population diversity (Austerlitz et al., 2000; Hamrick, 2004; Savolainen et al., 2007; Alberto et al., 2013). Adaptation of forests to climate change will depend upon the outcome of interactions between existing genetic diversity, phenotypic plasticity, and selection pressure over a relatively short period of time. However, adaptation in trees can be slow due to long generation times and low mortality of older, well-established, but increasingly maladapted trees that continue to contribute to the gene pool (Savolainen et al., 2007; Kuparinen et al., 2010). Long generation times can result in considerable genetic load with long lags between mean optimal genotype and existing climate (Kuparinen et al., 2010). Additionally, while phenotypic plasticity may allow some genotypes to maintain high fitness over a broad range of environmental conditions and aid in resilience to climate change in the short-term, it may slow down or hinder adaptation and persistence in the longer-term (Valladeres et al., 2014).

Adaptation in trees may be accelerated when new conditions or agents lead to high levels of mortality and directional selection in favor of heritable traits associated higher fitness and survival. For example, Kuparinen et al. (2010) used computer simulations to investigate rates of adaptation to longer thermal growing seasons and found that mortality of established trees was the key factor regulating the speed of adaptation with dispersal ability and maturation age having substantially lesser effects. Disturbances caused by agents that use selective behaviors in choosing individual trees, such as herbivorous insects that respond positively to tree stress, can elicit rapid microevolution even in slow-growing tree species (Petit and Hampe, 2006). Such agents may benefit forests in the long-term by increasing mortality of poorly adapted trees, enhancing the reproductive potential of surviving better-adapted trees, and reducing genetic lag loads in affected populations (Kuparinen et al., 2010; Pedlar and McKenney, 2017).

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The mountain pine beetle (MPB) (*Dendroctonus ponderosae*) is a highly selective insect that chooses hosts based on a complex array of chemical cues whose production by the tree is influenced by both tree condition and genotype (Emerick et al., 2008; Blomquist et al., 2010). Secondary metabolic chemicals produced by the tree are used by MPBs to distinguish among tree species as well as to assess the relative strength of defenses of individuals (Blomquist et al., 2010; Raffa et al., 2017). Such chemicals also likely signal adequacy of nutritional content for brood production given that beetles avoid hosts of very poor quality (Taylor et al., 2006; Dooley et al., 2015). Using such cues, a MPB will decide whether or not to enter a particular tree and initiate a mass attack. Once in the tree, the insect converts some terpenes to pheromones important in initiating and sustaining the mass attack required to kill the tree (Blomquist et al., 2010). When MPB populations are low to moderate in size, weakened trees with poor defenses that require fewer beetles to overcome defenses are most often attacked (Boone et al., 2011). However, during outbreaks, MPBs may switch to attacking healthier trees that, although better defended, possess thicker phloem and higher nutritional contents for brood development (Boone et al., 2011). Interestingly, some trees escape attack even when MPB populations are present in high numbers and suitable hosts become increasingly scarce.

In this study, we investigated whether trees that survive MPB outbreaks are genetically different than those that are selected for colonization and killed. Our overarching hypothesis was that surviving trees do not escape by chance, but rather possess genetically based characteristics that confer resistance. The basis for resistance, whether it is the ability to tolerate warmer drier conditions without a reduction in defenses, a chemical profile that negatively affects MPB host location or selection, or some other phenotypic trait, is likely to be under genetic control (González-Martínez et al., 2006; Keeling and Bohlmann, 2006).

MPB outbreaks are triggered by extended periods of warm weather and drought (Meddens et al., 2012). The recent MPB outbreak in western North America was a magnitude larger than any recorded in the past and affected millions of hectares of pine forest (Meddens et al., 2012). The outbreak was primarily driven by climate although its severity was intensified in some areas by past logging practices and fire suppression (Taylor et al., 2006; Creeden et al., 2014; Buotte et al., 2017). Climate change also supported movement of MPB further north in British Columbia and eastward across Alberta into naïve forests (those with no prior history of MPB) of lodgepole pine and jack pine (*P. banksiana*, a novel species for MPB) (Burke et al., 2017). While the size and extent of the recent outbreak was far outside the historic norm, outbreaks of MPB are not unusual and have likely occurred for millennia. Selection by MPB during outbreaks, as well as persistent low-level activity during non-outbreak periods, are believed to have been a major force shaping constitutive and induced defenses in host pines (Raffa and Berryman, 1987; Franceschi et al., 2005). MPB activity in naïve forests can be expected to exert especially rapid and strong selection for host resistance because of high levels of susceptibility. Indeed, naïve lodgepole and jack pine forests exhibit lower defenses to MPB attack than those with a co-evolutionary history with the beetle (Clark et al., 2010; Cudmore et al., 2010; Raffa et al., 2013, 2017; Burke et al., 2017).

We focused on two tree species that have suffered high mortality by MPB in the recent outbreak. One is a relatively naïve host, whitebark pine (*Pinus albicaulis*), and the other is a highly co-evolved host, lodgepole pine (*P. contorta*). Whitebark pine is a high elevation tree that is considered a keystone in western subalpine ecosystems of the United States and Canada (Tomback et al., 2016). Historically, outbreaks in whitebark pine appear to have been rare and limited in size (Logan et al., 2010). During warm periods, beetles sometimes moved upslope from lower elevation outbreaks (Bartos and Gibson, 1990) where they killed some whitebark pine, but either did not reproduce successfully due to winter mortality, or completed only one or a few generations before the return of cold conditions once again limited them to lower elevations (Logan et al., 2010). The recent outbreak in whitebark pine has been extensive and has been driven by chronic warm temperatures that allowed the beetle to move into the subalpine and to persist there for an extended period (Buotte et al., 2016, 2017). With climate change, the presence of MPB in high elevation whitebark pine forests is expected to be persistent rather than occasional (Buotte et al., 2016, 2017). Whitebark pine exhibits many of the characteristics of a naïve host, including lower levels of defense chemicals and resin (Raffa et al., 2013, 2017). Reduced snow packs may also result in greater drought stress that may increase susceptibility (Larson and Kipfmueller, 2012). Outbreaks in this tree have been devastating in some areas, including the Greater Yellowstone Area, contributing to the recommendation that it be listed as an endangered species (United States Fish, and Wildlife Service [USFWS], 2011).

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The second species studied was lodgepole pine, a co-evolved host that has experienced repeated extensive outbreaks in much of its range, likely over a long evolutionary period. Vigorous lodgepole pine typically exhibits strong constitutive and inducible defensive responses to beetle attack (Burke et al., 2017; Raffa et al., 2017). Outbreaks of MPB in lodgepole pine are considered natural disturbances that, much like fire, help maintain lodgepole pine forests by periodically regenerating new stands free of many diseases, initiating nutrient cycling, and stimulating regeneration, understory productivity, and supporting biodiversity (Dordel et al., 2008; Diskin et al., 2011; Pec et al., 2015).

Our objective in this study was to investigate whether whitebark and lodgepole pine growing in a mixed high elevation stand that survived the outbreak are genetically distinct. If so, this may indicate an increased potential for these pines to persist in the face of the more frequent and extensive outbreaks predicted due to a changing climate. We would expect genetic change at loci underlying beetle resistance but not at a genome-wide scale. Without knowing the basis for resistance in survivors, we chose to use inter-simple sequence repeats (ISSRs) to develop genetic profiles for whitebark and lodgepole pine. ISSRs target highly variable sequences within microsatellite regions (Parasharami and Thengane, 2012). Because ISSR markers can be used to detect high levels of polymorphism and are highly reproducible, they provide a powerful approach for comparing genetic diversity between individuals as well as within and among populations of plants including pines (Mehes et al., 2007; Parasharami and Thengane, 2012; Lucas-Borja et al., 2016). In many studies, ISSR profiles have been useful in marker assisted selection when particular markers were associated with particular traits (REFS). In our screens, we looked for patterns that indicted differences between survivors and susceptible trees.

Materials and Methods

Site Description

This study was conducted at Vipond Park, a high-elevation plateau supporting a patchwork of grassland and open forest stands located on the Beaverhead National Forest, Montana, United States (2,501 m elevation, 45.6974°N, 112.9106°W). The site is relatively xeric with an understory of sagebrush and a diverse mixture of annual and perennial forbs. Vipond Park was chosen to take advantage of the high mortality to pines that occurred there during a recent high elevation outbreak of MPB (2009–2013) when approximately 93 and 75% of mature *P. albicaulis* and *P. contorta*, respectively, were killed. The relatively flat topography of the plateau combined with its location at the transition zone between lodgepole and whitebark pine-dominated forests allowed us to study the effects of MPB selection on more than one pine species growing under the same conditions and experiencing the same level of beetle pressure. Although *P. contorta* existed at lower numbers than *P. albicaulis* at the site, they were abundant enough to allow sufficient sampling to make comparisons with whitebark pine. Additionally, white pine blister rust infection incidence and severity were very low reducing the potential for the presence of the disease to influence the choice of individual host trees by the beetle (Six and Adams, 2007).

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Transects

Transects were established in 2015 (*P. albicaulis*) and 2016 (*P. contorta*). These were variable length belt transects 2 m in width that started on the edge of a stand and then followed a randomly chosen bearing until another edge was reached at which point a new bearing was adopted to establish a new transect in the same or an adjacent stand. This process was continued until the desired number of trees per species per treatment were measured. When trees occurred in clumps (resulting from seed caching by Clark's Nutcrackers), we restricted measurements and samples to one tree per clump to avoiding sampling trees potentially originating from the same cone/parent.

Determination of the Diameter Distribution of Mountain Pine Beetle-Killed Pines

In initial transects, the diameter at breast height (DBH, 1.4 m above the soil line) of 100 *P. albicaulis* and 45 *P. contorta* killed by MPB were measured to estimate the diameter distribution of MPB-killed trees for each species. This distribution was used to inform our sampling of "survivors" (mature trees that survived the outbreak) so that a similar distribution was achieved, and to determine the diameter below which trees were not attacked.

Collection of Samples for Genetic Analysis

In 2015, transects were established as previously described. Thirty survivor *P. albicaulis* with diameters representative of the diameter distribution of MPB-killed *P. albicaulis* were located on the transects. For each tree, DBH was measured and each was rated for white pine blister rust infection severity using the method of Six and Newcomb (2005). Then, approximately 30 current-year needles were collected and placed in a small plastic bag that was sealed and placed on ice in a cooler. In the lab, needles were placed into silica gel for drying and preservation. In 2016, this procedure was repeated for *P. contorta* (n = 20) (except for rust rating) in the same stands sampled the previous year.

The smallest diameters of *P. albicaulis* and *P. contorta* killed by MPB were 12 and 18 cm, respectively. Because beetle-killed trees did not yield DNA, we used this information to choose a second set of living trees for sampling of each species we designated as the "general population." These trees were expected to approximate the genetic structure of the population of each tree species at the site without beetle selection and so should contain a mix of survivor and "susceptible" genotypes. If our hypothesis was correct that survivors were genetically distinct from beetle-susceptible trees, then we expected only a few general population trees would have genotypes matching those of survivors (roughly reflecting the proportion of mature survivors to mature MPB-killed trees at the site). To sample general population trees, we established similar transects as before, but collected needles from trees between 9–11 and 14–17 cm DBH for *P. albicaulis* (n = 36) and *P. contorta* (n = 20), respectively.

DNA Extraction and Amplification

Needles (3–5) from each sample were ground to a fine powder in liquid nitrogen using a mortar and pestle. DNA was then isolated from each sample using a Qiagen DNeasy Plant Kit (Qiagen, Valencia, CA, United States) following the protocol provided by the manufacturer.

Five ISSR primers were chosen for use (Table 1). Not all primers worked equally well for both species of trees. Therefore, we chose three primers for use with *P. albicaulis* and four for *P. contorta*. Two primers overlapped in use for both trees (Table 1).

TABLE 1

(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-t001.jpg)
TABLE 1. Primers used for ISSR amplification.

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For amplification we used a 25 μl reaction mixture consisting of 12.5 μl Promega Master Mix (Promega, Madison, WI, United States), 2.5 μl RNA-free water, 8 μl of 0.5 M primer and 2 μl of DNA template. Reactions were run individually with one of the five ISSR primers. PCR was conducted with one cycle denaturation at 95°C for 5 min, followed by 42 cycles of denaturation at 95°C for 1.3 min, annealing at 47°C for 2 min, and extension at 72°C for 1 min. A final cycle was conducted at 72°C for 1 min and final products were held at 6°C (Parasharami and Thengane, 2012).

PCR products were visualized in a 1% agarose gel prepared using 1× tris borate buffer (TBE) to which 2 μl ethidium bromide per 100 ml gel was added. A 100 bp ladder (Promega, Valencia, CA, United States) was placed in the first lane of each gel to provide a reference for scoring bands. Amplified DNA was loaded into the remaining lanes with bromophenol blue as a running dye. Each gel was run with 1× TBE as a running buffer at 70 mA until the dye moved 3/4 of the length of the gel. Gel images were captured using a UV table. Any sample that gave ambiguous results (no, faint, or smeared bands) was repeated. Approximately 20% of samples were rerun and compared to check for consistency in results. Only samples exhibiting clear bands were included in the final analysis. Bands were scored manually.

Data Analysis

Diameter Distributions

A two-sample *t*-test was used to compare mean diameters among groups (survivor, general population, and beetle-killed) using Statistix 7 (Analytical Software, Tallahassee, FL, United States).

Genetic Analysis

Bands were scored as present (1) or absent (0) to develop a binary matrix combining data for all primers by tree species. The matrices were analyzed in Popgene v. 1.32 (Yeh et al., 1997) (assuming each group was in Hardy-Weinberg equilibrium) to calculate percent polymorphism, the Shannon information index (I), Nei's gene diversity index (h), total genetic diversity (H_T), genetic diversity within groups (survivor, general population) (H_S), and evidence for deviations from neutrality (selection) with an overall Ewens–Watterson test for neutrality. Population genetic structure was investigated using STRUCTURE v. 2.3 (Pritchard et al., 2000). The *admixture* model was used with a 10,000 burn-in period and 10,000 Markov Chain Monte Carlo replications. Twenty runs were performed with each value from 1 to 10 to estimate the optimal number of clusters (K) using the ΔK statistic (Evanno et al., 2005).

For each tree species, we examined genetic variation between groups using analysis of molecular variation (AMOVA) in GenAlEx 6.5 (Peakall and Smouse, 2006). We then conducted a principle coordinates analysis (PCoA) in GenAlEx based on genetic distances between individual trees in the two groups for each species of tree. Genetic distance matrices were developed for each tree species in the *Restml* program and then imported into *Neighbor* in PHYLIP 3.67 (Felsenstein, 2005) to produce an unweighted neighbor-joining tree. The tree was visualized using TreeView 1.6.6 (Page, 1996).

Results

Diameter Distributions and Blister Rust Infection Severity

The mean, median, and range of diameters of beetle-killed and survivor *P. albicaulis* were similar (Table 2). The mean diameter was not significantly different between survivor and beetle-killed trees, while the diameter of general population trees, as expected, differed significantly from both groups (Table 2). The same was true for *P. contorta* (Table 2). Similarly, mean diameters of MPB-killed and survivor *P. albicaulis* and *P. contorta* did not differ from one another. However, the minimum size of tree attacked by the beetle differed by tree species resulting in the choice of different diameter distributions for sampling general population trees (Table 2). Blister rust infection severity was overall very low at the site, but significantly lower in survivors (mean = 1.3, *SD* = 1.8) than in general population trees (mean = 1.7, *SD* = 2.4; *F* = 1.63, *df* = 65, *P* = 0.013; potential range 0–18).

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TABLE 2

(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-t002.jpg)
TABLE 2. Summary statistics for diameter breast height (cm) of *Pinus albicaulis* and *P. contorta* by group.

Genetic Analyses

Pinus albicaulis

Three primers (17899A, HB12, and UBC807) resolved well for *P. albicaulis* and were used for ISSR analysis. A total of 28 loci (bands) were resolved using the three primers (Table 3). Mean percent band polymorphism (BP) for all primers for all trees (general population and survivors) combined was 96.4% and this value was similar to the BP for each group individually. The Shannon information index and Nei's gene diversity was lower in general population trees compared with survivors (Table 2). Nei's unbiased measure of genetic identity between the survivor and general population trees was 95% while genetic distance was a corresponding 5%.

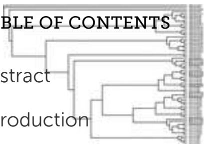
TABLE 3

(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-t003.jpg)
TABLE 3. Percent band polymorphism (BP), number of observed (N_a) and effective (N_e) alleles, Shannon's Information Index (*I*), Nei's gene diversity (*h*), and diversity between (H_T) and within groups (H_S), presented by tree species and group.

H_T, the total genetic diversity between the two study groups, was 0.26, and the diversity within groups, H_S, was 0.24. Seven of 28 loci (25%) exhibited significant differences between observed and expected frequencies of bands between the two groups (data not shown). However, no bands were unique to either group. The Ewens–Watterson test for neutrality detected only one marginally non-neutral locus. AMOVA indicated 87% of the variation exhibited existed within groups and 13% existed between groups.

The neighbor-joining tree resolved most general population trees together in the basal clades while one major terminal clade contained all survivor trees as well as eleven general population trees that were distributed throughout the clade (Figure 1). The results of Bayesian clustering using STRUCTURE indicated that the optimal *K*-value was 3 with the general population dominated by one cluster (red, Figure 2) and survivors dominated by the other two (blue and green, Figure 2). The eleven general population trees that clustered with survivor trees in the neighbor-joining tree exhibited predominantly blue and green profiles in the STRUCTURE bar graph (shown with asterisks) indicating similarity to survivors (Figure 2). In the PCoA, the first two principle coordinates explained a total of 33% of the variation associated with the two groups. Adding the third, 43.55% was explained. In general, the eleven general population trees that clustered with survivors in the neighbor-joining tree resolved separate from other general population trees and with survivors in the PCoA (Figure 3).

FIGURE 1



(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-g001.jpg)
FIGURE 1. Neighbor-joining tree from ISSR data for *Pinus albicaulis*. General = general population trees (with no *Dendroctonus ponderosae* selection). Survive = mature trees surviving *D. ponderosae* outbreak. Trees in boxes correspond to trees with arrows in Figure 2 and in ellipses in Figure 3.

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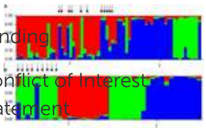
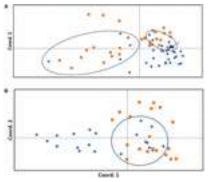
FIGURE 2



(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-g002.jpg)
FIGURE 2. Results of Bayesian clustering using STRUCTURE. Individual trees are represented by vertical bars. Colored segments represent the tree's estimated proportion similarity to each of the three clusters (red, blue, and green) optimally defined by STRUCTURE. **(A)** *Pinus albicaulis*. Arrows denote general population trees that resolved with survivors in neighbor-joining tree in Figure 1. **(B)**. *Pinus contorta*. 1 = general population trees. 2 = survivor trees.

FIGURE 3



(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-g003.jpg)
FIGURE 3. Principle coordinates analysis of general (blue diamonds) and survivor (orange squares) trees. **(A)** *Pinus albicaulis*. The first and second coordinates explain 19.29 and 13.67% of the variation among trees, respectively (total 33%). **(B)** *Pinus contorta*. The first and second coordinates explain 10.98 and 10.55% of the variation among trees, respectively (total 21.5%). Ellipses surround general population trees that clustered with survivors in the neighbor-joining tree (Figure 1 for *P. albicaulis*, Figure 4 for *P. contorta*) and correspond to trees marked with an arrow in the STRUCTURE analysis (in this figure). Arrow indicates one general population tree within the ellipse that did not cluster with survivors in the neighbor-joining tree.

Pinus contorta

Four primers resolved well for this species (17899A, UBC807, UBC901, and UBC811). Using these primers, we were able to resolve a total of 85 bands. The mean percent BP across all primers and groups was 98.82. This was considerably higher than BP for the general population (89.4%) and survivor (88.2%) trees (Table 2). The mean number of effective alleles was slightly lower than the mean number of observed alleles. Shannon's information index was similar within and across groups while Nei's gene diversity was lowest in survivors and highest for both groups combined (Table 2). Nei's unbiased genetic identity and diversity between the two groups was 93 and 7%, respectively.

H_T was 0.26 and H_S was 0.25, similar to values for whitebark pine. Allele frequencies were significantly different between survivors and general population trees at 12 of 85 loci (14%) (Table 3). No bands were unique to either group. The Ewan–Watterson test for neutrality indicated that six loci in the general population and nine loci in the survivors were outside the 95% CI indicating non-neutrality. All had positive *F*-values greater than the upper bound indicating a potential for directional selection. AMOVA indicated that 89% of variation occurred within groups while 11% occurred between groups.

The neighbor-joining tree partitioned general population and survivor trees into several clades (Figure 4). Most (55%) general population trees resolved in one clade. The remainder resolved into two clades interspersed with survivors (Figure 4). The general population trees that resolved with survivors in the neighbor-joining tree shared clusters with survivor trees in the STRUCTURE analysis (Figure 2) and also partitioned with survivor trees in the PCoA (Figure 3). The first two principle coordinates in the PCoA explained 21.5% of the variation between the two groups. Adding the third component explained 31%.

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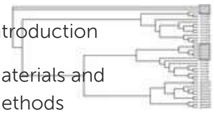
FIGURE 4



(https://www.frontiersin.org/files/Articles/382338/fpls-09-00993-HTML/image_m/fpls-09-00993-g004.jpg)
FIGURE 4. Neighbor-joining tree from ISSR data for *Pinus contorta*. General = general population trees (with no *Dendroctonus ponderosae* selection). Survive = mature trees surviving *D. ponderosae* outbreak. Trees in boxes correspond to trees with arrows in Figure 2 and in ellipses in Figure 3.

Discussion

Knowledge of the effects of bark beetle outbreaks on host tree population genetic structure and resistance to attack will be increasingly valuable as climate change drives more frequent outbreaks and facilitates the movement of beetle species into naïve forests. Outbreaks of MPB seldom kill all mature trees despite high beetle numbers during population peaks. Our results suggest that surviving trees possess a wealth of information that can be used to inform our understanding of the genetic and phenotypic bases for resistance and to develop management approaches that support forest adaptation.

We found that surviving mature trees in a high elevation forest of whitebark and lodgepole pine were genetically distinct from “general population” trees that were assumed to represent the genetic structure of the population pre-outbreak and without selection by the beetle. In line with our hypothesis, a low percentage (<10%) of “survivor” genotypes were identified within the general population. The proportion of these survivors roughly mirrored the proportion of mature trees that survived the outbreak at Vipond Park. The neighbor-joining tree, the PCoA and the STRUCTURE analyses each indicated strong differentiation between survivors and “susceptible” individuals and identified the same trees as survivors within the general population. In the STRUCTURE analysis for both whitebark and lodgepole pine, susceptible trees belonged to one cluster while survivor trees belonged to two other clusters. This separation can also be seen in the PCoA. Further research will be needed to determine whether the patterns we detected are indeed indicative of resistance, and if so, whether there are multiple or overlapping factors that account for survivorship.

We found surprisingly high levels of differentiation between survivor and general population trees in both species of pine. For whitebark pine, Nei’s genetic distance between survivor and general population whitebark pines was 5%, a value that would indicate moderate differentiation if these comparisons had been made between tree populations. Likewise, AMOVA indicated 13% of the genetic variation present existed between groups. Considering that the trees in this analysis were not from different populations, but rather grew intermixed at the same site, these values seem strikingly high. Likewise, for lodgepole pine, Nei’s genetic distance was 7%, and AMOVA indicated 11% of variation occurred between the groups.

These results indicate the presence of genetically based resistance in both pine species and that trees with resistant genotypes are not selected for attack. It has been thought that once MPB achieve high population levels during outbreaks, the selection of individual trees based on tree-produced compounds and condition becomes swamped by high levels of aggregation pheromone production and competition for increasingly rare hosts (Safranyik and Carroll, 2006). However, our results suggest that beetles remain selective even as outbreaks peak and collapse.

We chose ISSR profiling as a first step to determine whether survivors were different than trees chosen by MPB for colonization. This PCR-based method detects high levels of polymorphism, is highly reproducible, and allows the screening of a large number of trees relatively rapidly and economically. Unfortunately, this method cannot tell us why survivors are different, only that they are. Further study will be needed to further investigate whether survivors are indeed highly resistant and, if so, to determine the actual basis behind resistance. Ongoing studies are investigating correlations among genetic profiles of survivor and "susceptible" trees with phenotypic traits including defensive chemistry and growth rates in relation to climate. Genomic approaches will also be extremely useful to elucidate the basis of resistance.

This study corroborated the findings of other studies that found that MPB colonizes smaller diameter whitebark pine than lodgepole pine during outbreaks (Dooley et al., 2015). The mortality of younger whitebark pine trees indicates a more severe impact of MPB outbreaks on whitebark pine forests, at least in the short term, because advanced regeneration is killed along with large trees. However, the loss of large and mid-diameter trees may serve to open areas for nutcracker caching of seeds from the remaining resistant trees, potentially increasing the frequency of those genotypes and phenotypes at the site and within the larger population.

In a previous study, Six and Adams (2007) found that as infection severity increased so did the likelihood of attack by the beetle. However, while we found that white pine blister rust infection severity was significantly higher in general population trees than survivors, the mean level of infection severity at the site was very low and the size effect between means for survivors and general population trees was very small. Therefore, we feel it is unlikely blister rust played a significant role influencing beetle dynamics at the study site.

A caution is in order in interpreting our results. We were unable to amplify DNA from MPB-killed trees which forced us to use smaller diameter "general population" trees as a substitution for "susceptible" trees. These trees were mature reproductive trees and only slightly smaller than trees selected by the beetle for colonization; however, some or all may constitute a cohort that regenerated under different environmental conditions resulting in a genetic structure unrepresentative of the larger trees that were available for selection by the beetle. However, the proportional distribution of survivor and "susceptible" trees in the neighbor-joining trees, PCoAs and STRUCTURE analyses indicate that the general population samples were likely appropriate proxies.

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With climate change supporting the invasion of aggressive bark beetles into naïve forests, and predictions of more frequent and severe outbreaks, it is increasingly important to understand the capacity of trees to adapt and persist (Millar et al., 2007; Ramsfield et al., 2016). While the massive mortality of pines in western North America in recent years is cause for concern, we should also look at these hard-hit forests as opportunities to learn. In almost all cases, affected forests are not completely dead–they retain many living large diameter trees. If these trees are genetically different than those selected and killed by the beetles as our study suggests, these trees may aid in *in situ* adaptation and persistence. They may also be key to developing management and trajectories that allow for forest adaptation. For example, retaining surviving trees as a primary seed source, rather than removing them during salvage operations could support *in situ* adaptation. In contrast, the effects of natural selection in these stands could be instantly negated by clearcutting or replanting with general seed stock.

Supporting forest adaptation is critical in this time of rapid change (Millar et al., 2007). Given the great expanses of forest that are being affected by climate change and the fact that most will need to adapt *in situ*, it is imperative we begin to move past structural approaches to consider the genetic capacity of forest trees to adapt. The high degree of standing genetic variation found in most forest trees indicates many will have considerable ability to adapt. We need to be cognizant of adaptation that is occurring so that our management approaches act to support rather than hinder natural selection for traits needed under future conditions.

Author Contributions

DS conceived of the project, participated in field work, conducted data analysis, and wrote the manuscript. CV conducted lab work on whitebark pine and participated in field work and data analysis. MC conducted field and lab work on lodgepole pine and contributed to data analysis.

Funding

This study was partially supported by the U.S. Geological Survey under Cooperative Agreement No. G16AC00372 awarded to DS, an NSF EPSCoR Institute on Ecosystems grant to CV, and a Whitman College Summer Internship Grant to MC.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Keywords: *Pinus albicaulis*, *Pinus contorta*, *Dendroctonus ponderosae*, whitebark pine, climate adaptation, climate change, natural selection

Citation: Six DL, Vergobbi C and Cutter M (2018) Are Survivors Different? Genetic-Based Selection of Trees by Mountain Pine Beetle During a Climate Change-Driven Outbreak in a High-Elevation Pine Forest. *Front. Plant Sci.* 9:993. doi: 10.3389/fpls.2018.00993

Received: 03 April 2018; **Accepted:** 19 June 2018;
Published: 23 July 2018.

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