United States
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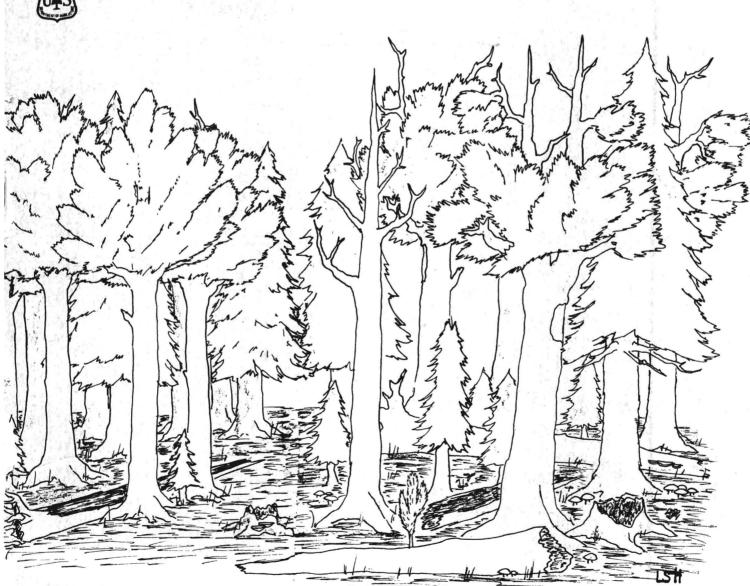
Rocky Mountain Forest and Range Experiment Station

Fort Collins, Colorado 80526

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Old-Growth Forests in the Southwest and Rocky Mountain Regions Proceedings of a Workshop

March 9-13, 1992 Portal, Arizona



Mature forest

Old growth

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Old-Growth Forests: What Do We Know About Their Ecology and Management in the Southwest and Rocky Mountain Regions?¹

Merill R. Kaufmann, W. H. Moir, and W. W. Covington²

This paper reviews the science and management of old-growth forests and summarizes discussions among 30 participants at a workshop in Portal, Arizona, March 9-13, 1992.

Concepts of old-growth forests -- the perceptions, values, definitions, characteristic features, ecological functions, and landscape importance -- vary widely. Because concepts are complex, scientists, resource managers, and the public will continue to bring old growth into clearer focus as knowledge is gained. Regardless of the concepts chosen for viewing old growth, on an ecological basis old-growth forests represent a stage in forest development characterized by certain structural, functional, and compositional features.

Managers are concerned with how much old growth exists, where it is, and what condition it is in. Improved inventory procedures are needed, including both remote-sensing technology and conventional on-the-ground procedures. Where will tomorrow's old growth be found, and how soon will younger stands attain old-growth conditions? Pathways of forest succession into old growth are poorly known for most forest types. We need better knowledge about how disturbances such as fire, insects, forest diseases, exotic organisms, pollution, and changing climate affect old growth and forest succession.

Allocation is another problem for planners. How much old growth is enough? How many stands should be old growth at any given time, what are the sizes and shapes of the stands, and how should they be distributed over various forest habitat types? How should old-growth stands be connected by forest corridors, and how are their functions modified by their setting? These are difficult but researchable questions. Lacking clear answers to these questions, should managers find clues from pre-European settlement forests? Is it reasonable to attempt to restore forests to their natural conditions? Or have changes since settlement precluded returning to earlier conditions?

In this paper, we review our knowledge of the influence old-growth stands on biogeochemical cycles and the roles of wildlife, decomposer organisms, cryptozoans of logs and snags, and other kinds of "hidden diversity." To what extent are the legacy of old trees and other genetic reserves in old-growth forests carried into the future? We know little about how present old-growth influences the development of future forest generations.

We conclude by looking at some tools for old-growth management. How can managers use fire or silviculture to assure future old-growth supplies, while at the same time meeting present and future extractive demands? Can younger stands be "treated" to hasten their development into old growth, or can existing old growth be altered without seriously compromising old-growth value?

INTRODUCTION

This volume of papers, given at a workshop on old-growth forests, represents much of what is known about old-growth forests of the central and southern Rocky Mountains and Southwest. This summary paper reviews the current state of knowledge available to

guide forest management and presents the most critical research needs. It is not our intent in this summary article to review the literature. Rather, we refer to specific papers in this volume for relevant literature on individual topics.

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Old-growth forests in the central and southern Rocky Mountains and Southwest have important biological and social values. Certain ecological characteristics of old-growth forests are unique, and because of these features such forests provide a necessary component in the forest landscape. Important biological values of old growth include habitat for a variety of animal and plant species, biodiversity and pools of genetic resources, and long-term biological records of climate. Old-growth forests also are valued for supplying economically important forest products, recreational experiences, and cultural (spiritual) heritage. Of these, perhaps the most

¹ Summary paper of the Old-Growth Forests in the Rocky Mountains and Southwest Conference (Portal, AZ, March 9-13, 1992).

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compelling mandate for old-growth conservation is its role as habitat for organisms which, over evolutionary time, have become dependent upon old-growth conditions.

Many geographic areas in the Rocky Mountains and Southwest have experienced a sharp decline in virgin forest in the landscape, and in some forest types, old-growth forest has been reduced to a fraction of the amount existing before settlement. Nonetheless, there is a tremendous opportunity for retaining or enhancing biological features unique to old-growth ecosystems. In Europe and Asia, in the rainforests of Brazil, and in the eastern United States, many forest areas have been either exploited through intensive and often repeated harvest or impacted by deterioration in air and soil quality to the point that the existence of old-growth forests in a historical condition is nearly impossible. That point has not yet been reached in the central and southern Rocky Mountains and Southwest, but threats to old-growth forests in the landscape are real and substantial.

Perceptions of Old Growth

An issue surfacing repeatedly at the workshop and elsewhere is the application of the term "old growth." The subjective "feel" of what constitutes high quality old-growth forests varies tremendously among individuals and may differ from scientifically determined ecological conditions that characterize old growth. It is important to recognize these differences because they represent the range of expectations placed upon forest lands by the various viewers and users.

Consider three contrasting forest scenarios discussed at this conference. These scenarios are described to illustrate that the issue of old-growth quality is very complex. First is a mature Engelmann spruce/subalpine fir ecosystem found low on a north-facing slope near the riparian zone (Fig. 1). This forest has multiple canopy layers, a number of large trees (some of which are in poor health), a number of snags and large down logs, and a few very old stumps. Second is a ponderosa pine forest having relatively few very large, old trees intermixed with many smaller trees in several additional canopy layers (Fig. 2). Large and small down logs occur, but there are no signs of prior harvest or other silvicultural intervention. Third is a small stand of very old limber pine trees on a rocky outcropping with little soil (Fig. 3). The trees are only a few meters tall and are widely spaced.

These stands may be viewed very differently by various individuals. The spruce/fir stand may be rated by most viewers as the highest quality old-growth forest of the three described because of the complex

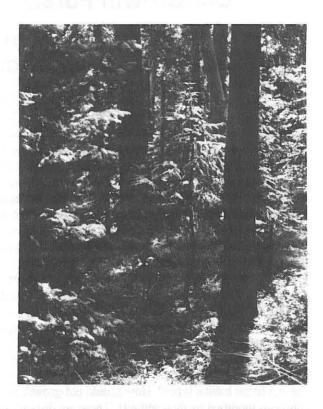


Figure 1. Mature Engelmann spruce-subalpine fir stand in the San Juan Mountains, Colorado.

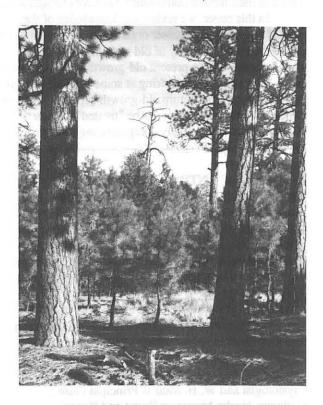


Figure 2. Old ponderosa pine with saplings filling in a small meadow. From the Monument Canyon Research Natural Area, New Mexico.



Figure 3. Limber pine trees 1,500 years old near Red River, New Mexico (photo by Ann Lynch).

stand structure, numerous big trees, and the large amount of dead and down material. However, a close examination may reveal that the oldest trees are only 200 years old and hardly approach the maximum age or size supported on that site. Furthermore, the dead and down material may have resulted from normal thinning as the stand matured and not from the decline of the oldest trees in the stand. Thus from a stand development view, the stand may barely qualify as old growth at all. Such a stand may satisfy a viewer's perception that "large" means "old," and it may well meet wildlife needs for a diverse stand structure, but ecologically the stand may not even be old growth.

The ponderosa pine stand has majestic old trees and no signs of disturbance. Many viewers might judge this stand to be ideal old growth because of the relatively high tree density and multiple canopy layers plus the presence of large old trees and dead and down logs. Yet this stand may be a far departure from the classic old-growth ponderosa pine forest of pre-European settlement times, because fire suppression has allowed the development of several younger age classes of trees and the accumulation of dead material on the forest floor (Covington and Moore, this volume).

The limber pine stand meets few viewers' expectations for an old-growth forest. The trees are

very small and widely spaced, giving the stand little "feel" that it is old growth. Yet these trees may exceed 1,500 years in age and the stand is truly an ancient forest (Swetnam, this volume).

Researchers and managers of all disciplines interested in old-growth forest structure and function, as well as individuals and groups attaching significance to old forests perceived to be old growth, must strive to adhere to scientifically credible terms and concepts. Doing so will help reduce conflicts over the many and often conflicting goals that old forests are expected to serve. In this regard, it is important that hidden agendas be addressed clearly and openly. While issues such as maintaining roadless areas, providing habitat for threatened or endangered species, sustaining the economic viability of a community through timber harvest, and honoring the cultural heritage of forests are very important, it is also important to apply those issues to old-growth forests only when the issues are appropriately linked specifically to the old-growth condition. By being clear about definitions and goals, it may be possible to limit conflict and misunderstandings and better resolve resource management problems, especially when forest lands are expected to meet goals that may not involve the requirement for true old-growth conditions.

DEFINING OLD GROWTH

The process of defining old-growth forests has been difficult because of the range of issues related to the old-growth condition. Because of this confusion, no single value has been universally accepted as the defining characteristic of old-growth forests. For example, in silviculture, forest ecology, and ecophysiology, the successional pathways and structural and functional aspects of stand development may be critical in definitions of old growth (Moir, and Kaufmann, this volume). In dendrochronology, the presence of very old trees may be the most important feature (Swetnam, this volume). For animal habitat, stand structure may be highly important (Reynolds, this volume), and for planning purposes, an easily applied forest structure/composition/age classification may be necessary (Mehl, and Lowry, this volume). For spiritual value, the presence of large trees and the lack of obvious human disturbance may be critical (Kramer, this volume).

Definition versus Characterization

In some cases the term "old growth" has been used in ways that distort or at least blur the ecological basis for distinguishing old growth from other stages of

forest development. Thus stands having features similar to those of certain old-growth forests, including multiple canopy layers with mature trees and considerable amounts of dead and down material, may be incorrectly termed old growth because they lack *old* trees. Stands having large trees that are not old may be perceived as old-growth stands even when the trees have not reached an old age for that site. Alternately, stands having old trees that are not large may not be perceived as old growth when they really are.

Another difficulty in characterizing "old growth" stems from applying strictly structural concepts in perceiving old-growth forests, when functional concepts also are important (Kaufmann, this volume). Functionally, old-growth ecosystems are characterized by having a component ("cohort") of old trees that have a biochemistry of secondary metabolic products, some of which may provide high resistance to insects and disease. Relative to younger trees, the oldest trees have approached their maximum size and have nearly ceased height growth, and the tree crowns may be in various stages of decline. On average, the rate of production of new biomass is offset by mortality and respiration, and net productivity of the ecosystem is near zero. These functional aspects provide important additional constraints as to which forest stands qualify for the old-growth designation and which do not.

A final difficulty in old-growth characterization is deciding the extent to which old growth should resemble primeval or presettlement conditions. Livestock grazing, fire suppression, and logging have brought about substantial changes in most western forests, so much so that current forest conditions may be decidedly "unnatural" from an evolutionary point of view. Where this is the case, certain species dependent upon presettlement ecosystem structures and functions may be at risk. Thus from a biological conservation perspective, contemporary "old growth" conditions may be inadequate habitat in many western forest types. Under these circumstances, ecological restoration treatments (e.g., elimination of exotic species, reintroduction of native species, prescribed burning, thinning, snag or down tree creation) may well be necessary for providing critical habitat (Covington and Moore, this volume).

As a step toward better understanding of old-growth ecology and management, scientists in the U. S. Forest Service and in universities and other agencies have gone to considerable effort in recent years to develop a general definition for old-growth forests. Given some of the confusion regarding how the term "old growth" is used, it seems worthwhile to present the definition developed by the U. S. Forest

Service and approved by the Chief of the Forest Service, and to discuss how it applies specifically in the Rocky Mountains and Southwest.

Agency Generic Definition

The Generic Definition (USDA Forest Service 1990) is as follows:

Old-growth forests are ecosystems distinguished by old trees and related structural features.

Old-growth encompasses the later stages of stand development that typically differ from earlier stages in several ways including tree size; accumulations of large, dead, woody material; number of canopy layers; species composition; and ecosystem function.

Workshop attendees suggested that for certain forest types, most notably ponderosa pine that historically was influenced by frequent fire, this definition is somewhat restrictive, particularly regarding the accumulation of coarse woody debris, number of canopy layers, and species composition. The group suggested the following General Definition for Old-Growth Forests in the Central and Southern Rocky Mountains and Southwest:

Old-growth forests are ecosystems distinguished by old trees and related structural features. Old growth encompasses the later stages of stand development that typically differ from earlier stages in structure, composition, function, and other attributes. This definition is broad and workable for communication, but the definition does not permit us to recognize old-growth stands. For this we turn to structural characteristics, which in turn reflect functional ecosystem processes. The group suggested slight rewording of the old-growth description to make it more appropriate for the central and southern Rocky Mountains and Southwest. The reworded **Description** is:

Structural features that characterize old growth in the central and southern Rocky Mountains and Southwest vary widely according to forest type, climate, site conditions, and disturbance regime. Old growth is characteristically distinguished from younger growth by some but not necessarily all of the following attributes:

- · Large trees for species and site.
- Wide variation in tree sizes and spacing between trees.
- Relative to earlier stages, high accumulations of large, dead standing and fallen trees.
- Decay in the form of broken and deformed tops or bole and root rot.
- · Multiple canopy layers.
- · Canopy gaps and understory patchiness.

"Old" is not necessarily virgin or primeval.

Structure and function of an old-growth
ecosystem may be influenced by its stand size
and landscape position. Given sufficient time,
old growth can develop following human or
natural disturbances, such as logging or wildfire.

While there has been some concern expressed that old-growth forests in the Rocky Mountains and Southwest are different from those in the Pacific Northwest, the definition and description published in 1990 as slightly refined here are appropriate in both geographic regions if properly applied. For example, only some of the descriptive elements above may be appropriate. The accumulation of large amounts of dead and down material and multiple canopy layers may be significant characteristics of some forest types (e.g., old-growth spruce-fir). But in presettlement old-growth ponderosa pine stands, the frequency of fire contributed to open stands of large trees having little dead and down material and perhaps only one canopy layer (Covington and Moore, Harrington and Sackett, this volume). Similarly, very old limber or bristlecone pine trees may develop in highly stressful sites and reach only a few meters in total height, but for those sites the trees are large.

Variables in the Characterization of Old Growth

Missing from the old-growth definition and description above is any mention of specific tree age or size, or density of old trees in the stand. While initial attempts to inventory old-growth forests have required the development of preliminary quantitative descriptions for each forest type (Mehl, this volume), it is clear that certain features of old-growth stands vary depending on site productivity and geographic location. Within a forest type, old-growth stands may be found in a number of habitat types and across a wide range of physiographic settings (Robertson, this volume).

Thus the characteristics defining the old-growth condition, particularly those involving tree size, age,

stand density, canopy structure, and the accumulation of dead materials, may be very different among sites and habitat types within a forest type. This precludes a strict use of "minimum" characteristics in old-growth definitions when "old growth" is meant to include all forest stands meeting ecological criteria for this stage of forest development.

Two particularly pressing research needs are to determine how presettlement forest conditions varied among forest types, habitat types, and site conditions, and to clarify how the minimum criteria should vary accordingly. Such research requires an extensive field data base including samples from a matrix of site/habitat combinations. In the absence of such a data base and analysis, it is nearly impossible to determine the criteria to be used in the inventory and management of old-growth forests in the landscape without either excluding a number of true old-growth stands on poorer sites or including marginal old-growth stands on better sites. It may be possible, if the data base is large enough, to develop a classification model in the form of a key for old-growth conditions that accounts for variation in old-growth characteristics among habitat types and sites.

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OLD GROWTH QUALITY

Many of us have been conditioned to believe that stands of big trees are old growth, when biologically such stands may not be good examples of late developmental stages for the forest type in its specific site condition. Some of us believe that signs of human disturbance such as skid roads and stumps seriously weaken the quality of an old-growth stand, when from an ecological point of view such evidence of disturbance may have little to do with the structural and functional features characterizing old growth or its value as animal habitat. A recreationalist seeking time in a pristine forest, or an individual seeking spiritual value, may be disturbed by rotting stumps in an old-growth forest but may be satisfied by an unroaded and undisturbed mature forest not meeting old-growth criteria. Some people may view a pine forest having multiple canopy layers and many down logs as ideal old growth, while from an ecological view such forests reflect significant disturbance in the form of fire exclusion.

We propose that the approach to old-growth definition in the previous section is the most appropriate one in many cases because it is ecologically sound and it is useful in decision-making processes regarding the inventory and management of old-growth forests in the landscape. We recognize that other values also are important, and we suggest, in

keeping with earlier remarks in this paper, that other terminology or concepts be used when dealing with wildlife habitat, visual or spiritual issues, etc., that in some cases may not require old-growth conditions to be present.

Disturbance and the Issue of Quality

Evidence of prior disturbance may affect how observers view an old forest. Some old-growth stands may have survived many centuries with no human intervention and with little change in history of biotic or abiotic disturbance. The question of disturbance is not a simple one, however. Many stands have no evidence of prior silvicultural activities, but fire has been effectively removed as a natural process during most of this century, and in some cases insect or disease control treatments have been applied. Thus large areas of presumably undisturbed forest have, in fact, taken on a structure quite different from what might have existed had natural disturbance regimes not been interrupted.

Many ponderosa pine forests, for example, historically had fire return intervals of less than every decade. But since the beginning of this century, fires have been excluded almost completely, with the result that new age groups of trees and considerable amounts of dead material exist in stands that otherwise might have had the classic, park-like appearance with numerous grassy openings characteristic of presettlement times. Fire suppression has resulted in much higher numbers of trees per area and the loss of most openings. And when fires occur, they often are of such intensity that the entire plant community is replaced.

Ecologically, many forested areas that now exist should be considered disturbed by fire suppression even though no other signs of human disturbance are found. Little is known, however, about how various observers and users of forest lands view fire suppression and other signs of human disturbance (such as evidence of silvicultural activities) as impacts on the quality of old-growth forests.

OLD-GROWTH FORESTS IN THE LANDSCAPE

Landscape Issues

Old-growth forests historically constituted a significant component of the landscape mosaic, providing an array of features not found in forests at other developmental stages. Many very important questions are being asked about old-growth forests in the landscape. Some of these questions have been

addressed above, such as why old-growth forests are needed and how they are recognized. Numerous other issues emerge when Forest Plans are appealed or subject to revision or when the ecology of old-growth forests is considered:

- How much old growth is enough?
- How serious is the impact of various management practices upon fragmentation, and how is fragmentation measured?

- Are old-growth forests found more frequently in some plant associations than in others?
- How large should old-growth stands be, and how should they be buffered by mature forests or by corridors that connect to other old-growth patches? Are the concepts of corridors and distribution useful in a naturally fragmented landscape?
- What organisms do patches and corridors serve?
- How do different alternatives in Forest Plans affect biological diversity within patches and the overall landscape diversity?
- What were the structure, composition, and geographic/topographic forest patterns (which included old growth) during presettlement times?
- How has fire suppression (or other broad-scale changes) during the last century affected old-growth conditions for wildlife habitat, epicenters of insects or plant pathogens, or the propagation of large-scale disturbances?
- How are ecological processes different in old-growth forests compared with other stages of development?
- How can the transitions into and out of the old-growth state be evaluated?
- What is the role of old growth in the development of subsequent forests on a site?

It is noteworthy that the important management questions also are priority research questions.

Scientists and managers attending the workshop suggested that cooperation of researchers and managers is essential when dealing with landscape issues.

Because of the large scales of space and time that are relevant for landscape processes, it is necessary that science and management cooperate in making scientifically sound management decisions while being aware that experimentation to answer a number of landscape questions may not be practical. The most

likely contribution of science to management at a landscape scale will be the development of appropriate ecosystem models that can be used to assist managers with landscape issues.

Biodiversity

Old-growth forests are considered by scientists and managers to be an important component of biological diversity, or "biodiversity," which is the richness and distribution of different forms of life in an area. The contribution of old growth to biodiversity occurs at all spatial scales. In the landscape, old-growth stands provide structural and functional contrasts to younger forests. The number of old-growth forest stands and their sizes and arrangement in the land contribute to landscape diversity. Scientists need to test various measures of landscape diversity for usefulness to forest managers. A research problem is to relate measures of landscape diversity to how landscapes are functioning in terms of various treatments and outputs such as water yield, nutrient cycling, recreation visitor days, or wildlife population levels.

Old-growth forests may be the preferred habitat for certain microbes, fungi, bryophytes, and higher plants (Romme et al., this volume). They are known to be the preferred habitat for a number of vertebrate species, such as martens, flammulated owls (Reynolds, this volume), or animals requiring tree cavities for reproduction. Animal populations of species preferring old growth are limited not only by the size of old-growth stands, but also by the number and arrangement of stands in the landscape. However, research lags far behind the manager's need to know about minimum viable populations, as illustrated for example by the Mt. Graham red squirrel on the Coronado National Forest in Arizona.

Much of the diversity within old-growth forests is associated with the numerous detrital and other heterotrophic food webs (e.g., metabolism based upon respiration rather than upon photosynthesis). Old-growth stands are rich with fungi and other microorganisms (such as nitrogen-fixing bacteria associated with rotting wood). These in turn support myriads of cryptic (hidden) micro-arthropods and other invertebrates in intricate food webs. Many small mammals include fungi in their diet; furthermore, their fecal pellets may function as mycorrhizal inoculum or fertilizer for germinating seeds. Several carnivores, such as woodpeckers, plethodonid salamanders (Scott, this volume), certain kinds of hymenopterans (e.g., bees, ants, wasps), or roaming black bears cap these food webs. This diversity is more complex in

old-growth forests than in younger stands in part because of the numerous kinds and amounts of chemical energy accumulated in wood and litter. For example, decaying wood is an important microsite governing ectomycorrhizal activity in forest soils (Larsen et al., cited in Moir, this volume).

At the genetic level, old-growth forests may harbor genotypes of species adapted to later stages of forest development and thus different from their genetic cousins in younger forests. Considerably more work is needed, however, to elaborate upon this theme. Indeed, the difficulty facing forest managers and researchers is that so little is known about the requirements of most of the species in old-growth ecosystems. Although animals such as Northern goshawks or Mexican spotted owls may symbolize old-growth dependency, knowledge about the breadth of ecological and habitat tolerances is often lacking even for them.

Research also is needed on the manner in which the biodiversity of old-growth forests contributes to the functional health of forests that follow. This has important implications in residue management and other practices that provide a structural link between successive forest generations.

Ecophysiology of Old-Growth Trees and Stands

The behavior of old-growth forests with regard to the carbon, nutrient, and water resources is understood in a general sense, but many specific questions have not been answered. It is known that at the late developmental stage we refer to as old growth, the net productivity of the ecosystem approaches zero and may even become negative. This means that newly produced biomass is offset, on average, by heterotrophic respiration plus mortality of individual trees or tree parts such as foliage, branches, and roots. It is also believed that as trees age, they not only experience a decrease in productivity in the form of reduced leaf area and growth, but they also undergo certain changes in secondary product metabolism resulting in biochemical changes in plant composition that may be related to increased resistance to insect or disease attack.

Many of the details of these processes are not understood for each forest type, nor is it clear exactly how the ecophysiological characteristics of old trees can be used to judge when a mature stand reaches old-growth status or when an old-growth stand deteriorates to the point it no longer functions as an old-growth ecosystem. It seems clear, however, that a stand does not qualify for the old-growth status if none of the oldest trees have reached the conditions in which

general vigor is being lost and no structural and functional changes accompanying longevity and senescence processes are occurring.

It is also obvious that some conditions required for achieving old-growth status can occur in stands that have had prior silvicultural treatment (including harvest), and it may be possible to influence, through silvicultural intervention, the development and persistence of the old-growth condition. Recent analyses of the growth history of old lodgepole pine trees has shown that trees presently having low leaf area and approaching mortality grew more rapidly during their first 100 years, compared with neighbor trees of the same age, height, and bole volume but currently having high leaf area (Kaufmann, this volume). This suggests that trees growing rapidly early in the life of the stand became the first trees reaching old-growth status. The trees growing slower initially but surviving to old age now extend the time during which the old-growth status occurs.

How this applies to even-aged stands of other forest types or to uneven-aged conditions is not known. It seems reasonable, however, to suggest that manipulation of stands early in their development may have considerable influence over their old-growth characteristics, and careful treatments may improve the character and longevity of old-growth stands. This is discussed more below.

Forest Development and Synchrony of Old-Growth Characteristics

Forest community development is both a stochastic and a deterministic process. The incidence and intensity of stand-altering events such as fire, climatic fluctuations, windthrow, insect attack, disease outbreak, regeneration success, stress-induced mortality, and other biotic and abiotic variables are highly unpredictable. The developmental trajectory by which forest communities reach the old-growth condition may vary widely within forest types both within and across geographic regions. Consequently the desirable features of old-growth stands may not peak at the same time in different environments, and considerable latitude is required in classifying stands. This is why, in the old-growth description given earlier, only some of the descriptive characteristics can be expected to occur simultaneously. Furthermore, certain characteristics are not equally expressed for all forest types. For example, the accumulation of coarse woody debris and development of multiple canopy layers are important for old-growth spruce/fir forests, but perhaps the best examples of old-growth ponderosa pine would be the rare cases in which fire has continually limited

the accumulation of coarse woody debris and the development of younger age classes of trees.

Relatively little is known about the range of successional pathways that can lead to old growth, nor is much known about how the different paths affect the quality of the resultant old-growth stands. It is important to understand that the old-growth condition is temporary. While stand-replacing disturbances may be very infrequent in some locations, eventually they are likely to occur. Some of the highest-quality old-growth stands, such as the Engelmann spruce/subalpine fir old-growth forest in Bowen Gulch near Rocky Mountain National Park in Colorado, may have had no significant disturbance for many centuries, but such stands are the exception rather than the rule, and even for those stands there is no assurance that a major stand replacement disturbance will not happen in the near future.

Seral stands can acquire old-growth characteristics and can be classified as old growth. Seral stands are expected to be transient, provided conditions are appropriate for stand structure and composition to change. However, climax stands also are transient when considered at more comprehensive scales of space and time, and there is little reason to distinguish between seral and climax forest communities when evaluating the old-growth condition. The likelihood of more rapid loss of old-growth characteristics may be higher in some seral stands (e.g., aspen), however, and this may be a factor in determining the role of seral old-growth stands in landscape management.

In areas where low-intensity fires had been frequent before settlement, the absence of fire during most of this century has resulted in very different developmental trajectories for stands. From an ecological perspective, some old-growth characteristics may still have developed, but the forests represent a new kind of old-growth condition. The degree to which novel stand conditions might be classified as old growth depends on the role of functions or conditions such as biodiversity, ecosystem health, and stability. To answer this question correctly, information is needed both about the ecological impacts (especially on biodiversity) of the altered developmental trajectory and the willingness of old-growth forest users to accept a modified type of old-growth forest.

MANAGING OLD-GROWTH FORESTS

The Baseline of Comparison

The issue of whether or not to use management techniques to affect the amount and quality of

old-growth forests, and whether any intervention is permissible at all, must be evaluated against the changes that have already occurred in all forests since settlement by Europeans. All old-growth forests have been impacted by man, whether or not the effects are obvious. The most apparent impacts in the central and southern Rocky Mountains and the Southwest involve timber harvest in ponderosa pine, which has sharply reduced the acreage of old-growth forests, and fire exclusion, which has altered the structure of old-growth stands that historically had frequent low-intensity fires.

Other impacts also have occurred. For example, the pattern of old-growth forest distribution in the landscape has been changed dramatically since presettlement times, with much of the remaining old-growth forest now relegated to less accessible areas and perhaps to less-productive sites. The atmospheric concentration of CO₂ has increased 40 % since the mid-1800's, and this may have far-reaching effects on the development and stability of old-growth stands. And there have been order-of-magnitude increases in atmospheric deposition of certain chemicals containing nitrogen, sulfur, etc., into forest ecosystems.

Given the variety of past, present, and future impacts, an important question, in those situations where managing for old-growth qualities is appropriate, is the baseline of comparison. From a biodiversity standpoint, presettlement conditions may be the most desirable baseline, because those conditions represented the natural system in all its detail and complexity (Covington and Moore, this volume). Yet over the near term, presettlement conditions may be difficult to restore on any extensive basis, because of the major impacts timber harvest and human community development have had in forested areas. It may not even be possible to restore presettlement old-growth conditions on any spatial scale, because of the unknown impacts of increased CO2 in the atmosphere and increased atmospheric deposition of chemicals.

Thus the question of old-growth management and the issue of selecting an appropriate baseline requires increased knowledge about changes that have occurred since settlement impacts began and the degree to which present physical and chemical environments affect old growth and other ecosystems. These are difficult issues, and it is likely that old-growth management decisions often will have to be made with inadequate knowledge of the ecological and environmental consequences. It is important that all management decisions, and even the decision *not* to intervene with the normal ecosystem processes, be done with clear understanding of the scientific knowns and unknowns.

Silvicultural Treatment

It was suggested earlier that, given enough time, it is quite possible for old-growth conditions to develop in stands where prior human disturbance had occurred. For example, a subalpine forest may have old lodgepole pine trees in various stages of decline, with a significant stand component of Engelmann spruce and subalpine fir that has developed after harvest near the turn of the century. Such stands may have a complex structure and considerable amounts of coarse woody debris, but also skid roads and very old stumps. The oldest trees in these stands, chiefly lodgepole pine, were left during the earlier harvest, and presently they help the stand meet some old-growth criteria.

While for certain uses past or future disturbance is not considered acceptable, there may be important situations in which silvicultural intervention is highly desirable to improve the quantity, quality, distribution, or duration of old-growth forests in the landscape. An example is ponderosa pine along the Front Range in Colorado, where old-growth stands are scarce. It may be possible and desirable to enter such stands and alter the structure, age distribution, and amount of coarse woody debris to favor the development of old-growth features. Such an effort could be part of a program to restore some of the desirable qualities of the ecosystem (biodiversity, etc.) that had existed before settlement, harvest, and fire suppression so drastically altered the landscape.

Reintroducing Fire

It is clear from discussions above that fire suppression since settlement of the West has had major effects on forests. It was the conclusion of the workshop participants that fire be used in forest ecosystem management because historically it has been a very important ecological process in most, if not all, forest types in the central and southern Rocky Mountains and Southwest. There are several forest types in which fire is a critical natural element in the forest landscape, and the effects are reasonably well-understood. There are other types, however, for which relatively little is known regarding the impacts of fire, although it is known that total fire suppression in the landscape is unrealistic.

The reintroduction of fire in landscape management is not easy. The buildup of fuels has reached such a level in many forests that any fire is likely to be so intense that the entire forest community will be replaced. Thus where fires historically were frequent enough to help maintain old-growth conditions, now fires may totally destroy the trees that

might otherwise have been protected by more frequent fires (Covington and Moore, Harrington and Sackett, this volume). Furthermore, human communities have developed in many forested areas that typically had frequent fires (particularly along the Front Range in Colorado), and both the accumulation of fuels and the presence of buildings severely limit prescribed burning in most situations. Intense fires in some cases even result in the destruction and replacement of the human community development.

The accumulation of fuels during the extended period of fire suppression has resulted in the accumulation not only of large amounts of coarse woody debris, but also in large amounts of litter beneath large trees. Thus far researchers have not been able to develop reliable techniques for using fire in ways that prevent lethal temperatures from developing at the base of trees as this accumulated litter burns, even when fire is used in cool, moist seasons of the year (Harrington and Sackett, this volume). Considerable research is needed to determine how fire can once again be made a more significant part of landscape ecology. It may be possible to achieve some of the structural effects resulting from fire by using silvicultural techniques not aimed at timber harvest. Research is needed on the potential for using silvicultural treatments to simulate the effects of fire.

Inventory Techniques

Inventories of old-growth forests and of forests that have potential for transition into the old-growth condition are extremely important in forest planning. It is critical that inventories are conducted using guidelines with a sound scientific basis. Presently, most inventory of old-growth forests is conducted using some type of scorecard, often with both quantitative and qualitative features (e.g., Lowry, this volume). This has been a useful interim approach, but considerable modifications are needed (Robertson, this volume). The main problem with existing approaches is that they almost totally exclude old growth on poorer sites, because the scorecards make use of minimum criteria relating to tree size and stand structure (Mehl, this volume). Furthermore, certain scorecards favor structural diversity that in some cases (e.g., ponderosa pine) should be considered a quality-reducing factor rather than a quality-enhancing factor, and little attention is given to functional features that distinguish old growth from other successional stages.

Several rating systems have been used to quantify dead material on the forest floor, but not all systems have been used to quantify all of the standing and down dead material important in characterizing old growth. Convenient methods are needed to evaluate all portions of the accumulated dead materials in forest communities, including their states of decomposition.

Research also is needed to improve inventory techniques for detecting old-growth forests at the landscape scale. The scorecard approach has evolved on individual National Forests, often with major differences in criteria among Forests for distinguishing old growth in similar forest types. General guidelines are needed for conducting inventories over large geographic areas. This research requires not only increasing our understanding of how old growth varies among sites and habitat types within forest types (see discussion above), but also improving the technology for completing accurate inventories. The development of remote sensing techniques (Nel, this volume) holds considerable promise for conducting broad-scale inventories.

Ecological Knowledge for Management

Synthesizing current and future scientific knowledge into a format useable in natural resource management is a formidable task. The necessity for addressing the likely ecological consequences and environmental impacts of various management scenarios (including no action) at comprehensive spatial and temporal scales overwhelms conventional approaches for integrated resource analysis. A central conclusion of working sessions at this meeting was that spatial and temporal ecological modeling coupled with formulations of desired future conditions is needed to support analyses not only for old-growth management decisions but also for landscape management in general.

Additionally, we concluded that management experiments and demonstration areas at the landscape level would be necessary for testing hypotheses and developing models that can aid decision-makers in guiding both research and management. To accomplish these tasks, improved access to remote sensing technology, geographic information systems, process-based simulation models, and other advanced technologies is necessary both for researchers and for managers.

CONCLUSIONS

It is clear from the wide array of topics covered in this volume that although much is known about old-growth forests in the central and southern Rocky Mountains and Southwest, many important questions remain unanswered. It is the responsibility of researchers to address these questions, because without

adequate scientific answers, it is likely that serious mistakes will be made that could have long-term negative environmental and ecological consequences.

At the same time, it is the responsibility of forest managers to incorporate the most up-to-date scientific knowledge in making decisions about the management of forest landscapes to protect and enhance the unique values of old-growth forests. It is also important that scientists and managers acknowledge those areas in which scientific knowledge is inadequate, to proceed cautiously when that is the case, and to inform researcher leaders and interested members of the public of such problems.

Some of the changes imposed on the forest landscape since settlement began presently restrict management options in the near future. Yet we have a tremendous opportunity to turn the pattern of change into a more positive one. This can be done through appropriate integration of sound scientific principles into guidelines for managing forests in ways that meet both present and anticipated future needs. It cannot be done by science alone, or by management alone, or by overreacting to the demands of narrowly focused interest groups. Managing old-growth forests in the landscape requires a long-term landscape perspective supported by informed communication among scientists, resource managers, and the public.

Ancient Forests – The Human Aspect¹

Carveth V. Kramer²

A get-together with our ancient forests -- the idea was to bring together people's hearts, heads and our ancient forests. This field workshop brought people together to develop common ground on what the ancient forest means to us. We all listened and talked about the ancient forests and their link to the options of the future. This get-together provides the framework around which we discuss the human aspects of the ancient forest. Are people *a part* of the forest? Or, are people *apart* from the forest? Can we any longer talk of people as something separate and alien from the environment?

INTRODUCTION

There are ancient stories called Koans, which are centuries old allegories on the meaning of life. This story is of a Zen Buddhist master.

A young, world renown expert on our ancient forests went to visit this master. The master greeted him with a bow. His guest explained that he knew much about the ancient forests, but he was not able to reach his goal. "I want to be able to use all that I have learned on the ancient forests and help people. But it seems that the more I learn, the harder it is to help. For as I learn, it opens up the doors on knowledge even wider and I see all that I do not know. It is becoming harder for me to help others, not easier."

As his guest spoke, the master reached for a pot of tea. He handed his guest a cup and started to pour the tea. The cup slowly filled. The tea came to the top. He kept on pouring. It overflowed. He kept on pouring. "Stop! Stop!" cried his guest. "My cup is full! My cup is full!" he exclaimed.

"This is true," said the master. "You are filled with your own judgments and speculations. You must return to our ancient forests as a child, with an empty cup," he explained.

Many of us come with cups full. We come with

a sincere desire to share and help others. This we must do. But let us not forget to come as children, with an empty cup, a cup which we will use to listen and to learn. Let us make new connections about our ancient forests. Let us put on new growth.

And this is your first step. This paper is like no others. Some will say, "It's out of place and unscientific." Others will say, "It's right on!" They will all be right. It is out of place, unscientific and right on.

I was asked to prepare this paper to help set the stage, to develop a context for the symposium,



Figure 1. Luis Torres talks of rebirth in the ancient forests.

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to place a different perspective on our ancient forests. As John Keats said, "The only means of strengthening one's intellect is to make up one's mind about nothing -- to let the mind be a thoroughfare for all thoughts." (John Keats. Letter to George and Gorgiana Keats, September 17-27, 1819).

The title of this paper, "Ancient Forests -- The Human Aspect", was carefully chosen. Some will feel uncomfortable with my choice of the words "ancient forests" -- preferring "old growth". Let me explain why both terms, ancient and forests, are key.

I use the term "forest" to refer to the entire ecosystem. The term forest conjures an image of a complete package. I see the air, birds, trees, fallen leaves, streams, soil, ants, fungi, mirco-organisms, all the chemical processes and yes, human beings.

Some may not prefer the word "ancient" because it is a word in vogue with many in the general public. They feel it may not appear "scientific". Also, it conjures up the idea of "old", yet more. So old, it elicits respect. As it is said, ...the ancient is wisdom; and as the days lengthen, so does understanding. It is precisely in this context that I use the word "ancient".

With this background, I present -- our ancient forests; all the wisdom and understanding enshrouded in millennia of the intertwining ecosystems of our earth.

PEOPLE... ...A PART OF THE ENVIRONMENT? ...APART FROM THE ENVIRONMENT?

Think of the hydrologic cycle. The moisture collects in the clouds. It rains. Water runs off into streams and lakes. Water infiltrates into the ground. Water is taken up by the plants. They transpire moisture to the air. Water evaporates from the oceans. Moisture condenses in the air. The cycle starts anew.

If we were to remove the clouds from this cycle, we'd immediately exclaim, "How absurd, there is a key element of the cycle missing." I would agree. And if we removed any one of the other elements in the cycle we'd exclaim the same thing, "Something is missing." Well, the ancient

forest model used by many has something missing. A key piece of the puzzle is left out -- people.

Understanding the whole forest cycle is much like putting together a jigsaw puzzle -- a puzzle with many pieces -- a puzzle of pieces within pieces (fig. 3). We often overlook the pieces we don't readily see -- the soil and the soil's inhabitants. Fortunately, we are gaining a better understanding, acceptance and support as to what the different pieces are and how they interrelate. But of all the pieces, there is one that is by far the largest, the most obvious, the most multicolored. the most complex, has the greatest impact on all the other pieces and can rearrange or destroy the other pieces -- yet is the least understood. That keystone is us, we HUMAN BEINGS. I ask you to join in increasing our understanding of our proper role in the forest puzzle. Let's do something to help all to better understand how the forest puzzle fits together. Let us interact within the puzzle and work with the larger global puzzle. Let's discover our humanness within the forests.

Animals pass through the forests. They follow their needs. We are the same. We too have needs of the forests. The difference is that we latch on. We learn. We understand. We modify our behavior. We bring the forests to us and us to the forests. We must look upon the forest and us as one. To do otherwise is to pit one against the other. To do otherwise is to ignore one piece of the puzzle -- people.



Figure 2. A log nutures new growth.

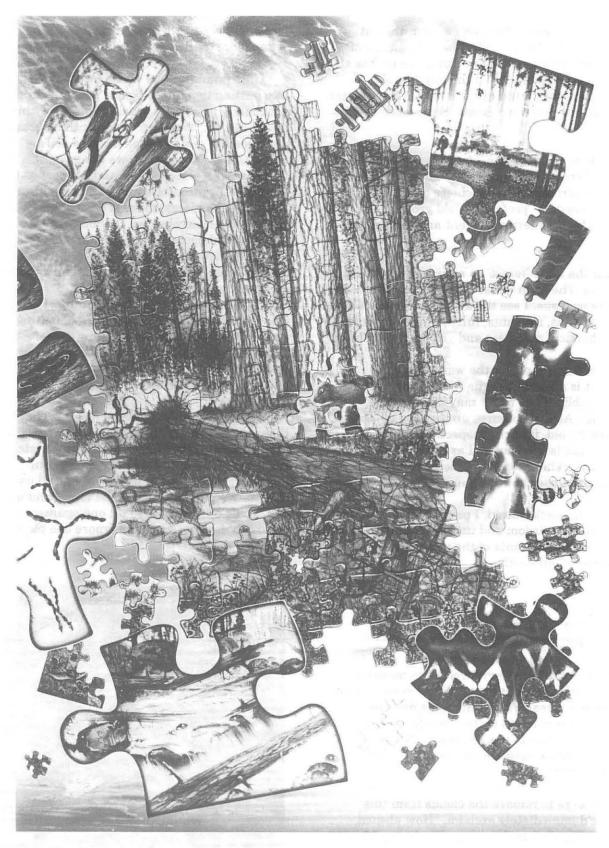


Figure 3. Artist Peter Lloyd depicts *Our Forests, Where Nature Celebrates Itself.* This visually depicts many of the key concepts developed in the Ancient Forests Get-Together held on the Carson National Forest. It emphasizes that we often overlook those parts of the forests we don't see.



Figure 4. At the Ancient Forests Get-Together, we saw, heard and felt ourselves and the ancient forest.

Let me take you back to a get-together we had on the Carson concerning our ancient forests. I do this to show how current scientific understanding can and must be married with thoughts of the public to result in management on the ground.

On August 14-17, 1989, the Carson National Forest had an Ancient Forests Get-Together. The first two days were classroom-style with each speaker talking on various aspects of the processes going on in a forest. We heard from:

Chris Maser -- The Biological Processes of the Ancient Forests. Maser is a consultant and author on sustainable forestry.

Bruce Milne -- Landscapes in the Southwest, the Importance of the Size and Spacing of the Plants, Millions of Acres at a Time. Milne is a professor at the University of New Mexico in Albuquerque. Dave Perry -- Soils (the part of the forest cycle we often pay too little attention to). Perry is a professor at Oregon State University in Corvallis.

Bill Mannan -- Role of Snags, Cavity-Nesting Birds. Mannan is an associate professor of wildlife ecology at the School of Renewable Natural Resources at the University of Arizona in Tempe.

Stan Gregory -- Healthy Streams, the Importance of Wood in Streams. Gregory in on the faculty on Oregon State University in Corvallis.

Ray Lujan -- The Native American Soul and the Ancient Forests. Lujan is from Taos Pueblo.

Luis Torres -- The Hispanic Soul and the Ancient Forests. Torres is a native of Northern New Mexico.

The next two days were in the field. We looked at the processes and relationships discussed the

previous days and saw how they operate in the Carson National Forest landscape.

On the last day Carson National Forest employees got together and discussed what we heard and where we wanted to go from here. The public went along and "kept us honest".

The Carson forest supervisor set up a group to work out a game plan on what to do next. It included members of environmental organizations, timber industry officials and employees of the Carson National Forest. Together, they drafted a proposed definition of old growth, a statement of reasons to manage for old growth and an amendment to the Carson Forest Plan.

The committee's recommendations were combined with documentation of the four-day get-together into a newspaper supplement. This supplement received wide distribution locally. It was also distributed throughout the U.S. and parts of Canada. In the supplement, we asked for further feedback. Videos and audio tapes of the four day get-together were also made available on loan to anyone wanting to use them.

From the interaction of participants and our ancient forests many comments were expressed on the value of the ancient forests.

- o They are banks of knowledge about the intricate, complex interrelationships occurring in the forest ecosystem. They serve as blueprints for the natural forest processes.
- o They ensure that future generations will have the opportunity to enjoy the benefits of ancient forests and continue to expand upon our knowledge and make informed decisions. They guarantee that our children will have options regarding the future of our forest ecosystems.
- o They represent a high degree of biological diversity that is essential for plant, animal and human survival.
- o They mirror our feelings, values, ethics and attitudes toward our environment. The conditions of our environment reflect our ability to co-exist in harmony with our environment. Our ancient forests are a favorable reflection.

- o They are an important part of our national heritage which we will pass on to future generations.
- o They are a source of inspiration, a place to reflect upon ourselves and on the natural wonders and mysteries of nature. They challenge us to think about our role in nature.
- o They provide a living story of nature in balance, a story of life and death, predator and prey, change and stability.
- o They produce healthy feelings and emotions which tend to bind us with nature. Nature communicates to us through the ancient forests in a spiritual sense that is beyond verbal communication and seems to reach directly through our souls.
- o Aldo Leopold, a former forest supervisor on the Carson, suggested an ethical aspect to wilderness that could be extended to the ancient



Figure 5. We are a piece of the puzzle. We acknowledge the need to manage the whole cycle, and the need to leave options open for the future. We must manage for a sustainable forest, a sustainable forest we have a profound influence upon.

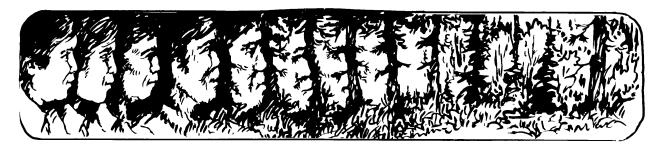


Figure 6. We all must see more than the trees. We must manage as a blending of the land and the people. It is no longer wise nor possible to separate the two.

us not be accused of being indifferent to any aspect of the environment -- including people.

As scientists we have important knowledge about a key concern, the ancient forests. We must make ourselves aware of how our knowledge can and should be used, for information out of context is meaningless.

As noticed in our Get-Together, some people cannot easily, or don't feel the need, to convert their feelings into numbers or terms used by scientists and managers. That is our job. We must listen to what they say, and what they don't say. Then we need to ask ourselves, how can we interrelate their feelings with what we know of the forests. Only then can we present information in the proper form and context.

So, in our discussion and resulting technical report, we need to be sure we give a firm foundation. People need to know:

- o What is wanted (i.e. How would they recognize it if they saw it?)
 - o Where it is wanted.
- o When it is wanted (Could be a point in time or schedule. Also over what period of time?).
 - o Why it is wanted.
- o How much is wanted and how we might get there.

Chris Maser is unique in bringing science and the people together. In his book, The Redesigned Forest, he uses a strong analogy. "We, the people of the United States, are like a great American quilt. We too often pursue our science and our technology in intellectual isolation of their long-term consequences to the environment. Our science and our technology are like isolated pieces of a great, patchwork quilt with a largely random arrangement and without a thread to either relate the pieces one to the other or to hold them together. ...we must adopt the ...values of

relatedness to the land and apply them to our values of science and technology. Thus, as we the people elevate our personal, environmental and social consciousness, the constant human struggle, we begin to take our rightful place in the universe -- not as conquerors, for we have conquered nothing, but as universal custodians. In this way we can both design our quilt and sew it together for all generations to enjoy (Maser 1988, page 190)."

So as we work, we must be aware of the overall quilt. We need to relate all the pieces together and to the rest of the ecosystem. We must bring our humanity to the issue. We must use our humanity as the thread to relate the pieces, one to another.

Are people apart from the forest? Or, are they a part of the forest? Can we any longer talk of people as something separate and alien from the environment? I think not. We all must see more than the trees. We must manage as a blending of the land and the people. It is no longer wise nor possible to separate the two.

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Ecological Concepts in Old-Growth Forest Definition¹

W. H. Moir²

Abstract.—A generic definition for old growth is applied to forests of the Southwest and southern and central Rocky Mountain region. Old growth is presented as a stage of forest succession and structural development, and therefore requires time to develop. While certain structural features, like patchiness and abundant snags, can occur in younger forests, they are best expressed in old-growth forests. Old-growth forests also are characterized by complex ecological relationships, such as detrital food webs, mycotrophic dependencies of vascular plants, fungal-invertebrate, and fungal-invertebrate-vertebrate relationships, and preferential wildlife use by some species. There have been few quantitative studies to separate mature, old-growth, and post-old-growth forest stages. However, the age and size of dominant trees, as well as other structural features, and complex relationships between organisms help distinguish old-growth from other stages of forest succession.

OLD GROWTH AS A STAGE OF FOREST SUCCESSION

A generic definition of old-growth forest in current use by the U.S. Forest Service states that old-growth forests are "later stage(s) in forest development which may be distinctive in composition but are always distinctive in structure from earlier (young and mature) successional stages." The words, "development" and "successional", are essential- they may or may not imply a subtle distinction. Succession informs us that the composition of the plant community in earlier stages differs predictably from the plant community of later stages. Thus, old-growth sprucefir may contain old lodgepole pines in mid-succession and lack living pines at climax. Development implies that the structure of old growth differs predictably from the structure of earlier stages. Both concepts may be necessary or useful. Old-growth forests develop structurally and successionally from younger forests only after sufficient time has elapsed. In a word, old-growth forests are "old" forests, as determined by the oldest surviving trees from the earliest cohort established after a stand-replacing disturbance. An example of old growth as a successional stage is given in figure 1 (after Fischer and Clayton 1983).

Although structural and other features may help characterize old-growth forests, forest age is the essential feature. Many of the structural features described below are also found to some degree in earlier stages of forest succession.

In the successional sequence, old-growth forests develop from the mature forest stage (fig. 1). Early foresters recognized the distinction when describing old growth as "overmature" or "decadent" forest

¹Paper presented at Old-Growth Forests in the Rocky Mountains and Southwest Conference (Portal, AZ, March 9-13, 1992).

(clearly a timber-oriented language). The development of old growth from mature forests is usually accompanied by both compositional and structural changes discussed below. Quantitative attempts to separate mature and old-growth forests using ordinations and stepwise discriminant analysis are reported for Douglas-fir forests in the Pacific Northwest (Spies and Franklin 1991; see also Robertson, this volume).

The old-growth stage of forest development ends with a catastrophic (stand-replacing) disturbance, such as blowdown, severe insect epidemic, holocaust fire, clearcutting and partial cuttings (see literature cited for examples). The La Mesa fire in New Mexico caused replacement of old-growth ponderosa pine forest by an early seral stage dominated by herbs (fig. 2). Without catastrophic disturbance, the old-growth stage may persist in accordance with climax theory. Descriptions of climax or near-climax forests in the Southwest and Rocky Mountain regions are plentiful in the literature of forest classification and stand dynamics (for review see Muldavin et al. 1990). But age structures of some old-growth stands do not suggest persistence. They may lose sufficient numbers of old trees to mortality without replacement, and attain a post-old-growth structure which resembles earlier stages of forest succession (see, for example, Veblen et al. 1989, Miller 1970, Schmid and Hinds 1974).

Development of forests into old growth is gradual, so that distinction between mature and old-growth stages may be subjective. Evaluation criteria which help define the distinction are discussed below. The basic criterion, however, remains stand age. Old-growth stands are always older than mature stands. The clock starts running at the time of stand initiation, which is usually assumed to have been a stand-replacing event such as the La Mesa fire. But, if the implied catastrophic event is in the distant past, the stand condition at the onset of settlement by Europeans is commonly used as the starting point (e.g., Cooper 1960, Brisson et al. 1992).

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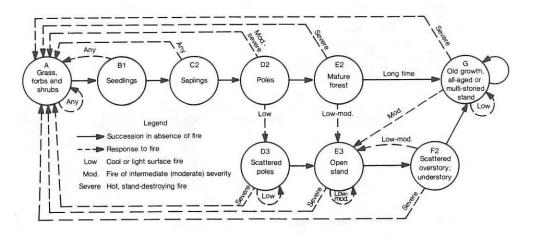


Figure 1. Hypothetical fire-related successional pathway.

Old-growth forest is a *stand* condition that is attained through time, not a count of how many old trees are present. It is important to recognize that



Figure 2. Ponderosa pine snags and logs on the Pajarito Plateau, July 17, 1986, nine years after the La Mesa fire, New Mexico.

most old growth described in the literature developed with minimum human interference prior to about 1880 (fig. 3). The degree to which humans affect stand development and thus the transition into old growth, or to which they alter old growth through treatments so that stands are no longer old growth, has not been resolved (see Gottfried and Ffolliott, this volume).

HOW OLD IS OLD GROWTH?

Old-growth forests are identified on the basis of ages of dominant trees. At what age does a forest become old-growth forest? The age criterion is usually judged from forest dynamics and the nature of tree mortality. In a mature forest stands have developed on the basis of competition between trees, self-thinning, and the occasional play of other mortality factors upon tree populations (Peet and Christensen 1987). In old-growth forests competition among dominant trees is minor, but senescence and a wide variety of mortality factors assume considerable importance (Waring 1987, Franklin et al. 1987, Clark 1990). Trees in the oldest cohorts are nearing their natural longevities as influenced by site and environment.

Table 1 indicates average tree longevities and maximum ages that might be found in the Southwest and Rocky Mountain regions (for trees of exceptional old age, see Swetnam, this volume). Old-growth forests evolve as the clock of forest succession approaches the time span of natural tree longevity. Natural mortality of older, dominant trees then becomes a major process of internal stand dynamics (Harcombe 1987, Moir et al. 1992).

Successional stages of many forest ecosystems in the Rocky Mountains have been described by Fischer



Figure 3. Forest ranger, accompanied by a lumberman, marking National Forest timber for sale.

and Clayton (1983), Stromberg and Patten (1991), Moir and Dieterich (1988), Dye and Moir (1977), and Veblen (1986b). There is less information on the *time* required to attain the late successional, near-climax, and climax stages- any of which can be old growth as the natural longevities of dominant trees are approached and natural old-tree mortality becomes important in stand development.

The use of stand age alone to characterize old growth has been criticized because some 200-300-year-old stands may not have developed some or any of the expected old-growth characteristics (Habeck 1988). This illustrates the difficulty of giving precise definition to old-growth forests or of using age alone

Table 1. Average longevities and average maximum ages (in years at breast height) of trees in old-growth stands of the Southwest and southern to central Rocky Mountains.

Tree	Average	Maximum	Notes
Abies concolor	200		5
Abies lasiocarpa	< 200	400-450	1
A. l. var arizonica	300-350		3
Picea engelmannii	500-600		1
Picea pungens		600	2
Pinus edulis	400	800-1000	2
Pinus contorta	350-400		4
Pinus ponderosa	400-450	600	2
Populus deltoides	<100		2
Populus tremuloides	<220		2,ramet
Populus tremuloides		>1000	2,clone
Pseudotsuga menziesii	700	2	

Notes 1 - Alexander 1987, 2 - Burns and Honkala 1990, 3 - Dye and Moir 1979, 4 - Moir et al. 1992, 5 - Moir unpublished field notes. to characterize them. In my experience old-aged stands that are successionally beyond the mature forest stage and that have minimal disturbance from management (including altering the historical fire regime, see Covington and Moore, this volume) will display a variety of the old-growth features discussed in the following section.

FOREST STRUCTURE THAT ACCOMPANIES "AGING" INTO OLD GROWTH

In the northern Rocky Mountains, Pfister (1987 cited in Habeck 1988) reported some structural features of old growth forests that provide reliable criteria for recognizing old-growth across a variety of major forest types (see also Spies 1990). These criteria are applicable in the Southwest and central and southern Rocky Mountains where forest habitat types are the same as, or similar to, habitat types east of the Continental Divide in the northern Rockies. Some combination of the following six criteria help characterize old-growth forests.

1. Large, old trees

Dominant trees in the stand attain large sizes. How large they are depends on site potential, and to a lesser extent on stocking density (Clark 1990). In extremely severe environments, trees may be exceptionally old but unimpressive in stature (Swetnam and Brown, this volume). The vicissitudes of age are reflected in crown and stem deformities in some, if not most, old trees. These are the cull trees or defect noted in many timber assessments. Old trees may

exhibit trunk rot, plant parasitism (mistletoe), rusts, herbivory by vertebrates and invertebrates, and other signs of *involvement with other organisms*, as well as mechanical and/or weather damage to crown and stem.

2. Low stem densities of larger trees

Old-growth descriptions in most unmanaged stands are characterized by dominant and codominant trees at *lower densities* than found in earlier stages (fig. 3). However, where fire suppression has been in effect during the last century, many old-growth stands have become densely stocked with young and advanced regeneration.

There are unresolved questions concerning how low old-tree densities can get through natural mortality or select harvest logging and still retain the old-growth character. Similar questions arise for post-old-growth forests in which old trees die without replacement by another old-tree cohort. Scientists have not addressed these questions, but guidelines can be suggested based on the proportion of microsite dominance by remaining live old trees, or by cultural criteria described by Kramer (this volume).

3. Snags and logs

The content of snags and logs in old-growth stands depends on fire history, insect epidemics, blowdown, tree longevities, and decay rates. In old-growth stands the greatest mass and volume of snags and logs are produced by old-tree mortality, and can accrue erratically (individual trees die here or there) or episodically (groups or cohorts of trees die simultaneously). Except in some fire-recurrent environments (for example, fig. 3), the number of large snags and logs is generally high. Decay classes 2 and 3 may be most abundant in forests approaching equilibrium between dead-tree input and wood decay (Arthur and Fahey 1990). Where measurements have been made. the pulse of dead wood at stand initiation appears to have disappeared by the old-growth stage (Harmon et al. 1986, Moir et al. 1992).

4. Tree gaps and spatial patchiness

Old-growth forest structure is a function both of age and stand history. Gaps and spatial patchiness result from internal stand events which occur both continuously and in episodes (Debell and Franklin 1987). Mortality of dominant trees creates a patchy gap pattern in some forest types (e.g., Veblen 1986a). Agents of gap formation include fungal diseases, parasitic plants, insects, tree herbivores, wood rots in combination with windbreak, windthrow (the blowdown of otherwise healthy trees), fire hot spots, lightning, and human activities. As development proceeds, the gaps fill with regenerating trees. In wetter forests gap formation has been studied both experimentally and theoretically (Ffolliott and Gottfried 1991, Nikolov 1992). In drier forests mosaics of different-aged tree patches result from recurrent, low-intensity fires. Armillaria and other diseases may create dead-tree pockets in ponderosa pine forests (Wood 1983). Some old-growth forest structure reflects insect epidemics and fires interacting at

various intensities to create a patchwork of tree sizes and densities. For example, severe western spruce budworm epidemics may eliminate regeneration of host trees locally, but dominant trees survive. The stand appears "stagnant," composed of large, old mother trees but no regeneration. Elsewhere in the stand where defoliations are less severe, regeneration of host trees creates a multistoried canopy. Such arrangement of fuels in turn affects the behavior of fires (Jones 1974, Dieterich 1983, Baker and Veblen 1990).

In contrast to old-growth forests, stands in younger stages may be more uniform, because time has been too short for patch-forming events to take place.

5. Structures utilized by wildlife

Sometimes we cannot adequately describe all the significant structural variations attained by oldgrowth. We may not perceive critical structural elements of an old-growth stand, but old-growthdependent wildlife can. In cases where our criteria for old-growth classification are marginal, the presence or absence of key wildlife may be decisive. The use of some old-growth structures by wildlife may affect old-growth structure; for example, bears tearing up logs while feeding (LeCount 1992) or debarking trees at squirrel midden sites (Smith and Mannan, this volume). The interpretation of oldgrowth structures from wildlife usage must be exercised carefully. There are examples where microhabitats occupied by vertebrates are coincidentally found in old-growth forests as well as in other environments (e.g., Scott, this volume).

6. Tree regeneration

In old growth of mixed tree species, regeneration is dominated by climax species, although seral trees, such as aspen or oaks, may persist from old rootstock or within large canopy gaps. In fire-dependent old growth, regeneration may be dominated by fire-tolerant species, such as pines or Douglas-fir. Tree regeneration criteria are useful but not definitive, since the same rules may apply to mid-successional or mature stages of some forest types.

OLD-GROWTH FORESTS FROM ECOLOGICAL RELATIONSHIPS

Old growth differs from mature forest in the complexity of its ecological interrelationships. Except in a few instances of vertebrate species, the living interrelationships of old-growth forests have not received much study in the Rocky Mountain or Southwestern regions. But we have reason to believe that complexities exist here which are similar to those described in other temperate old-growth forests.

Old-growth forests have complicated detrital food webs. This includes the "hidden diversity" involved in decay processes of logs and snags (Hornibrook 1950; Hinds et al. 1965, Hinds and Hawksworth 1966, Maser and Trappe 1984). Food webs of old-growth forests involve fungal-small mammal relationships (Maser et al. 1978), and arthropods and other microzoans inhabiting the "cities of the soil" in deep forest litter (Evans 1968), and within decaying stems of old living trees, whose decay may involve nitrogen fixing (Aho et al. 1974, Larsen et al. 1980). There are food webs associated with mistletoes (Bennett 1991), and plant-to-plant dependencies such as mycotrophy (i.e., nutrition from fungi) of vascular plants without chlorophyll, as in many of the Orchidaceae and Ericaceae (Furman and Trappe 1971). There may be mixed communities of cryptogams and associated invertebrates on tree branches and stems (for example, pinyon-juniper woodlands, see Wetmore 1976). Consider the abundance of ectomcorrhizae in decaying wood (Harvey et al. 1980), together with rotting wood as a reservoir of moisture and nutrients and as cover for rodents that disseminate mycorrhizal spores in fecal pellets: all this implicates logs and snags to be important carryovers between old-growth forests and the forest generation that follows. Decaying logs in subalpine forests last about 150-200 years (where measured in Colorado, see Moir et al. 1992); they may be a major reservoir of the biological diversity that connects old growth to the forests that follow. The ecological functions of this linkage need more study in this region.

Lastly, the etiology of gap processes is complex in old-growth forests (although not limited to old growth), and is often mediated by fungi and associated microorganisms. This complexity of living interrelationships in old-growth stands apparently serves the process of forest change (Wood 1983; Worrall and Harrington 1988).

CONCLUSIONS

Exact definitions of old-growth forest of the Southwest and southern and central Rocky Mountains cannot be given because of the great variation in forest environments and old-growth conditions. However, certain ecological principles may be applied to help conceptualize old growth. Old growth may be considered a late stage of forest succession, which differs in structure and composition from earlier stages. The gradual development of old growth results in dominant trees which are old relative to their natural lifespans. Old trees are large, occur in low densities, and exhibit the scars of age as crown and stem deformities. These features, as well as longevity itself, are conditioned by the stand environment. In absence of stand-replacing disturbances, old tree mortality is a conspicuous feature of forest dynamics. As a result, old-growth stands have developed a high degree of patchiness, and where fires are infrequent or of long intervals, have accumulated large amounts of snags and logs.

Ecological relationships include the prominence of detrital food webs and organisms involved in decay processes. Certain animals have preference for oldgrowth forest and can be used as indicators when adequately studied over the range of their environmental tolerances.

In summary old-growth forests are "old" forests, with well-developed structures and living interrelationships that help set them apart from younger stands.

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Oldest Known Conifers in the Southwestern United States: Temporal and Spatial Patterns of Maximum Age¹

Thomas W. Swetnam and Peter M. Brown²

Tree-ring collections obtained from Arizona and New Mexico oldgrowth forests were used to assess age structure and maximum ages of conifer stands and trees. Mean ages of the oldest Douglas-fir, ponderosa pine, and piñon trees in stands selected for maximum age varied from about 270 to 290 years. Mean ages of the oldest Douglas-fir trees in northern New Mexico old-growth stands not specifically selected for maximum age were about 200 years. Trees older than about 400 years (establishing before 1590) were less common in Southwestern forests, and trees older than about 500 years (establishing before 1490) were rare. A decrease in numbers of sampled trees in age classes establishing before about 1590 and an increase in numbers of trees in early 1600s age classes may be related to a severe drought in the late 1500s, and a subsequent wet period in the early 1600s. Many of the oldest stands ("super old-growth") in the Southwest are characterized by stunted trees growing in sites with steep, dry, rocky slopes. Some of the super old-growth stands, however, have more stereotypical old-growth characteristics of closed, multilayered canopies, large and small diameter trees, and presence of abundant snags and logs. Scientific values, particularly tree-ring resources, of old-growth are high and important to studies of past global change.

INTRODUCTION

A fundamental attribute of old-growth forests is the presence of old trees. Despite the obviousness of this statement, it is not clear how old is "old", nor is it clear that tree age can or should be used as a primary criteria for identifying old-growth. Interim definitions of old-growth list minimum tree ages, but most of the emphasis in classification has been on structural, compositional, and ecological attributes that are age-

related, but not necessarily age-specific (Franklin et al. 1981, Franklin and Spies 1986, Spies and Franklin 1988, Franklin and Spies 1989, Southwestern Region Old-Growth Core Team 1992). For example, Pacific Northwest old-growth stands must contain trees at least 200 years old, and the stands should have broad diameter distributions with some trees greater than 30 inches dbh. Proposed minimum tree age in Arizona and New Mexico old-growth is 150-200 years, and trees should have diameters of 9 to 20 inches dbh (depending upon forest cover type). Deep, multi-layered canopies and a minimum number of snags and logs per unit area are also specified. Actual tree age distributions within regions or within oldgrowth stands have not been considered in the context of old-growth definitions. However, the implicit importance of tree or

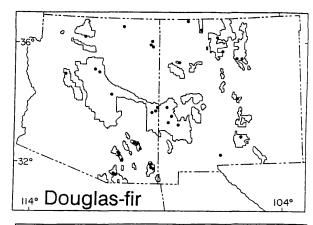
^{1.} Paper presented at Workshop on Old-Growth Forests in the Rocky Mountains and Southwest: The Status of Our Knowledge, Portal, AZ, March 9-13, 1992.

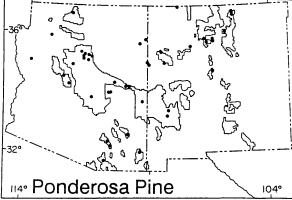
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stand age is evident in assessments of stand structure indices as a measure of "old-growthness", since actual stand ages are the standard against which the indices are tested (Franklin and Spies 1989).

Franklin and his colleagues argue that old-growthness in the Pacific Northwest is a continuum rather than a discrete state; one cannot identify a single set of attributes and quantities that will classify all stands as either old or young growth. Local disturbances and site-related differences have led to a wide variety of tree ages, stand structures, and species compositions across the landscape. Given this ecological variability, and the many resource values contained in old-growth (e.g., wildlife habitat, forest industry jobs, esthetics, etc.), it is quite reasonable that definitions should include a broad assessment of attributes. While we agree that multiple age-related attributes must be considered, we submit that scientific understanding of old-growth ecosystems, and decisions on old-growth preservation, can benefit from a more specific examination of actual tree ages within regions and within old-growth stands. Assessments of tree age distributions (how old is "old"?) are needed as a baseline to determine the rarity and uniqueness of particular trees and stands.

The main subjects of this paper are the age structure and character of the oldest known Southwestern old-growth stands. We will describe temporal and spatial distributions of maximum ages of the four most widespread and economically important conifer species - ponderosa pine (Pinus ponderosa), Douglas-fir (Pseudotsuga menziesii), piñon pine (Pinus edulis), and white fir Abies concolor. We will also emphasize the distinctive characteristics of the "oldest" old-growth stands ("super" oldgrowth) in the Southwest, since qualitative and quantitative features of these stands are not well known among land managers or natural resource scientists. Ancient trees and stands in the southwest also have high scientific values, and we will discuss some of these values.





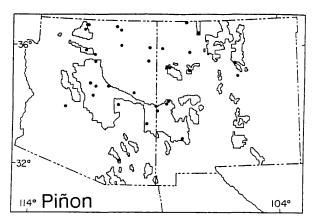


Figure 1. Location of tree-ring collections (dots) in Arizona and New Mexico, sorted by species. National Forest boundaries are shown (approximately). Because of close proximity, two or more sites are sometimes shown as a single dot.

METHODS

The Data Set

We used a unique data set to develop an estimate of maximum tree ages in the Southwest. A set of ring-width measurements of more than 2,800 trees in 164 sites dispersed throughout Arizona and New Mexico was analyzed (Fig. 1). These data were collected mainly by dendrochronologists working at the Laboratory of Tree-Ring Research (LTRR), University of Arizona. Since 1904, when A. E. Douglass began his tree-ring research in the Southwest, thousands of trees have been sampled, dated and measured using the techniques he pioneered (Webb 1983). Early in the history of LTRR these collections were extended throughout the western U.S. and North America, and data bases now contain collections from most temperate and boreal forest regions of the world. Most of these collections have been obtained for the purpose of investigating past climate variations, and for the dating of past events, such as construction dates of ancient dwellings. Although collections are globally dispersed, the Southwest still has the highest concentration of sampled sites of any region (Hughes et al. 1982, Hughes 1989).

Southwestern tree-ring collections have been obtained and used for a variety of purposes, but a common sampling strategy has been to maximize the length of the treering record by selecting the oldest stands and trees. An additional strategy in most sites, but not all, has been to maximize climatic sensitivity. In the Southwest these two strategies are often complementary because the oldest trees in arid and semiarid regions are commonly found in stressful sites (Schulman 1943, 1954, 1956) where year-to-year ring-width variations tend to be high (sensitivity), positively correlated among trees, and closely coupled with climate variations (e.g., rainfall or temperature) (Fritts 1976, 1991). Although most of the sites in our data base were at least partly selected for climatic sensitivity, the data includes samples from a broad range of habitats from low to moderate productivity sites, in piñon-juniper woodlands at elevations of about 1,350 m up to mixed-conifer forests at elevations of 3,200 m.

In general, the collection of tree-ring samples from the Southwest is a highly stratified data set. They are the result of more than 80 years of efforts by dendro-chronologists to find the oldest trees and stands. The selective nature of these collections has advantages and disadvantages in assessing age structure. On the one hand, clearly, they cannot be used to characterize the overall age structure of Southwestern conifer forests. On the other hand, they are a very useful data set for assessing maximum tree and stand ages in this region.

We began data compilation by reviewing individual site collections contained in a ring-width database used at LTRR. Because of time limitations only sites from Arizona and New Mexico (referred to here as the "Southwest") were included in our sorting of the data (Fig. 1). Future investigations could extend the analyses to portions of the Colorado Plateau in southern Utah and Colorado, and in the Southern Rockies in Colorado, where the densities of sampled tree-ring sites are as high, or nearly so, as in Arizona and New Mexico.

In addition to 143 sites from throughout Arizona and New Mexico we also compiled and analyzed a systematically sampled set of 21 stands from the Carson and Santa Fe National Forests in northern New Mexico. These stands were selected for a study of western spruce budworm history in this region (Swetnam and Lynch 1989, Lynch and Swetnam, this volume). These stands were old-growth mixed-conifer with Douglas-fir and white fir as primary components, and they have had minimal or no human disturbance. Douglas-fir and white fir trees were sampled at evenly spaced points along transects. Three or four evenlyspaced transects were approximately centered in the stands and the nearest Douglas-fir and white fir to each point were cored. Tree sizes down to about 20.3 cm dbh (8 inches) were cored. A total of about 15 trees of each species were sampled in

this manner. We also selectively sampled an additional five of the oldest appearing Douglas-fir and white fir in each stand to obtain the longest (oldest) tree-ring record possible for each stand. Hence, this data set contained a broader range of size and age classes than the larger regional data set, but oldest trees within the stands were still disproportionally represented.

Analyses

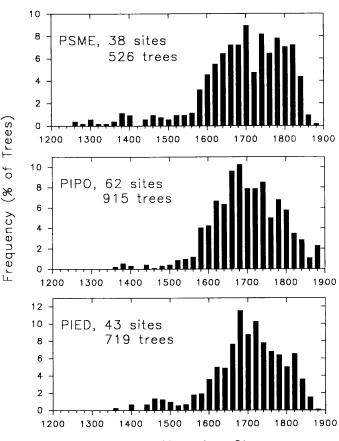
Each of the site data files typically contained two radial measurement series from each of at least 10 trees. In some cases, many more trees were sampled per site (e.g., 30 or more). The year of the first measured ring was extracted from each radial series from each site. The shortest of the two series from the same tree (later innermost ring date) was deleted. The resulting data was a list of inner-most measured ring years (dates), identified by site, tree, and species.

The inner-most ring years were not germination or establishment dates. The samples were increment cores taken from the lower trunk from at a height of about 1.5 m to about 25 cm from ground level. The pith was infrequently included in the samples (we estimate less than 10% of the time), although most cores probably extend near to the pith, so that in the majority of cases inner-most measured rings were within a few years to a decade of the pith. Thus, we estimate actual germination dates of the trees usually varied between about 5 and 20 years earlier than the inner-most ring dates. Because of these uncertainties, we grouped the inner-most ring dates into 20year age classes for assessment of temporal patterns. Frequency distributions were compiled for each species and plotted on the first year of the 20-year age classes.

RESULTS

Regional Maximum Age Distribution

All three of the major conifer species had a maximum age distribution that is more or less bell-shaped, with means and modes centered around the late 1600s and



Twenty-Year Age Classes

Figure 2. Distribution of all trees sampled within sites in Arizona and New Mexico, sorted by species. The percentages of inner-most ring dates of trees falling in each age class are plotted on the first year of the twenty-year age classes. For example the age class shown at the 1600 tick mark includes trees with innermost ring dates falling between 1601 and 1620. Species abreviations are:

PSME = Douglas-fir, PIPO = ponderosa pine, PIED = piñon.

early 1700s (Fig. 2). The mean ages (years) of all trees in the data sets, and modes of the twenty-year age class (innermost ring dates) were, respectively: Douglas-fir 289 years, 1700; ponderosa pine 279 years, 1680; and piñon 278 years, 1680. The age distributions also had a long "tail" of fewer older trees that established before about 1580 (Fig. 2). The lower percentages of trees in more recent age classes (i.e., post-1800) are mainly a reflection of the sampling strategy which typically targeted only

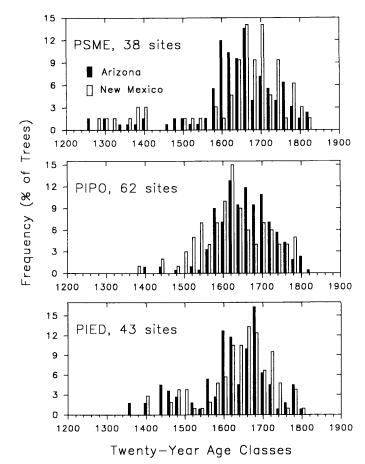


Figure 3. Distribution of five oldest trees from 143 sites in Arizona and New Mexico, sorted by species and state. As in Fig. 2, percentages falling in each age class are plotted on the first year of the twenty-year period.

the oldest stands, and oldest trees within stands. A sorting that included only the five oldest trees within each site had a similar pattern, although modes of the Douglas-fir and ponderosa pine were shifted to older twenty-year age classes (1660 and 1620, respectively) (Fig. 3).

Age distributions of Douglas-fir and white fir sampled systematically in the 21 stands from northern New Mexico (Fig. 4) reflect the dominance of younger age classes that would generally be expected in uneven-aged stands with a pattern of more-or-less continuous recruitment and mortality. The lower number of individuals in age classes after 1920 was probably due a lack of sampling of trees smaller than 20.3 cm

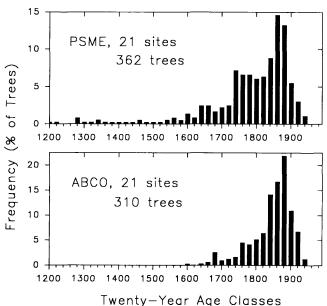


Figure 4. Distribution of all trees systematically sampled in 21 mixed-conifer stands in northern New Mexico. ABCO = white fir.

dbh. White fir were generally younger than the Douglas-fir (Fig 4.), although we suspect that the lack of older inner-most ring dates is partly due to the fact that many of the oldest trees of this species had heartrot and hollow interiors.

The oldest Douglas-fir trees in these stands were considerably younger than the oldest trees in the larger regional set (Figs. 2 and 3). For example, the median age of the larger regional set was about 275 years (establishing before 1716), whereas less than 23% of the Douglas-fir sampled in the 21 northern New Mexico stands were older than this. An even smaller percentage of such older trees (relative to all trees) are present in the northern New Mexico stands, because we also sampled at least five of the oldest appearing trees. This suggests that the oldest trees within the regional data set of old-growth stands (as described by distributions in Figs. 2 and 3) may comprise a relatively small proportion of the total stocking of more typical old-growth stands of northern New Mexico (i.e., those not specifically selected for maximum age).

Dendrochronologists working in the Southwest have known for a long time that trees up to about 350-400 years of age

(establishing in the period from about 1600 to 1640) could usually be found in most mountain areas, but trees older than this were more difficult to locate. This phenomenon is reflected in the decline in innermost ring dates before 1600 (Fig. 2 and 3), especially in Douglas-fir. This pattern shows up most clearly in Fig. 3, especially as fewer trees in the mid to late 1500s age classes, and larger numbers of trees in the early 1600s age classes. Ponderosa pine in New Mexico appear to be an exception to this pattern. The classification by twentyyear periods, necessitated by uncertainty in the relation between our inner-most ring dates and actual germination or establishment dates, tends to obscure the actual date of decline in number of trees sorted by age class. However, the age distribution within many individual sites show the oldest trees (including pith dates) establishing in the early decades of the 1600s, with only a few, or no trees establishing earlier. The lower number of inner-most ring dates before the late 1500s could be a reflection of higher mortality rates, lower regeneration rates, or both, before this time. This pattern could also simply be measure of some physiological age limit for these species, although the fact that we can find some trees and stands that are much older seems to counter this argument.

These observations led us to hypothesize that an event or events in the late 1500s and early 1600s affected the mortality and regeneration patterns of conifers throughout the Southwest. An obvious possible cause for such a pattern is climate change. Tree-ring width chronologies are the best available source of information on climate variations on these time scales, but the decline in sites with trees old enough to reflect changes during the late 16th and early 17th century somewhat limits our ability to examine climate change during this period. Fortunately, a tree-ring chronology network derived from living trees and archaeological specimens (beams and timbers from ancient dwellings) has recently been used by dendrochronologists to reconstruct the past 1,000 years of winterspring precipitation (D'Arrigo and Jacoby 1991) and spatio-temporal variations in tree-

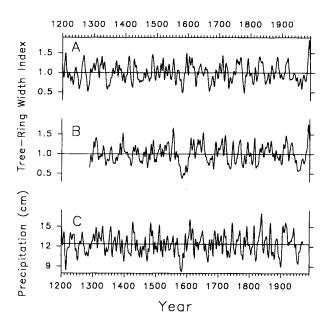


Figure 5. Precipitation variations in New Mexico can be inferred from the treering-width index chronologies from ancient limber pines at the Elephant Rock site (A) and Douglas-fir at El Malpais site (B). These time series were smoothed with a 13-weight symmetrical filter (Fritts 1976). See text for descriptions of the sites. Dendroclimatic study (Grissino-Mayer et al., in preparation) shows that the limber pine have a strong spring-summer precipitation response. The El Malpais Douglas-fir reflect primarily winter-spring precipitation. Tree-ring reconstructed winter precipitation from living tree and archaeological samples from northwestern New Mexico is shown in the bottom plot (C) (modified from D'Arrigo and Jacoby 1991). All three time series show the severe late 1500s drought, especially the El Malpais indices (B) and the winter precipitation reconstruction (C). The reconstruction ends in 1970.

Table 1. Oldest known living trees (at time of sampling) of various tree species in Arizona and New Mexico.

Species	Date of * Inner Ring	Date g Sampled	Number of Years	f Site Name	Location
ponderosa pine (Pinus ponderosa)	1243	1984	742	Mount Bangs	Mt. Bangs S.E. of Littlefield, AZ
Douglas-fir (Pseudotsuga	1062	1991	930	Bandera	El Malpais National Mor south of Grants, NM
menziesii) piñon (Pinus edulis)	1295	1960	666	Mariano Lake	N.W. of Gallup, NM
bristlecone pine (Pinus aristata)	547	1984	1,438	San Francisco Peaks	San Fran. Peaks N. of Flagstaff, AZ
limber pine (Pinus flexilis)	±320	1989	1,670	Elephant Rock	Sangre de Cristo Mtns. E. of Questa, NM
Southwestern white pine	± 1454	1991	538	Camp Point	Pinaleño Mtns. S.W. of Safford, AZ
(Pinus strobiformis) white fir (Abies concolor)	1655	1987	333	Alamitos	Sangre de Cristo Mtns. S. of Angostura, NM
Engelmann spruce (Picea engelmannii)	1696	1990	295	Emerald Peak	Pinaleño Mtns. S.W. of Safford, AZ
gambel oak (Quercus gambelli)	± 1587	1987	401	Beaver Creek	Beaver Creek S. of Flagstaff, AZ

^{* ±} indicates inner-most ring date is estimated from a ring count only, while other dates are dendrochronologically crossdated.

ring growth (Graybill, pers. comm.) in northwestern New Mexico and northeastern Arizona. We also have recently discovered ancient tree sites in north central and west central New Mexico that provide an estimate of climate variations through the relevant time period (Grissino-Mayer et al., in preparation).

The tree-ring width data indicate that a severe drought occurred in the late 1500s, followed by very moist conditions during the early 1600s (Fig. 5). Spatial analysis of tree-growth variations in the archaeological tree-

ring set indicate that this response, particularly the drought, was more pronounced in northwestern New Mexico than in northeastern Arizona (Graybill, pers. comm). The sorting of oldest trees within sites by state (Fig. 3) generally shows fewer trees establishing or surviving before the late 1500s in New Mexico (no Douglas-fir are included in the 1560 age-class) although ponderosa pine does not show an obvious sharp decline in numbers of trees before 1600. A pronounced increase in numbers of innermost ring dates in the early 1600s age classes is observed in Arizona sites, especially Douglas-fir and piñon (Fig. 3).



Figure 6. Strip-bark limber pine at the Elephant Rock site, west of Red River, New Mexico. Scattered trees and steep slopes visible in the background are typical of this site and other super old-growth stands.

"Super" Old Growth

Many other tree-ring collections from the most ancient stands and trees in the Southwest are not included in the data set compiled for the age distributions discussed in the previous section. This is because they are from other species not considered, or ring-width measurements have not been obtained from them yet. The oldest known trees of various Southwestern species are reported for the first time here (Table 1). Recent discoveries of very ancient Douglas-fir trees in several sites, and the oldest known trees the Southwest limber pines in the Sangre de Cristo Mountains - deserve special descriptions because they illustrate several characteristics of "super old-growth" in this region.

Elephant Rock Limber Pines

In many ways this site epitomizes the "classic" type of site that dendrochronologists look for to sample maximum age conifers with climate-sensitive ring-width

patterns. It is located on a very dry, steep, south facing slope (Fig. 6). The trees are widely spaced, stunted, and many have spike-tops, and "strip-bark" growth form. Numerous living trees at this site are over 800 years old. The oldest tree we have sampled so far is well over 1,600 years old (Table 1).

This site is on the Carson National Forest, a few kilometers west of Red River, New Mexico. Although the site is clearly not suitable for timber harvesting because of the extreme low productivity and steep slope, it could be threatened by future road building, or mining activity (a large molybdenum mine is only a few kilometers away).

Before we discovered this stand, the oldest known trees in the Southwest were the ancient bristlecone pines on the San Francisco Peaks near Flagstaff, Arizona (Table 1). As in many super old-growth stands, remnant snags and logs on the ground surface also contain ancient and valuable tree-ring records (Fig. 7).

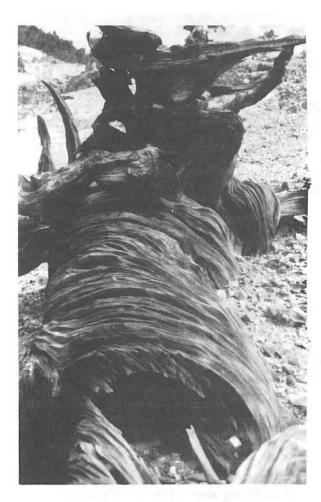


Figure 7. Ancient snags and logs, such as this partially buried limber pine log at the Elephant Rock site, are a valuable treering resource because they help extend the tree-ring record back in time. A short increment core was taken from the outer shell of this hollow log. The innermost ring, which was obviously quite far from the original pith, was crossdated at A.D. 767, and the outermost ring dated at A.D. 1231.

El Malpais Douglas-Fir

This site also appears to be an extreme situation for conifer growth. Very stunted Douglas-fir trees are growing in crevices and small pockets of soil accumulated on the Bandera lava flow in El Malpais National Monument, south of Grants, New Mexico (Fig. 8). Although the lava field is broken and undulating, the trees are apparently in stable and more-or-less level micro-sites. We have sampled dozens of trees here with

inner-most ring dates in the late 1200s to early 1300s. The oldest living tree sampled so far has a pith date of A.D. 1062. This is the oldest inland Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) that has ever been reported. Maximum ages of the coastal variety of Douglas-fir (*P. menziesii* var. *glauca*) reportedly exceed 1,000 years (Hermann and Lavender 1990).

The harsh conditions of this site have severely stunted the trees, but they are not subject to significant competition or spreading fires. Even though moisture is limited, and the annual rings have high year-to-year variation, good thermal insulating or water retaining properties of the lava may provide the trees with a relatively consistent water supply through the centuries that rarely is



Figure 8. Oldest known inland Douglas-fir growing in a small pocket of soil on the Bandera lava flow in El Malpais National Monument, south of Grants, New Mexico.



Figure 9. Ancient tree site on Mount Graham, near Safford Arizona. The oldest trees found on this site are among the large boulders on the steep slope (center of photograph), but other ancient trees, living and dead, are also found nearby.

so low that trees die from drought stress. The surprising lesson of this stand is that very ancient stands sometimes occur in highly unusual habitats that do not fit the usual expectations of where to find super old-growth, or of what it looks like.

Mount Graham Douglas-fir

In terms of moisture stress this site could be characterized as intermediate. Like the Elephant Rock site, it is on a steep slope, but tree density and overall site productivity are higher. The oldest trees are found on a rocky, south facing slope of Mount Graham just below a relatively level bench where road construction and logging has taken place in the recent past (Fig. 9). Several 600 to 700 year old Douglas-fir trees have been sampled here. The oldest tree has an inner-most ring date A.D. of 1257. The inner-most ring of a snag was dated at A.D. 1102, and fire-scarred logs of southwestern white pine (Pinus strobiformis) have been dated back to A.D. 1380. We are unaware of any immediate threats (such as road building or harvesting) to the ancient trees we know about on this mountain, but the overall environmental sensitivity of this area is well known as a

result of the heated controversy over the endangered Mt. Graham red squirrel (<u>Tamiasciurus hundsonicus</u> subspecies <u>grahamensis</u>) and the building of an astronomical observatory, which is only about 3 km from the ancient trees (Pennisi 1989, Waldrop 1990).

Rito Claro and Bonita Douglas-fir

These stands are quite different from the other super old-growth stands just described. Both sites are in Cabresto Canyon on the Carson National Forest east of Questa, New Mexico. The Bonita site (Fig. 10) would probably easily classify as oldgrowth based on the presence of many relatively large diameter Douglas-fir and white fir, multiple canopy levels, and abundant snags and logs. Although structurally this stand appears similar to many other old-growth forests we have sampled in northern New Mexico (see Lynch and Swetnam, this volume), it is unusually old and contains many trees (especially Douglas-fir) that established in the 14th century. Part of the stand is on a north facing slope, but many of the oldest trees are on a relatively level bench just above the canyon floor.



Figure 10. The Bonita stand east of Questa, New Mexico. This stand has typical old-growth characteristics that would probably match interim definitions, but maximum ages of trees are atypical. Many trees here are over 600 years old.

At first glance it is not at all obvious that the Rito Claro stand is ancient. In fact, it is one of the oldest Douglas-fir stands ever sampled in the Southwest. The site is on a south facing slope that is not especially steep (about 20%), tree diameters are generally small (most trees < 30 cm dbh), tree density is moderate, and the stand is primarily composed of Douglas-fir. Snags and logs are present, but they are not as abundant as in the Bonita stand. We sampled more than 60 trees in this stand, and among this collection ten trees had inner-most ring dates in the mid to late 1200s, and four other trees had inner-most ring dates before 1230. The oldest living Douglas-fir had a pith date of 1210 (Fig. 11).

Figure 11. Oldest Douglas-fir tree in the Rito Claro stand (left of center, with forked stem).



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DISCUSSION AND SUMMARY

The Southwestern tree-ring data we have analyzed represents only a small proportion of stands that potentially qualify as old-growth. However, this data set is useful as a documentation of the maximum ages of conifer trees that can be found in this region. Because these data are the product of many years of effort to identify the oldest stands, and the oldest trees within stands throughout the region, we argue that the compiled age distributions (Figs. 2, and 3) offer an estimate of what is "rare" in terms of age. The maximum age distributions of three major conifer species -Douglas-fir, ponderosa pine, and piñon - all confirm what dendrochronologists have generally known for many years: Super oldgrowth stands with trees over 400 years old (establishing before ca. 1590) are somewhat rare, and stands with trees over about 500 years old (trees establishing before about ca. 1490) are very rare.

The available tree-ring chronologies that extend back through the 1500s and earlier show that a very pronounced drought occurred in the late 1500s (Fig. 5). This offers a possible climatic explanation for the temporal pattern of decreased numbers of inner-most ring dates before about 1600. Our sorting of inner-most ring dates by state (Fig. 3) was arbitrarily defined by the stateline, and the resulting distribution by species and state do not show entirely consistent patterns. For example, ponderosa pine in New Mexico does not show an obvious decline in numbers of inner-most ring dates in the late 1500s, but both Douglas-fir and piñon in both Arizona and New Mexico do exhibit such a decline. The Arizona Douglas-fir and piñon sites have a more pronounced increase in numbers of inner-most ring dates in the early 1600s than the New Mexico sites.

Overall, the specific importance, if any, of the late-1500s drought or the subsequent wet period, to the dynamics and age structure of these species is not clear. We do not know if the important effect is on mortality or regeneration rates, or both. The co-occurrence of these climate changes and

the age distribution changes could be coincidental, or the relations could be indirect through other climate-related factors, such as disturbance (e.g., fires and insect outbreaks). Better time resolution in the age distributions (annual to decadal) may be needed to verify that a real change in age structure has occurred during this particular time period, especially since it occurs near the tail of the more-or-less bell shaped curves of the overall distribution (Fig. 2).

The super old-growth stands that are highly valued by dendrochronologists for scientific reasons (see discussion below), are distinctly different from the conception of old-growth that many land managers, and the public may have. The controversial endangered species issues of the Pacific Northwest (i.e., the spotted owl) have imprinted the image of old-growth as stately monarch trees with shafts of sunlight streaming down through tall, dense canopies. The Southwest does contain oldgrowth stands that fit this stereotype, but many of the oldest conifer stands in the Southwest do not. Structurally they are more "woodland" than "forest". The stands are often very open with sparse understory, and trees may be stunted in diameter and height. Sites are typically on steep slopes, with shallow rocky soils, and consequently, productivity (especially tree growth rates) is very low. Most of these sites are unlikely to be targeted for timber harvest. However, they are occasionally threatened by other human disturbances, such as fuelwood cutting, road building, or other development. Currently, the definitions for oldgrowth do not clearly include this special kind of old-growth.

It is also true that not all Southwestern super old-growth stands fit the descriptions given above. The Bonita stand, and to a lesser degree the Mount Graham stand, are examples of closed-canopy forests that more closely approximate the interim definitions of old-growth, and could be (and have been in the case of the Bonita stand) included in timber sales. While economically harvestable stands containing structural

aspects fitting the broader definitions of oldgrowth, such as Bonita, might be protected in some measure in the future, other potentially harvestable super-old-growth stands, such as Rito Claro, may "slip through the cracks". We have no clear solution to this problem, other than suggesting that timber sale planning and preparation include an assessment of maximum tree age within stands by taking increment cores and counting the rings. Dendrochronologists and other scientists who know about ancient stands with high scientific values should make an effort to point out these stands and their values to land managers.

Most of the foregoing discussion presumes that there are inherent resource values in super old-growth, distinguished primarily by exceptional old age, that are worthy of special consideration (e.g., preservation). As dendrochronologists our professional interests (bias!) in old trees are obvious, but we do feel that the scientific values of old-growth are very broad-based and significant. For example, tree-rings in old-growth contain information on past variations in rainfall, temperature, streamflow, forest fires, insect outbreaks, pollution, and many other aspects of forest ecosystems (Fritts and Swetnam 1989). Many different kinds of measurements of treerings, such as width, density, and isotopic composition have been used to learn about long and short-term changes in the environment. Tree-ring records, especially long ones, have been specifically targeted by U. S. national and international global change research programs as a key source of information on past changes that have occurred on the planet (EPA 1989, USFS 1990, IGBP 1990).

In a strict sense one could argue that even 700-year old trees are "renewable", however, the unique environmental histories they record are not. The history contained in these stands, in both the living and dead trees, is fundamentally an irreplaceable scientific resource, and this is a history we don't know enough about. Only a few dozen tree-ring records in the world extend back more than 700 years before present, but this period is of great interest and

importance to climatologists and ecologists because it encompasses significant shifts in global climate. For example, the medieval period (about A.D. 1000 to 1300) may have been marked by a general "warming", and then a cooling period known as the "Little Ice Age" (from about 1300 to mid-1800s) may have affected many areas of the world. However, the timing, magnitude, and spatial extent of these climatic events are poorly known, especially in North America. Improved understanding of these climatic phenomena is essential for developing and testing realistic predictive models of global change.

The Southwest happens to be one of the few places in the world where sufficiently long and sensitive tree-ring records can be found to study climate and ecological variations during the past millennium. At the very least, "salvage" of valuable tree-ring records prior to disturbing super old-growth stands is warranted. Long-term protection is also justified by the need to resample and study these sites in the future. Resampling in the future will offer the chance to apply new analytical techniques to new scientific questions. Additional years of independent environmental observations will also increase our ability to interpret and understand tree-ring records (Van Pelt and Swetnam 1990).

The emphasis of the preceding paragraphs has been on old-growth stands as a tree-ring resource. There are many other scientific uses of old-growth, including the study of population dynamics, genetics, nutrient cycling, community ecology, etc. We understand that many resource values other than purely scientific ones have dominated the public discourse on oldgrowth, particularly the values of endangered animal species, and jobs for people. Nevertheless, we hope that recognition of the rarity of certain ancient stands and trees in the Southwest, and their scientific values, will lead to a broader and more complete assessment of the resource values that are at stake.

ACKNOWLEDGEMENTS

The tree-ring data used in this paper were collected by several generations of dendrochronologists, and to them we are grateful. Chris Baisan and Henri Grissino-Mayer deserve credit for discovering the ancient stand on Mount Graham. Tony Caprio was involved in sampling and dating several of the oldest trees, including the Elephant Rock limber pine, Rito Claro Douglas-fir, and El Malpais Douglas-fir. Henri Grissino-Mayer and Rex Adams both sampled the oldest Douglas-fir at El Malpais. Tom Harlan discovered and dated the oldest ponderosa pine on Mount Bangs. Other oldest tree dates were provided by Don Graybill (bristlecone pine), Franco Biondi (gambel oak), Chris Baisan and Henri Grissino Mayer (southwestern white pine and Engelmann spruce). We thank Roseanne D'Arrigo and Gordon Jacoby for providing the values of tree-ring reconstructed winter precipitation shown in Fig. 5., and Lori Stiles, Henri Grissino-Mayer, and Ann Lynch for providing photographs. Funding for collection of the tree-ring data came from many sources, but most notably from the Laboratory of Tree-Ring Research (State of Arizona), National Science Foundation, Environmental Protection Agency, U. S. Forest Service and National Park Service.

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Carbon, Water, and Nutrient Relations – Distinguishing Functional Features of Old-Growth Lodgepole Pine Forests in the Southern Rocky Mountains¹

Merrill R. Kaufmann²

The vegetation in forest ecosystems is composed of carbon, water, and nutrients. Old-growth forests differ functionally from younger forests in patterns of distribution and in processes involving carbon, water, and nutrient resources. Old-growth forests store large amounts of carbon in live biomass, but net productivity of old stands is generally near zero because new photosynthate is offset by respiration and the mortality of trees and tree parts. Large amounts of nutrients may be unavailable for new growth in old stands because they are held in living or dead biomass. Leaf area of old-growth stands is generally lower than in more productive younger stands. Leaf area may vary dramatically in old trees of similar size and age, perhaps as a function of the early growth history of individual trees. Reduced leaf area in old stands may contribute to lower transpiration and interception of water, and perhaps to increased water yield from catchments.

INTRODUCTION

Traditionally, old-growth forests were viewed primarily as reservoirs of wood products. Old-growth stands were often selected for commodity production because high standing timber volumes and minimum investments made them economically attractive. In certain areas such as subalpine forests, an added benefit of harvest was the increase in water yield following clearcutting.

The last decade has seen a dramatic shift toward considering forest lands as ecosystems rather than tree farms. The change in views of forest managers has been remarkable, with the present view no longer exclusively focused on commodity production, but rather focused primarily on sound, sustainable ecosystem management. In the context of the function and management of ecosystems, new questions have arisen about the ecophysiology of old-growth forests.

The summary paper of this volume (Kaufmann et al. 1992) notes that old-growth forests not only have certain structural and compositional characteristics

Because nutrients and water interact with the carbon cycle and are involved in processes affecting carbon balance and distribution in forests, these materials also are critical in forest ecosystem function and the development and persistence of the old-growth condition. Nutrients are required both for plant growth and for decomposition. Because water provides the medium in which cellular activities occur and nutrients are transported, water deficits affect growth and decomposition processes. In many forest ecosystems, nutrients (principally nitrogen) and water limit the rates of plant growth and decomposition (Miller 1981).

This paper focuses on how carbon, water, and nutrients influence ecophysiological processes during various developmental stages of lodgepole pine forests.

related to community function, but they also have important ecophysiological processes that set them apart functionally from other successional stages. Carbon, water, and numerous macro- and micro-nutrients are the principal constituents of a forest community, and their study is helpful in understanding forest ecosystem function. Carbon in particular plays a major role in almost every distinguishing structural characteristic of old-growth forests (see the old-growth description given in Kaufmann et al. 1992). Carbon is the major constituent of live biomass (foliage, stem, and roots) and dead phytomass (standing and down woody debris, and litter and humus on the forest floor). The aggregate of changes in each of these components determines the carbon balance of a forest stand.

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PATTERNS OF CARBON ACCUMULATION

The pattern of carbon accumulation in forests depends on the forest type and the structure and successional pathway following disturbance. In an even-aged lodgepole pine forest (and also presumably in ponderosa pine) developing from a stand-replacing disturbance such as fire, a large amount of carbon may be present in dead wood from the previous forest. As this dead wood decays over time, new trees rapidly accumulate carbon in new biomass, perhaps for well over a century. Eventually the forest matures and the rates of height and volume growth decrease.

While individual trees may continue to grow and become a part of the old-growth cohort, the growth of these trees is often offset by mortality of other individuals. Mortality in a 300-year-old lodgepole pine stand on the Fraser Experimental Forest in Colorado is about 0.5 percent of the population per year and appears to be increasing as the stand ages (W. Moir, personal communication). This mortality rate is similar to rates of 0.5 - 1.0 percent per year found in younger stands.

Old-growth forests subjected to disturbance such as fire or insect attack are commonly reset ecologically to an earlier successional stage or, where seed sources are available, develop an uneven-aged structure through ingrowth and release of Engelmann spruce and subalpine fir. The frequency of fires is greater at low elevations and on south-facing slopes than at higher elevations and on north-facing slopes. Successional status and stand structure reflect these differences in disturbance history (Romme and Knight 1981). In forests with even-aged structure that have remained undisturbed for long periods of time or those subjected to only minor disturbances through time that favor development of multiple canopy layers, carbon accumulation may reach a stable point in which growth and mortality are roughly equal.

Whatever the initial structure, the development of the old-growth character includes a strong tendency for the production of new living biomass to be offset by mortality and respiration, so the net stand growth approaches zero and the total live biomass remains fairly constant (Jarvis and Leverenz 1983, Pearson et al. 1987, Waring and Schlesinger 1985). Furthermore, the growth efficiency (amount of biomass produced per unit of incoming solar energy) is lower in old stands than in young ones. However, successional stages, such as dog-hair lodgepole pine, may develop in which net productivity of the stand is reduced to zero before old trees exist, in which case the stand fails to meet old-growth conditions. Thus the functional stand feature of net productivity being near zero is not, by

itself, a distinguishing characteristic of old-growth forests any more than is structural complexity, which also may occur without old trees.

The spatial and temporal distribution of carbon among various components of a lodgepole pine forest is represented in Figure 1. These data were collected for several stand ages on the Fraser Experimental Forest in northern Colorado (Ryan and Waring 1992). Younger stands accumulated carbon in new wood rapidly, but the rate declined sharply after 50 years. No data were collected for the age period 100 to 260. During this time there was a slight increase in the amount of carbon in wood, but much of this may have occurred well before the trees reached 270 years of age. Thus while the rate of change in various carbon-storing components is not known at 270 years, there probably was little net carbon gain at this late stage of stand development. Individual trees undoubtedly still accrued carbon, but this was probably offset by losses from mortality, woodrot in living trees, and increased respiration.

Changes in carbon pools in a lodgepole pine forest result from differences in annual carbon flux to various constituents of the stand. The annual carbon flux to wood is highest early in the life of the stand (Fig. 2). This corresponds to the period of most rapid increase in total wood (Fig. 1). Foliage production reaches a maximum when the canopy fully closes and declines slightly through the remaining life of the stand. Litterfall includes foliage, branches, and bark and is slightly larger than annual foliage production. Root production remains fairly high throughout the life of the stand, but much of the annual carbon flux to roots is lost by fine root turnover.

A major portion of the annual carbon fixed is lost through respiration (Fig. 2). Two types of

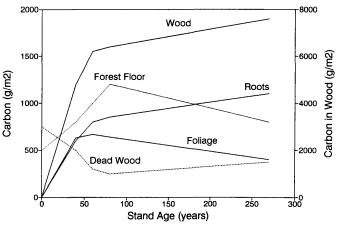


Fig. 1. Changes in carbon stocks for lodgepole pine over time. (Unpublished data of M. G. Ryan developed from allometric relationships; see also Ryan and Waring 1992.)

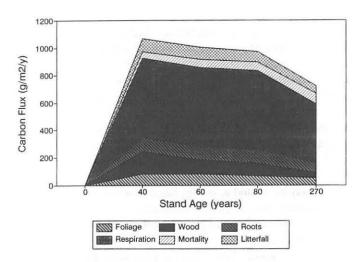


Fig. 2. Annual carbon fluxes over time for lodgepole pine (note non-linear lower axis). (Unpublished data of M. G. Ryan developed from allometric relationships; see also Ryan and Waring 1992.)

respiration occur. All living tissues require respiration to maintain the system (maintenance respiration), and growing tissues require additional carbon for respiration during the growth process (growth or construction respiration) (Amthor 1989). The relative importance of these two types of respiration changes over time (Fig. 3). Early in the life of the stand, more carbon is used for growth respiration and biomass is accumulating rapidly, while the total respiring biomass being maintained is still relatively low. As the stand matures, the growth rate decreases, but the live biomass has increased, resulting in a shift toward lower growth respiration and higher maintenance respiration.

Annual photosynthetic productivity may decline with age in lodgepole pine. The reason for the decline in growth of old trees and in productivity of old stands is not known, but it may involve reductions in photosynthesis. Net photosynthesis may be estimated in Fig. 2 as the sum of all components except litterfall (which is roughly equal to foliage production). The sum of all the carbon fluxes declines by 20 - 25 % from age 40 to age 270. Consistent with this, studies of photosynthesis on old and young lodgepole pine trees indicated that the maximum rates of photosynthesis were about 25 % lower during summer months in old trees (unpublished data of M. G. Ryan). Similar results have been observed in ponderosa pine trees (unpublished data of B. Yoder), suggesting that old trees may have less fixed carbon available for allocation to various uses. More exact estimates of carbon balance and allocation in old-growth and younger lodgepole pine forests are the subject of current research.

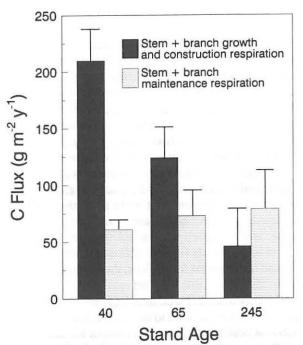


Fig. 3. Changes in growth and construction respiration and maintenance respiration over time for stems and branches of lodgepole pine (from Ryan and Waring 1992).

In lodgepole pine, the onset of the old-growth condition is probably best characterized by trees reaching an age at which height growth nearly ceases and the crowns of some trees become flat-topped (Kaufmann and Watkins 1990). As crowns deteriorate, mortality of some trees begins, and the stand enters a period, perhaps lasting many decades, during which trees are in various states of decline. The patterns of annual carbon flux and total carbon accumulation during the entire old-growth period depend largely on the changes that occur in the forest community. If there are no major biotic disturbances, the stand may decline gradually, indicated by decreases in amount of live wood and increases in amount of coarse and fine woody debris entering the decomposition cycle. Biotic disturbances such as herbivory and parasitism may accelerate the rate of decline, reducing the time period during which old trees persist, and they may create openings in which new trees develop, resulting in a more complex stand structure and carbon flux features reflecting the presence of young trees.

NUTRIENTS AND WATER IN OLD-GROWTH STANDS

As the live biomass of a forest increases, the mass of nutrients accumulated in living tissues also increases (Fahey et al. 1985). This may reduce the supplies of nitrogen and certain other macro- and micro-nutrients in the soil and litter for new growth,

and place a premium on internal retranslocation of nutrients from tissues having lower nutrient demands to tissues having higher demands (Nambiar and Fife 1991). More research is needed to clarify nutrient resources and requirements. Some nutrients are also derived from dead biomass in standing and down trees and from litter on the forest floor (Fahey 1983). Nutrient demands (especially nitrogen) of decomposer micro-organisms add to restrictions in amounts of nutrients available for plant growth. Thus old-growth forests normally are nutrient poor in the sense that most of the nutrients in the ecosystem are immobilized in plant tissue and temporarily unavailable for growth. One role of low-intensity fire is to release nutrients held in dead tissue on the forest floor, thus making a pulse of nutrients available for plant uptake.

Old-growth forests with little ingrowth of younger age classes may tend to have lower leaf areas than stands at peak production. The reasons for this are unclear, but they may include limitations in nutrient resources for foliage production and the effects of tree height and size on the development of water stress in the tops of large trees. Several hydrologic processes are affected by leaf area. Transpiration by the overstory is directly linked to leaf area, as is the interception and evaporation of rain and snow (Kaufmann 1985). Furthermore, leaf conductance to water vapor may also be lower in old trees. The net result of these factors is that total evapotranspiration may be lower in old-growth stands than in stands at earlier stages of development, and water yield from such forests may be higher than from the younger, more productive stands. Research is needed to obtain more precise comparisons between young and old stands.

LEAF AREA AND GROWTH HISTORY OF OLD TREES

As trees enter the old-growth period, leaf area is decreased either by the death of the top or branches, or through reduced annual production of needles and a shortening of the branch length bearing live needles (Kaufmann and Watkins 1990). Data collected from the Fraser Experimental Forest in Colorado illustrate the differences in leaf area that can occur in a small stand (1 ha) of lodgepole pine trees having similar height, diameter, and age (Table 1). These data are for trees selected to have a similar size but a wide range of leaf areas. The leaf areas for these trees ranged from as low as 10 to as high as 224 m². Trees with low leaf areas were obviously in a state of decline.

Preliminary analyses of the history of volume growth for these trees, using tree-rings and

cross-sections along the bole, indicate that the trees having the lowest leaf areas at the time of sampling consistently grew the fastest during their first 50 - 100 years, whereas those trees having high leaf areas at sampling grew more slowly when young (Fig. 4). Furthermore, the trees with high leaf area at sampling were growing more rapidly in recent years. This suggests that the growth pattern of trees in old stands may depend strongly on the growth pattern of the trees when the stand was young. While the later growth patterns may be related to earlier stand structure and competition, the role of genetic differences cannot be discounted, and research on genetic properties of trees having contrasting growth patterns is needed.

It is not known how these early growth patterns and the relative dominance position for these trees compared with those of the other trees making up the young stand, except that these trees were the survivors. Nonetheless, the available data suggest that the longevity of an old-growth condition may be a direct result of the growth patterns when the stand was young. For example, the trees growing rapidly when young were undoubtedly the first trees reaching maximum size and developing crown deterioration features characteristic of old-growth stands. The trees growing more slowly but surviving normal stand thinning (perhaps codominants in the younger stand) had high leaf areas at sampling and presumably provided for longevity of the old-growth condition, because they had not yet entered a period of significant decline.

The implications for stand management to achieve old-growth characteristics are not entirely clear, but it is possible that appropriate manipulation of stand conditions at an early age may influence the age at which old-growth conditions develop and the length of the period during which those conditions persist.

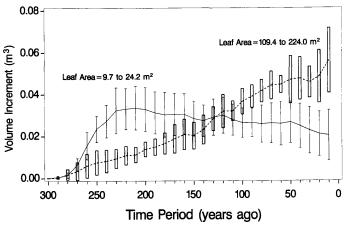


Fig. 4. Bole volume increments over time for five trees having low or high leaf areas (Low Set and High Set from Table 1). Bars indicate two standard errors. (Unpublished data of M. R. Kaufmann.)

Table 1. Difference in total leaf area of lodgepole pine trees having similar heights, diameters, and ages. Values are means and ranges for five trees having the lowest (Low Set) and highest (High Set) leaf areas out of a sample of 20 trees.

Variable	Lov	v Set	High Set		
	Mean	Range	Mean	Range	
Leaf Area (m ²)	20	10-25	152	109-224	
Height (m)	21.9	20.7-23.4	21.0	19.8-22.1	
DBH (cm)	30.3	28.5-32.7	31.3	28.6-33.2	
Age (yr)	273	260-286	270	251-282	

Research is needed to evaluate early stand conditions in relation to the old-growth features that result, and to determine if similar processes occur in other even-aged systems such as ponderosa pine. Research also is needed to determine if there is a genetic component to the differences in early growth rate and later decline.

Research is needed to determine how growth patterns, carbon balance, and nutrient and water resources of stands change over time, and how they are related to stand conditions at various stages of forest development. By examining growth patterns and carbon allocation at these various stages, researchers and managers may achieve a greater understanding of the manner in which old-growth stands develop, and how stands can be managed to favor the development of desirable mature and old-growth forests.

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Past and Present Fire Influences on Southwestern Ponderosa Pine Old Growth¹

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Abstract.—For centuries, the climate of the Southwest teamed with frequent natural fires to develop and maintain an open-structured ponderosa pine forest. Most pine regeneration died in competition with grasses or in the inevitable surface fires. Those that survived were sustained throughout the next several centuries by this fire sequence. Oldgrowth ponderosa pine was the rule before white settlement, rather than the exception as it is today.

The old-growth component of southwestern forests has been declining because of decades of timber harvesting, intensification of forest pest epidemics, and increasing severity of wildfires. Pest and wildfire losses can be directly or indirectly tied to suppression of natural fires. Because of the tenuous status of the remnant old-growth component, forest management should emphasize maintaining and improving growing conditions for perpetuating old growth. Furthermore, management programs should begin to create additional old-growth stands from current, younger stands. Because fire was the primary element in sustaining presettlement old growth by controlling fuel levels and stand densities, it should be relied upon again, possibly in concert with mechanical thinning and fuel reduction, to reestablish old growth prominence. However, in this process, large stand density reductions should be anticipated. This may represent shorterm economic losses, but will result in a long-term gain in large, high quality timber.

INTRODUCTION

Ponderosa pine (*Pinus ponderosa* Laws. ex Doug.) occupies 8 million acres of commercial timber land in the southern Rocky Mountain States of Arizona and New Mexico (Schubert 1974). Included in this acreage is one of the largest continuous pine forests in North America with an unbroken band 25 to 40 miles wide and about 300 miles long extending from northcentral to northeastern Arizona to west-central New Mexico (Cooper 1960). In addition to its expanse, other attributes make this a highly valued forest. These include high timber, wildlife, watershed, and recreational values. Many of these qualties are associated with the diversity contributed by old growth. However, during the past century, slow but dramatic changes in the structure and composition of southwestern ponderosa pine have likely altered these values.

HISTORIC FOREST CONDITIONS

Chronicles from 19th century explorers, scientists, and soldiers described a forest type quite different than what is seen today. Ponderosa pine forests were open and parklike with abundant grass and forb

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cover dominating the understory (Biswell et al. 1973). Stately, mature pines grew predominantly in small groups. Scattered clumps of young trees occurred infrequently in spaces between these groups. It seems realistic to assume that for the 150 years of historic documentation before the 20th century, and perhaps for centuries prior, most southwestern pine stands had an old-growth component. Furthermore, this component likely made up a large portion of the forest landscape.

Two interrelated, abiotic factors helped maintain this open-structured forest. Climate is a key factor in vegetation development. Regular precipitation patterns in this pine zone usually include enough winter snow to saturate the soils. Winter temperatures are relatively mild with monthly averages slightly above 30 °F (Schubert 1974). Annual precipitation minimums occur in May and June with many places receiving less than 0.5 inch of rain for each of those months. This dry period is also represented by increasing air temperatures, low humidities, and persistent winds. By early to mid-July, this drought is usually broken by a rainy period. July and August are the wettest and warmest months of the year. As temperatures cool in the fall, another dry period frequently occurs.

Fire is the other factor that has had a great impact on southwestern vegetation. Early explorers observed both lightning and Indian-ignited fires (Cooper 1960), but fire scar records from the ponderosa pine zone document fire history more precisely. These records authenticate the long-term recurrence of extremely short fire intervals. Within designated sites, mean fire intervals of 6 to 7 years have been documented in east-central Arizona (Weaver 1951), 2 to 3 years in north-central Arizona (Dieterich 1980), and 5 to 6 years in southwestern New Mexico (Swetnam and Dieterich 1985). Most southwestern ponderosa pine fire scar chronologies point to only a few periods as long as 15 to 20 years without fires during several centuries prior to 1900. These have been associated with abnormally wet cycles (Swetnam and Dieterich 1985).

The typical climatic patterns and presettlement vegetation dictated the frequent return of fire. The continuity of grass and pine litter fuels, frequent lightning, and the warm, dry spring and early summer weather contributed to high fire frequency (Pyne 1982). Highly flammable litter fuels built up rapidly after surface fires. Grasses resprouted and needle cast occurred annually providing fuel for subsequent ignitions. Large, woody fuels rarely accumulated over extensive areas. Mortality of large trees from surface fires was unlikely, and crown fires were exceptionally rare (Biswell et al. 1973). This was apparent even during the drought years of 1903 and 1904, when north-slope spruce-fir types were ravaged by crown fires, but south-slope pine stands survived (Kallander 1969). General tree mortality during presettlement times was usually the result of lightning, dwarf mistletoe, insects, windthrow, or senescence with old age. When single or small groups of trees died and fell, they were consumed by the inevitable surface fires. This more severe, but localized, fire treatment produced mineral soil seedbeds and reduced grass competition, creating a favorable microsite for ponderosa pine seedling establishment (Cooper 1960). Generally, tree seedlings died while competing with established grasses or were burned in fires, but within severely burned microsites with little fuel buildup, a few groups of seedlings infrequently survived. As these seedlings grew, their competitive ability kept grasses from flourishing nearby. In addition, as the pines aged their resistance to fire increased quickly. This pattern resulted in an uneven-aged forest with small, relatively even-aged groups (Cooper 1960).

POSTSETTLEMENT FOREST CHANGES

Changes in the old-growth ponderosa pine forests of the Southwest began during extensive livestock grazing in the late 19th century (Faulk 1970). Most herbaceous vegetation could not survive the intensified grazing, and its coverage declined drastically. This vegetation decline subsequently led to reduced fire spread because of the decrease in fine fuels, and an eventual increase in ponderosa pine regeneration because of reduced competition and fire mortality, and more mineral seedbeds (Cooper 1960). In the early 1900's, forestry practices, including fire suppression, further reduced the spread of fires, leading to unprecedented fuel accumulation and stagnation of seedling and sapling thickets (Biswell et al. 1973).

The ponderosa pine forests that have developed in response to these changes bear little similarity to the presettlement forest. In the uncut or lightly harvested stands, some old-growth trees remain. The open structure is gone, however, as dense sapling thickets and small pole groups have developed in the understory. Stand stagnation has been reported on many sites as several thousand saplings per acre are commonplace (Cooper 1960; Schubert 1974). Stagnation persists without natural or artificial thinning. Extremely slow growth is apparent with these stand densities. One northern Arizona site with over 5,000 stems per acre had 43-year-old trees that were growing at a rate of 1 inch in diameter in 33 years (Schubert 1971). After thinning to less than 500 stems per acre, the largest trees responded with a growth rate of 1 inch in 4 to 5 years, possibly representative of presettlement growth.

Slow growth indicates low vigor, high stress, and generally poor health, not only for the dense sapling class but also for adjacent age classes because of intense competition for moisture and nutrients. Older trees are susceptible to disease and insect attacks when they are highly stressed. Primary examples in the Southwest include armillaria root rot and mountain pine beetle (Schubert 1974). In addition, dwarf mistletoe is a major cause of mortality in the ponderosa pine belt. It can kill trees of all age classes. Fire was considered the primary natural control agent of dwarf mistletoe by thinning and pruning diseased trees (Hawksworth 1961). Without frequent fire, mistletoe infestations have increased substantially. Schubert (1974) states that disease (primarily dwarf mistletoe) and insects (primarily bark beetles) account for more than 75 percent of the Southwest's ponderosa pine sawtimber mortality. In addition to stand changes, 75 to 100 years of general fire absence has also led to abnormally large accumulations of surface and ground fuels (Kallander 1969).

The natural accumulation of pine needles and woody fuels is exacerbated by the very slow decomposition rates characteristic of the dry southwestern climate. The steady state weight of dead forest floor fuels, a level at which organic matter inputs equal organic matter decomposition loss, can range from 9 tons per acre in sapling thickets to almost 50 tons per acre on old-growth sites. Annual fuel accumulation on those sites ranges from less than 0.6 ton per acre per year to more than 3.5 tons per acre per year (Sackett and Haase, in preparation). The decomposition rate (k) (Jenny et al. 1949) is the ratio of steady state forest floor weight to the annual accumulation weight. The characteristics of needle litter and small woody fuel for 17 ponderosa pine overstory stands are:

	Sapling	Pole	Old growth
Steady state			
forest floor (tons/acre)	14.3	24.4	42.6
Annual forest floor			
accumulation (tons/acre)	1.09	1.43	2.12
Decompositon rate (k)	.076	.059	.050
2 ccompositori raco (12)			

These k values are considered quite low (Olson 1963). High decomposition rates, where k approaches 1.0, occur in very warm, humid climates.

Sackett (1979) reported average loadings of naturally created fuels at 22 tons per acre (ranging from 8 to 48 tons per acre) for 62 southwestern ponderosa pine stands. Harringon (1982) verified the heavy fuel loading, finding an average of 34 tons per acre in southeastern Arizona. Another formerly uncommon feature is the abundance of large, woody fuels, averaging about 8 tons per acre. Much of these down, woody fuels have accumulated in sapling thickets, creating an even greater probability for crown fires.

The changing forest conditions have alterated the herbaceous understory as well. The open, parklike structure of presettlement stands was accompanied by a luxuriant herbaceous layer. With more area occupied by ponderosa pine, understory vegetation has significantly diminished, reducing forage for wildlife and livestock (Arnold 1950). One study in northern Arizona showed that in an unmanaged condition, a stand with 210 square feet of basal area per acre produced no forage, whereas an adjacent stand thinned to 30 square feet produced 470 pounds of forage per acre per year (Schubert 1974).

In the past, pine regeneration generally developed in stand openings after fire had produced a grass-free, mineral seedbed. Now, when trees die creating openings in the stand, pine seedlings have little opportunity to become established in the poor quality, organic seedbed (Sackett 1984).

The dense stands and heavy fuel accumulation are the primary contributors to the increasing number of severe wildfires. Examples include the 1951 Gila Black Ridge Fire (40,000 acres), the 1956 Duddly Lake Fire (21,000 acres), the 1971 Carrigo Fire (57,000 acres), and the 1977 La Mesa Fire (15,000 acres) (Biswell et al. 1973; Cooper 1960; USDA 1977). More recently, six lives, many structures, and numerous acres were lost in the 1990 Dude Fire near Payson, Az. Fire reports from all southwestern agencies further reveal the increased potential for damaging wildfires. During the 75-year period from 1916 to 1990, wildfires burned over 100,000 acres is each of 16 years. Nine (56 percent) of these 16 large fire years have occurred in the last 12 years. Eleven (69 percent) have occurred in the last 20 years. This increase has taken place despite impressive advances in fire detection and suppression technology. In the first half of this century, the impacts of high-frequency, low-intensity fires were still apparent. Fuel and stand conditions had not yet deteriorated to hazardous levels, and intermittent cool, moist periods reduced the fire danger. More recently, with widespread hazardous fuel conditions, droughtlike weather has made large wildfires a regular occurrence. Old-growth trees, which survived numerous presettlement fires, now commonly succumb to highintensity crown fires.

In summary, changes within the past century have resulted in several undesirable conditions in the southwestern ponderosa pine forests. Extreme fuel

hazard is probably most apparent. Heavy forest floor fuel loadings and dense sapling thickets combine with the normally dry climate and frequent lightning- and human-caused ignition potential to create a severe wildfire threat (Biswell et.al. 1973; Harrington 1982). Additionally, trees of all sizes have generally poor vigor and reduced growth rates (Cooper 1960; Weaver 1951). Reduced soil moisture availability caused by intense competition and by moisture retention in the thick forest floor likely contribute to the stagnation (Clary and Ffolliott 1969). The thick forest floor also indicates that soil nutrients (especially nitrogen) are bound in unavailable forms, possibly resulting in nutrient deficiencies (Covington and Sackett 1984).

MANAGING OLD-GROWTH STANDS

The need to alleviate the stagnated and hazardous forest conditions was recognized decades ago (Cooper 1960; Weaver 1951). Much of current mortality of large ponderosa pine can be related directly or indirectly to fire exclusion for at least 75 years. For example, dwarf mistletoe, once held in check by periodic fires, is now a major cause of mortality. In addition, associated growth reduction and stress have resulted in destructive bark beetle epidemics. This stress is related to high competition due to overstocked stands, which was previously insignificant because of regular thinning by fire. A third significant cause of mortality is fire injury. The number of acres burned by wildfires fluctuates from year to year depending on climate, but a recent trend of increasing acres burned is apparent. Fires which formerly passed undramatically through the understories of these forests, now burn uncontrollably through the crowns of dense stands.

Southwestern forest conditions have been altered largely as a result of fire exclusion. The reintroduction of fire should figure into any attempt to relieve this condition. Management activities, including fire, must be evaluated for stands of all ages to provide optimum conditions for sustaining remnant old growth and to provide opportunities for establishing future old growth. This is because of the closeness and interaction of stands of different age classes. Widespread use of fire to achieve specific management goals has proceeded slowly. A shortage of prescription guidelines and insufficient fire effects information contribute to this reluctance.

Fuel Reduction

The use of prescribed fire for hazard reduction increased from the early 1950's to the early 1980's. However, concerns about smoke have led to burning constraints in recent years. Some of the earliest prescribed fire programs began on the Fort Apache Indian Reservation. Over 300,000 acres, containing primarily natural fuels with some logging slash, were burned from 1950 to 1970 for fuel reduction (Kallender 1969). A dramatic decline in wildfire size

and severity resulted (Biswell et al. 1973; Knorr 1963). Weaver (1952) reported that the number of wildfires in west-central Arizona was limited after prescribed burns consumed 55 to 80 percent of duff and nonslash woody fuels.

One important concern deals with the direct relationship of fuel consumption and tree injury. In one fire impact study, a relatively low-intensity, moderate-severity burn in Arizona ponderosa pine reduced surface, ground, and aerial fuels by 57% percent (Gaines et al. 1958). A contrasting burn under more severe weather and fuel moisture conditions initially consumed more fuel. However, when the fire-killed foliage, branches, and trees were added to the remaining surface fuel several years later, the reduction was only 15 percent. Documentation from two additional prescribed burning projects substantiated this finding. Burning in central (Davis et al. 1968) and west-central Arizona (Lindenmuth 1962) left sites with sufficient fuel reduction initially. After tree mortality, however, the net fuel loss on the sites was minimal.

Sackett (1980) and Harrington (1987) emphasized the important relationship of moisture content and consumption of forest floor fuels. Stand density and overstory type are also contributing influences. For example, with similar fuel moistures, forest floor reduction was 34 percent in sapling thickets, 52 percent in pole stands, and 89 percent in old-growth stands (Covington and Sackett in press). Because old-growth stands generally have the greatest forest floor loadings, this potentially high fuel consumption could represent a substantial impact, which will be discussed later.

Besides surface and ground fuels, extensive ladder fuels add to the fire hazard. In fact, it is this component that takes a surface fire into the crowns of the overstory, including the old growth. Vertical continuity can be broken with proper fire application. Some important live fuels are medium-sized shrubs, which are easily top-killed, but generally resprout. Gambel oak, for example, is quite flammable, but its height and canopy coverage can be kept low by repeated burning (Harrington 1985). Low crowns of ponderosa pine sapling thickets also increase crown fire threat. Scorching the lower portion of sapling canopies helps relieve this hazard, but the procedure is difficult (Harrington 1981).

Initially, the fuel hazard in these pine stands can be substantially reduced with understory burning. Removal of the litter layer reduces potential rates of fire spread and ignition. Reduction of duff, woody material, and ladder fuels decreases potential fire intensity, total heat release, and resistance to control. However, the fuel hazard is only temporarily reduced as up to 2 tons per acre of fine fuels are normally cast annually. Decidedly more can accumulate from fire-injured trees. This latter accumulation is the consequence of inevitable tree injury caused by consumption of unnaturally high fuel quantities in unnaturally dense stands. Consequently, repeated burning is essential to remove these fire-created fuels and

generally maintain a low fuel hazard. More detailed information on prescriptions and burning techniques can be found in Harrington and Sackett (1990).

Stand Density Reduction

Since the early 1900's, the remnant old-growth ponderosa pine stands that survived extensive logging and wildfire have been invaded by a profusion of pine regeneration. Reducing the densities of sapling thickets that cover millions of acres in the Southwest would produce many benefits. Besides reducing the crown fire hazard, herbaceous vegetation could be increased as more light and moisture become available (Clary and Ffolliott 1966). Because these "dog hair" thickets have encroached into oldgrowth sites, substantial decreases in the number of tree stems would lessen competition, possibly improving the health of young and old trees. Finally, most forest visitors find the dense stands inaccessible and esthically unappealing (Brown and Daniel 1986).

Managers have few options for reducing densities of these stands. Commercial thinning for pulpwood is possible where trees have grown into usable size. Precommercial thinning is probably the most common practice, but it is not economically feasible over extended areas. Additionally, the fuel resulting from large-scale thinning would encourage insect epidemics and create severe wildfire hazards. Obviously, no single treatment is the answer. The problem must be approached with a number of methods, depending on the circumstances and present conditions.

Thinning by fire was a natural process in ponderosa pine before white settlement (Cooper 1960). However, today's stand and fuel conditions are a drastic contrast to turn-of-the-century conditions. Fire thinning operations are complex, uncertain, and frequently viewed as wasteful, particularly given the high value placed on timber products. Guidelines for using fire as a thinning tool are scarce. Even though the smallest and least vigorous trees are the first to succumb to fire injury, fire is generally not very selective. A patchy stand with characteristics that cannot be predicted usually results. Most studies dealing with fire as a thinning agent have lacked a long-ranged process to accomplish the objectives. A number of fires are usually required to reduce fuels, change the stand structure, and overcome other alterations caused by decades of fire exclusion.

Several investigators have observed both positive and negative aspects of fire thinning. Weaver (1947) reported that 30 years after burning, a young ponderosa pine stand had fewer stems per acre, greater heights, and larger diameters than an adjacent unburned stand. In another study, Gaines et al. (1958) reported that even though younger, suppressed classes had been thinned, the commercial overstory suffered substantial injury. Lindenmuth (1962) studied the effects of fire in east-central Arizona and concluded that 24 percent of the potential crop trees were released from competition, but 17 percent were killed or severely damaged. Ffolliott et

al. (1977) reported that a positive thinning response followed prescribed fire in northern Arizona, but basal area was not reduced enough for optimal stand stimulation. Clearly, most research points out the imperfect nature of fire as a thinning mechanism. However, a single fire cannot be expected to correct forest stagnation that has occurred in the past 100 years. Additional information on burning techniques and thinning prescriptions is found in Harrington and Sackett (1990).

Thinning was also an important benefit in a more recent prescribed burning study in southeastern Arizona designed to reduce fuel hazards. A comparison was made between the impact of three distinct fires on sapling thickets and old-growth groups (Harrington 1981). The fires reduced tree densities by 24, 43, and 56 percent in stands with total fuel reductions of 13, 18, and 22 tons per acre, respectively, implying a relationship between fuel reduction and stand density reduction. Basal area in the oldgrowth groups was reduced only 2 percent, indicating that with a 26 percent reduction in stems per acre. most mortality was in the small size classes. However, observations several years after prescribed burning have revealed results that need special attention.

The impacts of 75 to 100 years of fire suppression can have quite serious impacts when fire is reintroduced into old-growth ponderosa pine. Frequent fire intervals of presettlement times (2-5 years) kept fuel accumulations to a minimal level (2-8 tons per acre) at the bases of mature trees. Today, total litter and duff accumulations in old-growth groups can amount to 30 to over 70 tons per acre.

Even though there are valuable fuel hazard, nutrient, thinning, and regeneration benefits derived from the consumption of heavy forest floors, there are also liabilities. Consumption of large quantities of fuel generates large amounts of heat. Studies at Fort Valley and Long Valley Experimental Forests in Arizona show very high mineral soil temperatures during burning (Sackett and Haase, in preparation). Lethal temperatures have been measured deeper than 8 inches in the mineral soil on some sites. The first burn in 100 years at the Chimney Spring Prescribed Fire Research Area at Fort Valley killed almost 40 percent of the old-growth ponderosa pines, which had survived numerous presettlement fires. Mortality did not appear until several years after the burns and has continued to be greater than on unburned sites.

Fires burning under these old-growth pines are often unspectacular, consuming only the litter layer in the flaming front. Most of the forest floor is consumed by smoldering combustion, which often goes unnoticed. As smoldering continues for up to 72 hours, ash is formed from the top down, creating an insulating cover. The insulation prevents heat from escaping causing it to penetrate the mineral soil. Burning for long time periods can result in either temperatures exceeding 140 °F, which causes instant

cambium or root death, or lower temperatures for longer durations which also can kill plant tissues.

Fuel loadings ranged from 32 to 86 tons per acre where temperatures were measured under old pines at Fort Valley and Long Valley. Consumption was always greater than 85 percent despite humus moistures up to 90 percent. In 22 of 25 cases, the temperature 2 inches below the soil surface reached 140 °F. At the 8-inch depth, temperatures exceeded 100 °F in 21 cases and averaged 138 °F. Even at 12 inches below the soil surface, temperatures greater than 115 °F have been reached.

Tree cambium can also be affected by forest floor consumption. Sloughed bark along with heavy duff compressed against the tree's bole generate additional heat during burning. Temperatures measured at the cambium where forest floor material is being consumed range from 61 °F to 231 °F. The average for 14 test fires was 144 °F, high enough to kill the cambium.

MANAGEMENT IMPLICATIONS

Forest management in the Southwest should include objectives that maintain or improve existing old-growth stands and that also begin to create supplemental old growth. Trees more than 200 years old are relatively scarce outside of research natural areas, experimental forests, and wilderness because of timber harvesting, and mortality from wildfire, insects, and disease. Therefore, the emphasis in forests managed for multiple use should be to generate conditions that will allow existing stands to development into healthy old-growth stands. Concurrently, growing conditions should be improved in the remnant old growth within experimental forests and wilderness areas and on isolated sites under general management.

Because recurrent fire was a primary element in sustaining presettlement forest health leading to the establishment and maintenance of old-growth stands, its use should be emphasized when restoring favorable conditions for ancient pine development. These conditions include low levels of dead organic matter (fuels) to lessen the potential of high fire intensity and severity, and open stand structure to reduce crown fire potential and intraspecific competition. Fire can be used to reduce fuel hazard, but its success has been uncertain and temporary. Failures denoted by too little or too much fuel consumption generally result from improper burn prescriptions and attempting to correct long-term fuel buildup with one treatment. Cooper (1960) questioned whether prescribed fire could be used in the restoration of deteriorated forests. He concluded that planned burning would either be too conservative and accomplish little, or would destroy the stand. While this observation has merit, with refined burning techniques as described in Harrington and Sackett (1990), it appears that fire could be applied sequentially to relieve the unnatural fuel and stand density status. However, it is apparent that considerable tree mortality will result, possibly representing an economic loss. This seems to be an inescapable cost, dictated by a century of forest degradation.

In extensive forest regions where old-growth pine groups are absent, designated areas based on site quality and existing stand types should be selected for creating future old growth. The best growing sites should be chosen because old-growth characteristics would be achieved more expeditiously there than on poor sites. Moir and Dieterich (1990) suggested that 150- to 200-year-old blackjack pines in open stands with no dwarf mistletoe be selected as the best stands to begin developing old growth. Through sequential silvicultural and fire treatments, the stands should be relieved of wildfire hazards and competition, allowing concentrated growth on a chosen group of trees. A long-term commitment is necessary, because another century may be needed before select oldgrowth pine is represented (Moir and Dieterich 1990). If younger stands are chosen for old-growth replacement, a greater commitment of time is required for thinning, slash disposal, commercial harvesting, and fire application.

Special attention should be given to the unnaturally excessive buildup of forest floor fuels in present old-growth sites. As mentioned, burning of these deep forest floor layers can mortally injure the roots and cambium of old pines, which previously survived many fires. Options for alleviating this atypical condition are not ideal. Managers could simply accept a 20 to 50 percent loss of old growth in a single fuel reduction burn as a cost of decades unnatural fuel buildup. Alternatively, heavy fuels could be manually reduced from the forest floor around old-growth groups before fire is used. This option would be limited by cost. Lastly, under the right fuel moisture conditions, fire might be used to peel the forest floor one layer at a time, eliminating the impact of a onetime heat shock. This option is speculative, since it has not been specifically attempted. If presettlement ponderosa pine stand and fuel conditions are approached, regular burning must be practiced to allow fire to play the primary role in sound ecological maintenance.

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Dendroctonus Beetles and Old-Growth Forests in the Rockies¹

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Abstract.--Dendroctonus beetles (Coleoptera: Scolytidae) are a major mortality agent in old growth pine, spruce-fir, and Douglas-fir forests of the Rocky Mountains. The frequency of recurring bark beetle epidemics depends on the size of the area being considered, how extensively the stand(s) was decimated by a previous epidemic(s), and how fast the stand(s) grows into the hazardous condition. Predictions of when epidemics will occur, their impact, and their duration are tenuous. Partial cutting may perpetuate old growth.

Dendroctonus beetles (Coleoptera: Scolytidae) are the significant mortality agent in old growth pine, spruce-fir, and Douglas-fir forests.³ Different species of *Dendroctonus* have killed tremendous numbers of trees in the different forest types of the West. Mountain pine beetle (MPB) (D. ponderosae Hopkins) populations during the period 1979-1983 infested over 4 million acres per year in the western United States and killed over 15 million lodgepole pine (Pinus contorta Douglas ex Loud.) trees per year (McGregor 1985). The MPB killed over 15 million trees in 1981 in British Columbia (Canadian Forestry Service 1982). The same species killed over 1 million ponderosa pine (P. ponderosa Lawson) in the Black Hills in the 1963-1974 period (Thompson 1975). The spruce beetle (SB) (D. rufipennis (Kirby)) killed millions of Engelmann spruce (Picea engelmannii Parry) during the infamous White River outbreak from 1939 to 1951 (Massey and Wygant 1954). The Douglas-fir beetle (DFB) (D. pseudotsugae Hopkins) killed 109 million board feet of Douglasfir (Pseudotsuga menziesii var. glauca (Beissn.) Franco) between 1970 and 1973 (Furniss and Orr 1978). In essence, a destructive Dendroctonus

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³Old growth as used herein refers to any stand with a number of susceptible-sized trees. Susceptible size may vary with different species of *Dendroctonus* but is generally a tree with a d.b.h. ≥ 8 inches.

species exists for each important coniferous species.

Effects of Epidemics

Bark beetle epidemics can decimate stands. Both the MPB and SB have killed over 90% of the live trees in a stand (Schmid and Frye 1977, McGregor et. al 1987). Mortality of this magnitude changes stand structure, species composition, and successional trends. For example, the MPB kills proportionately more large-diameter trees than small-diameter trees (Amman 1977) and thus alters the diameter distribution. Where lodgepole pine is the climax species, the MPB may create two- or three-storied stands (Amman 1977). Where lodgepole is seral, MPB epidemics may accelerate succession to other coniferous species in the absence of fire or, if fire occurs, help perpetuate the even-aged condition so conducive to extensive epidemics (Amman 1977). In the absence of fire in ponderosa pine stands in the Black Hills, paper birch (Betula papyrifera Marsh.) has become dominant in some old MPB epicenters (J.M. Schmid, personal observation).

In similar fashion, the SB has caused similar changes in spruce-fir stands. The White River SB epidemic killed 99% of the spruce over 10 inches d.b.h. (Schmid and Frye 1977) and altered species composition from 90% spruce-10% fir to 20% spruce-80% fir (Schmid and Hinds 1974).

Although major epidemics cause significant changes in stand structure over extensive areas, not all epidemics create these extreme impacts. Epidemics of lesser magnitude may kill 10% to 20% of the stand (Frye and Flake 1972) or only the largest-diameter trees within the stand (McCambridge et. al 1982). Mortality of this magnitude temporarily lowers the stand density by removing the large-diameter trees but may set up the stand for a more extensive epidemic in the near

future by creating more uniformity in diameter classes within the stand.

The death of the large-diameter trees, particularly in even-aged stands, generally means the loss of the overstory. This, in turn, allows understory vegetation to prosper. Herbage production of forbs, sedges, and grasses in a beetle-killed ponderosa pine stand increased to more than 500 pounds per acre in 3 years (McCambridge et. al 1982). Similarly, forbs, sedges, and grasses were denser in beetle-killed stands of spruce-fir than in green uninfested stands (Yeager and Riordan 1953).

The change in stand structure and the associated change in understory vegetation bodes well for some animal species and ill for others so the net result is diversity in animal species and their abundance. Species dependent on the old growth like the red squirrel (Tamiasciurus hudsonicus (Erxleben)) are adversely affected because of the loss of seed from the beetle-killed mature trees (Yeager and Riordan 1953). In contrast, chipmunks (Eutamias spp.) may benefit because of the increase in grasses and forbs. Wild ungulates may benefit from the increase in forage production in the short term but may not be able to use the forage in later years when fallen beetle-killed trees become an impenetrable jungle (Light and Burbridge 1985).

Populations of invertebrate and vertebrate predators of bark beetles may increase during the epidemic and then decrease dramatically after beetle populations become endemic. Foliagegleaning birds such as chickadees (Parus spp.) and kinglets (Regulus spp.) as well as bark-gleaning birds such as nuthatches (Sitta spp.) and brown creepers (Certhia americana) decrease in number with an increase in beetle-killed trees once the infested trees lose their foliage. In contrast, woodpeckers (*Picoides* spp.) may temporarily increase with the increasing numbers of infested trees because of the insect fauna under the bark of the infested trees (Bull 1983). In general, the influence of beetle epidemics on animal species will vary depending on the needs of the particular species. Even then, the effects will vary depending on the extent (geographic area) and intensity (percent of stand killed) of the beetle epidemic.

Epidemics of *Dendroctonus* beetles have ramifications well beyond the tremendous number of dead trees. Extensive epidemics have increased annual streamflow 1.6 to 1.9 inches (about 16%) for a spruce-fir watershed (Mitchell and Love 1973) and water yield 15% for a lodgepole pine watershed (Potts 1984). However, net precipitation

under small group infestations of the MPB was no different from under adjacent live trees (Schmid et. al 1991).

Both MPB and SB epidemics influence fire hazard and fire intensity, although fire hazard may be greater in pine stands than in spruce-fir stands. For both forest types, fire hazard is probably greatest during the two years following beetle attack when the dead needles and fine twigs are still on the trees. After needles and twigs fall, hazard decreases but still remains above preepidemic levels because of the increase in ground fuels. MPB epidemics create heavy fuel loads in lodgepole pine forests (Lotan 1976) and probably overshadow all other causes as a creator of fuel buildup (Lotan et. al 1985). This heavy fuel buildup increases the probability of high intensity fires (Brown 1975). SB epidemics also create heavy fuel buildups but fire hazard would not be as great as in beetle-killed pine stands except during the two years following beetle attack (Schmid and Frye 1977).

Frequency of Epidemics

Stands of dead trees in the pine and spruce-fir forests of the Rockies became the historical evidence of beetle epidemics from previous centuries when settlers immigrated into the forested regions. A SB outbreak killed mature Engelmann spruce on the Grand Mesa, Colorado, in the 1870's (Sudworth 1900) and MPB were infesting lodgepole pine in Utah around 1785 (Thorne 1935). One 400-year-old ponderosa pine tree showed evidence of seven unsuccessful MPB attacks during its life (Craighead 1925), thus indicating previous periods of MPB activity.

The historical evidence generally reflects Dendroctonus populations of epidemic proportions. But beetle populations are never in epidemic proportions continuously in a given stand. The frequency of epidemics depends on the size of the area being considered, how extensively the beetle population decimated the stand(s) within the area and modified its (their) stand structure, and how fast the stand again grows into the hazardous condition.

When the area under consideration is stand-size (i.e., 1-200 acres), the frequency of beetle epidemics depends on how extensively the previous epidemic decimated the stand. For example, some spruce stands subjected to the White River SB epidemic will probably be free of an outbreak of that magnitude for 150-200 years because 99% of

the spruce over 10 inches d.b.h. were killed (Schmid and Frye 1977). Similarly, where a MPB epidemic killed 84% of the pine basal area in 163 acres of ponderosa pine and reduced the basal area to 27 ft² per acre (McCambridge et. al 1982), the stand(s) would not be expected to suffer another outbreak for 50-100 years. In contrast, a stand surviving a short-lived epidemic or losing 10-20% of its basal area may be subjected to another epidemic within 20-50 years.

When the area under consideration is more regional such as river drainages or districts of national forests, the interval between epidemics is less. Intervals between MPB epidemics in ponderosa pine on the Kaibab National Forest ranged from 4 to 14 years from the end of one epidemic to the start of another (Blackman 1931), but the epidemics were not at the same locale. Frequency of MPB epidemics in lodgepole stands range from 20 to 40 years for any given area (Cole and Amman 1980). In ponderosa pine in the Black Hills, the frequency between epidemics was 5-35 years (Thompson 1975), but again the infestations were not in the same locale.

Intervals between epidemics can obviously be misleading because the duration of epidemics is also frequently contingent on what area is defined as common to each epidemic as well as our definition of the start and ending of epidemics. DFB epidemics generally last only 3-4 years (see McGregor et. al 1974) while the duration of MPB epidemics is variously estimated as: 6 years in lodgepole pine (Cole and Amman 1980), 7-12 years (Coulson et. al 1985), 2-5 years for short-term epidemics in ponderosa pine (see Blackman 1931), 7-13 years (see Blackman 1931) and 13 years (McCambridge et. al 1982) for long-term epidemics in ponderosa pine.

Although MPB epidemics in lodgepole pine usually last less than 10 years, epidemics may last for ≥30 years for the lodgepole type as a whole (G.D. Amman 1992, personal observation). For example, a MPB epidemic was reported on the Flathead National Forest in northwest Montana in 1909. During the succeeding 25 to 30 years, new infestations appeared in most national forests and parks between Flathead and the Cache National Forest in northern Utah (Evenden 1934). More recently, the reverse occurred with epidemics starting in the Wasatch National Forest in northern Utah about 1955 and eventually arising in most national forests and parks between Wasatch and the Kootenai National Forest in northern Montana over

the next 35 years (G.D. Amman 1992, personal communication).

Intervals are also complicated by the imprecise definition of when beetle epidemics begin and end, particularly in records before World War II. Even records of epidemics as recently as the 1960's and 1970's can be interpreted differently. Thompson's 1975 review of MPB activity in the Black Hills led him to believe that epidemics occurred in 1962, 1967, and 1972. These three MPB epidemics could also be considered one epidemic with various infestation loci caused by shifting MPB populations as well as lulls and increases in population levels during the epidemic phase. (J.M. Schmid 1992, personal observation).

Endemic Population Levels

Between epidemics, bark beetle populations are endemic, i.e., at a level where their presence is hardly noticeable. They exist in trees predisposed to attack by biotic agents or weather phenomena. MPB populations in lodgepole stands cohabit in trees previously infested by other small scolytids such as Ips pini (Say), Pityophthorus confertus Swaine or Pityogenes knechteli Swaine (Schmitz 1988), or in trees infected with Armillaria root disease (Tkacz and Schmitz 1986). In ponderosa pine in the Black Hills and southern Utah, endemic MPB populations can be found in Armillariainfected trees or in lightning-struck trees. SB populations inhabit wind-thrown or wind-damaged trees. DFB populations are also associated with wind-thrown trees as well as diseased and defoliated trees (Furniss et. al 1981).

On first thought, the incidence of predisposing weather or biotic phenomena would seem so infrequent that beetle populations would have difficulty maintaining themselves. However, weather phenomena are more insidious than might be imagined. Wind conditions in the central Rockies characteristically reach hurricane velocity at least once each year. Conceivably, winds of this magnitude would wind-throw a tree or tear the top from a mature spruce or Douglas-fir somewhere in every 200-300 acres. Both tree conditions would be suitable habitat for maintaining SB or DFB populations.

Similarly, lightning directly and indirectly predisposes trees. Lightning strikes from summer storms may average one per 20-50 acres in the Black Hills (R. Holle 1992, personal communication) and lightning-struck trees are potential sites for MPB infestation (J.M. Schmid

1992, personal observation). Lightning-caused fires scorch trees and thereby predispose them to beetle infestation (Fellin 1980, Amman and Ryan 1991), which in one case led to a DFB epidemic (Furniss 1941). Lightning-caused fires predispose trees to infection by root rot fungi, which subsequently predispose trees to beetle infestation (Gara et. al 1985). These various weather influences plus the number of trees predisposed by *Armillaria* and other scolytids could sustain MPB populations.

Because endemic bark beetle populations exist in the forest, their recurrence at epidemic levels in any particular stand becomes mostly a function of how quickly that stand reaches a hazardous state. As noted previously, this depends primarily on how extensively the previous epidemic modified the original stand structure. To a lesser extent, post-epidemic tree and stand growth will also influence how quickly the stand will return to the high hazard condition. If other disturbances such as fire, logging, etc., are injected into the stand development scenario, they may further affect the development of the hazardous state.

Hazardous Conditions

Highly hazardous stand conditions vary among Dendroctonus species but also have some striking similarities. For the MPB in lodgepole pine, stands with a number of large-diameter trees are hazardous (Cole and Amman 1969). More specifically, stands with average d.b.h. > 8 inches, average age > 80 years, and low elevation-latitudes are considered high risk (Amman et. al 1977, Hall 1985) when they are within the most suitable climatic zones of Safranyik et al. (1974). Stands of ponderosa pine with basal areas ≥ 150 ft² per acre and average d.b.h. ≥ 8 inches are considered highly hazardous for MPB infestations (Sartwell and Stevens 1975), although recent evidence suggests a basal area $> 120 \text{ ft}^2$ coupled with an average d.b.h. > 8 inches may constitute the critical threshold (Schmid and Mata 1992). Sprucefir stands are highly hazardous for SB infestations when the basal area > 150 ft² per acre, average diameter > 16 inches for live spruce above 10 inches d.b.h., proportion of spruce in the canopy >65%, and their physiographic location is a welldrained site in creek bottoms (Schmid and Frye 1976). High density Douglas-fir stands composed of > 120 year-old large-diameter trees are highly hazardous for DFB epidemics (Furniss et. al 1981). More specifically, stands with average diameter \geq 16 inches d.b.h., basal area \geq 150 ft² per acre,

and age \geq 100 years are highly hazardous when they are near root disease centers (K.E. Gibson 1992, personal communication).

Predicting Epidemics

Given a highly hazardous stand, can we predict when an epidemic will begin? Not really, at least not without supplemental information. Predicting an epidemic for any of these *Dendroctonus* species is like predicting a 100-year flood. We know that it will happen sometime during the next 100 years after a number of trees reach susceptible size, but we can't pinpoint the exact year. We can't predict the year of an epidemic because we don't precisely know the key factor(s) that trigger the change from the endemic to the epidemic. We can with Dendroctonus beetles, however, make shorter term predictions for the start of future epidemics if we have supplemental information. For example, the SB and DFB prefer to inhabit downed trees and most epidemics have arisen from populations originating from downed trees (Schmid and Frye 1977, Furniss et. al 1981). If a windstorm creates substantial wind-thrown or wind-broken trees in a high-hazard forest supporting endemic SB or DFB populations, then we would expect to see the start of an epidemic (some infested standing trees) 4-6 years after the blowdown. Without the information on windthrow, the forecast of an epidemic for either the SB or DFB would be more tenuous.

We also cannot predict with much certainty the duration of the epidemic and, therefore, the extent of the tree mortality in ponderosa pine, spruce-fir, and Douglas-fir stands. The duration of an epidemic is uncertain because our ability to predict population trend is limited to one year into the future (see Knight 1959, Knight 1960a, 1960b). Thus, given the start of an epidemic, we can predict the population level and its associated level of tree mortality one year hence but not how long a specific epidemic will last or the eventual magnitude of the tree mortality. However, we can do somewhat better for lodgepole pine because the duration of the MPB epidemic and its associated tree and volume losses can be estimated on an annual basis (Cole and McGregor 1983). For all Dendroctonus species, we can outline for the forest manager a series of epidemic scenarios and their respective levels of tree mortality based on the current stand conditions and historical evidence from past epidemics.

Beetle Management

Although our predictive capabilities for epidemic startup and duration are tenuous, our ability to minimize tree mortality through silviculture is substantially greater. For the MPB at least, partial cutting greatly reduced tree losses (fig. 1) in stands of lodgepole pine (McGregor et. al. 1987) and ponderosa pine (Schmid and Mata 1992). Maintaining ponderosa pine stands at basal areas of <100 will minimize tree mortality (Schmid and Mata 1992).

The success of partial cutting against the MPB in 80- to 125-year old pine stands suggests it could be used to perpetuate old growth pine stands. And we assume similar practices would be effective against the SB in spruce-fir stands and the DFB in Douglas-fir stands because DFB outbreaks have not been evident following any kind of commercial cutting (Furniss et. al 1981). However, over time, stands will grow into a hazardous state. How long the partial cutting will effectively maintain minimal

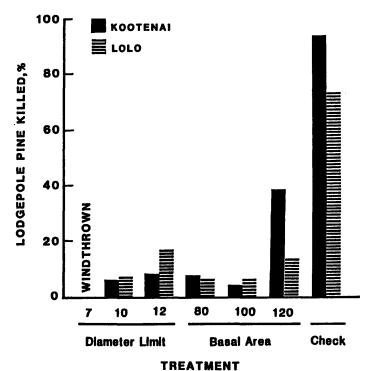


Figure 1.--Percent lodgepole pine (LPP) killed by mountain pine beetles in different partial cutting treatments, Kootenai and Lolo National Forests, Montana, 1980-1984 (from McGregor et. al 1987). Treatments indicate diameter limit cuts in which all trees ≥ 7 , ≥ 10 or ≥ 12 inches (d.b.h.) were removed, spaced cuttings leaving basal areas of 80, 100, or 120 ft² per acre, and uncut check.

losses is a function of the stand density (basal area) and tree growth subsequent to cutting (Schmid 1987) but we know the partially cut lodgepole pine stands of McGregor et. al (1987) have remained relatively free of MPB infestation since cutting (12 years). Using RMYLD (Edminster 1987), we can project when partially cut stands of various densities will reach the critical thresholds and become susceptible again. Assuming a basal area of 150 as the critical threshold for MPB epidemics (Sartwell and Stevens 1975), stands cut to basal area 60 would remain unsusceptible for 60-80 years, basal area 80 for 40-50 years, basal area 100 for 25-40 years, and basal area 120 for < 20 years (Schmid 1987). However, if the critical threshold is basal area 120 rather than 150 as Schmid and Mata (1992) propose, then stands would become highly hazardous much sooner; namely, about 50 years for basal area 60 stands, 25-30 years for basal area 80 stands, and 11-15 years for basal area 100 stands (table 1). Thus, stands may grow into a high hazard condition rather quickly, depending on their density.

Table 1.—Time required for partially cut stands of specific GSLs to reach basal areas (BA) of 120 and ≥150 ft² per acre as projected by RMYLD. Mean diameter (D) for each GSL under BA 120 and ≥150 represents the projected diameter when each GSL reaches those basal areas.

Area/	Stand co	Stand conditions		BA 120		BA > 150	
growing		Mean		Mean		Mean	
stock level	BA	D	Time	D	Time	D	
	(ft/ac)	(in)	(yrs)	(in)	(yrs)	(în)	
Brownsville	(PP)						
60	60.5	12.4	51	18.0	76	19.5	
80	80.8	11.5	29	13.4	51	15.7	
100	100.7	12.8	16	14.0	37	15.6	
Hinman (LP)						
80	79.8	12.8	24	15.8	40	17.6	
100	101.2	12.7	11	13.9	27	15.5	
120	118.1	10.9	1	11.0	13	12.3	
Brush Creek	(LP)						
40	40.0	9.8	73	17.7	90	19.6	
60	60.7	12.0	48	17.0	62	19.9	
80	81.3	10.0	26	11.2	40	13.6	
120	119.7	8.9	4	9.2	16	10.2	
White House	e (PP)						
60	59.0	12.5	50	18.0	75	20.1	
80	79.0	11.5	19	13.8	51	15.5	
100	100.7	11.6	14	13.6	35	14.4	

Although the high hazard condition in managed stands⁴ should be a red flag for forest managers and should stimulate silvicultural action, stands may exist in this state for years before beetle populations become epidemic. If annual forest pest management surveys reveal no change in the endemic status, then no action is necessary. However, if surveys indicate increasing trends in beetle populations, then forest managers must act promptly, particularly in pine stands where populations can rapidly increase and spread to adjacent areas. Forest managers will not be able to maintain old growth forever, and some trees will be lost even after partial cutting, but managers can extend stand life beyond the time when bark beetles perform their regulatory cut. The bottom line is, Will the general public allow forest managers to minimize beetle-caused mortality through partial cutting in order to perpetuate the old growth? Or, rephrased, Who will do the cutting--the forest manager or the beetles?

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Effects of Dwarf Mistletoe in Old-Growth Lodgepole Pine Stands at Fraser Experimental Forest, Colorado¹

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ABSTRACT – The distribution of dwarf mistletoe (*Arceuthobium americanum*) and its effects on basal area increment and pine mortality were studied in three 2.02 ha plots in old-growth lodgepole pine stands at Fraser Experimental Forest, Colorado. From 34 to 60 percent of each plot area was infested with dwarf mistletoe, but no isolated infection centers were found. Nearby 70-year-old stands had an average of 1.4 isolated infection centers per ha. Basal area increment of individual old trees was reduced significantly only among the most severely parasitized trees, where the reduction was 30% between 1960-1989. Young, pole-sized lodgepole pine stands throughout Colorado and Wyoming have considerably greater reductions among moderately to severely parasitized trees. Somehow, old surviving pines tolerate dwarf mistletoe parasitism with considerably less effect on their growth rates than do younger trees. However, mortalities of old pines from 1960 to 1989 averaged 0.43 %/year at sites without dwarf mistletoe and 0.75 %/year at infected sites, a highly significant difference.

INTRODUCTION

The dwarf mistletoe (Arceuthobium americanum Nutt. ex Engelm.) is a widespread parasite of lodgepole pine (Pinus contorta Dougl. ex Loud.) essentially throughout the tree's range (Hawksworth and Wiens 1972, Hawksworth and Johnson 1989). The mistletoe is particularly common on and damaging to the Rocky Mountain subspecies of lodgepole pine (P. contorta subsp. latifolia (Engelm. ex Wats.) Critch.), which is the host tree discussed here. Although considerable literature exists on the biology and effects of dwarf mistletoes in western North America, very little of it relates to old-growth stands. Longterm plots on the Fraser Experimental Forest in Colorado have enabled us to obtain ecological information on dwarf mistletoe in old-growth lodgepole pine stands.

Comprehensive analyses of 50 years of succession in three 5-acre (2.02 ha) plots in old-growth lodgepole pine at the Fraser Experimental Forest are presented by Moir et al. (1992). That paper discusses changes in stand density, basal area, extent of mortality, causes of mortality, above-ground net primary productivity, snag recruitment, downed woody biomass, and seedlings and sapling ingrowth. Here we describe in more detail the dwarf mistletoe effects upon both trees and stands in the three pine plots.

THE SETTING

Fraser Experimental Forest, located in Grand County in central Colorado, contains lodgepole pine and spruce-fir stands representative of high-elevation forests in the Central Rocky Mountains (Alexander et al. 1985).

The old-growth forests we studied were over 300 years old. Lodgepole pine forests grow on warm, dry sites at lower elevations (2600 to 3100 m) and are of the *Pinus contorta / Vaccinium myrtillus* habitat type (Moir 1969, Johnston 1987).

In 1938, three plots (designated B, C, and D) were established in old-growth lodgepole pine stands at 2800 to 2900 m elevation in the King Creek drainage of the Experimental Forest (Wilm and Dunford 1948). Each plot is 2.02 ha (5.00 acres) surrounded by an isolation strip (1.20 ha or 3.00 acres). At the time of plot establishment, each tree over 9.0 cm in diameter at breast height (dbh) was tagged and recorded for species, dbh, vigor class, and form defects. Plots were revisited in 1942, 1946 (plots B and C), 1947 (plot D), 1960, and 1989, when each tagged tree was remeasured and dead trees and proximate cause of mortality recorded (Moir et al. 1992). In this paper we refer to lodgepole pines tagged in 1938 as "old pines."

Dwarf mistletoe information was systematically recorded on the plots in 1990 when each lodgepole pine over 9.0 cm dbh was rated by the 6-Class system Dwarf Mistletoe Rating (DMR) (Hawksworth 1977). Also in 1990, each 5-acre plot was gridded into permanently marked, approximately 0.1 acre (0.04 ha) blocks, and the tagged trees in each block were recorded. Maps showing the distribution of dwarf mistletoe and habitat types in each plot were prepared.

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OBJECTIVES

Objectives of this study were:

- To compare diameter growth rates of trees without dwarf mistletoe to those in various infection classes.
- 2. To compare mortality rates in infested vs. uninfested blocks.
- To quantify occurrence of any isolated infection centers within the plots, and to compare these results with those obtained earlier in nearby younger stands.

SAMPLING AND ANALYSIS

Stand ages are based on a random sample of about 30 old pines in each plot. Ring counts were made on cores taken at a height of 1.4 m, so our tree ages are reported as years at breast height (ybh in table 1).

Table 1. Characteristics of the lodgepole pine study plots at Fraser Experimental Forest, Colorado.

PLOT ELEVATION		SLOPE & ASPECT	AGE	No. TREES	MEAN DBH	
	m	deg	ybh		cm	
В	2790-2830	3 W	179 - 293	1150	27	
С	2900-2930	22 NW	206- 328	1362	23	
D	2900-2970	30 W	161- 288	1607	23	

In each plot, all old pines tagged in 1938 and alive in 1990 were analysed. Individual measurements, including DMR, were obtained for 4,119 live old pines. Growth of each tree was computed as the

change in basal area (BA), measured at breast height. from 1960 to 1989. We refer to this variable as the average increment for each tree. We tested average increment of old pines in each DMR class for normality using both the Shapiro-Wilkes and Lilliefors statistics in the SPSS program (Norusis 1990), and for homogeneity of variance among classes using Levines statistic (Milliken and Johnson 1984). These tests were non-significant, and we then subjected average increment to analysis of covariance using tree diameter at breast height as a covariate and both DMR and plots as analysis factors. To help discriminate which levels of dwarf mistletoe infection might be associated with reduced basal area increment, we compared covariate-adjusted means among all paired combinations of DMR classes. The null hypotheses were that the average basal area increments were not different between any pair of dwarf mistletoe infection classes, and a Type I error of alpha = 0.05 was maintained across all comparisons using a Bonferroni correction of significance levels (Milliken and Johnson 1984).

To compare mortality rates in infested and uninfested areas, we stratified plots B,C, and D into infested and uninfested 0.1 acre blocks, based upon our mapping (figs. 2 and 3). We eliminated blocks that were not in the Pinus contorta/Vaccinium myrtillus habitat type, as well as ecotonal blocks shown in the figures. We also eliminated blocks partially within an infected area. A total of 44 blocks (23 uninfected, 21 infected) were used for analysis. In each block we computed mortality as the number of old pines that died between 1960-1989 divided by the number alive in 1960. We performed the same tests for normality and homogeneity of variance (see above) for mortalities in the two classes of blocks. These conditions were found to satisfy the tests, and we therefore used the two-tailed Student's t-test to test the null hypothesis that there were no differ-

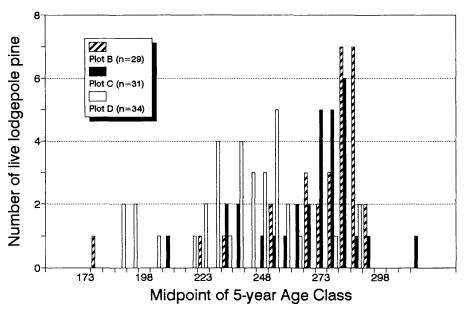


Figure 1. Age distribution of sampled old lodgepole pines in three study plots at Fraser Experimental Forest, Colorado.

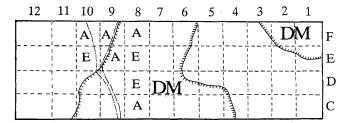
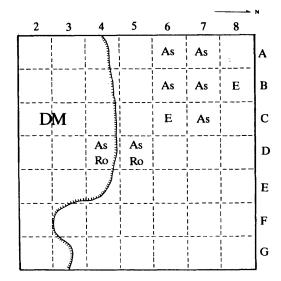


Figure 2. Map of plot B. The plot is 4 by 12.5 chains, or 5.0 acres (2.024 ha). The blocks in grid 1 through 11 are each 0.1005 acre (0.0407 ha); the 4 blocks in grid 12 are each 0.1443 acre (0.0584 ha). The distribution of dwarf mistletoe (DM) on lodgepole pine is shown. The area marked by dashed lines is a ravine. Unlettered blocks are in the *Pinus contorta/Vaccinium myrtillus* habitat type (HT). Lettered blocks are: A = wet area dominated by *Abies lasiocarpa* and *Alnus incana* (an undescribed HT), and E = blocks ecotonal to the two HTs.



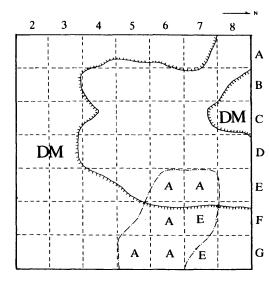


Figure 3. Map of plots C (lower) and D (upper). Each plot is 7.07 chains square, or 5.00 acres (2.024 ha). The 49 gridded blocks are each 0.102 acres (0.0413 ha). The distribution of dwarf mistletoe (DM) is shown. The dashed line indicates an area dominated by Abies lasiocarpa. Unlettered blocks are in the Pinus contorta/Vaccinium myrtillus habitat type (HT). Lettered blocks are: A = Abies lasiocarpa/Linnaea borealis HT, As = Aspen dominated, E = blocks ecotonal to two HTs, Ro = rock outcrops.

ences in mortality of old pines between the infested and uninfested blocks.

Mapping was aided by lines surveyed out (by compass) in a rectangular grid pattern to delineate blocks generally 0.1 acre (0.0407 ha) in area. Permanent markers (steel re-bar with yellow plastic caps) were installed at grid line intersections. Areas were mapped as infected whenever infected trees were less than 10 meters apart (the distance that can be travelled by an explosive seed discharge). The boundary to uninfected areas was mapped at the canopy edges of overlapping infected trees. We looked for "isolated" centers as pines of any size that were infected more than 10 meters beyond the edge in otherwise uninfected areas (Hawksworth et al. 1987).

RESULTS AND DISCUSSION

Summary plot data are given in table 1. Age distributions for old pines are shown in figure 1. The maximum ages measured were 293, 328, and 288 years in plots B,C, and D respectively. Since these are ages at breast height (ybh), it is reasonable to cite actual stand ages at over 300 years for each plot.

Maps of the three plots are given in Figures 2-3. From 34 to 60 percent of the lodgepole pine areas on each plot are affected by dwarf mistletoe (table 2). No isolated "satellite" infection centers were found on any of the plots. This was somewhat of a surprise because in a 70-year-old lodgepole pine stand 1-2 km west of these plots we found several isolated infection centers in otherwise uninfested stands (Hawksworth, unpublished data). In an intensively surveyed area of 14.6 ha we found 21 isolated infection centers, or 1.4 per ha (Hawksworth et al. 1987). The isolated centers ranged from 12 to 65 m (average 27 m) from the nearest infection source. These isolated centers are established by birds, of which the gray jay (Perisoreus canadensis) is apparently the primary vector (Nicholls et al. 1989).

Table 2 summarizes mistletoe infection states in all pine plots. Since only 30-37% of old pines were infected, the average plot DMR is low (1.3-1.7).

Table 2. Characteristics of dwarf mistletoe in the lodgepole pine study plots. DMI is the average infection of all infected trees in the plot (0 = uninfected, 6 = severely infected).

PLOT	INFESTED AREA %	INFECTED TREES %	PLOT DMR	PLOT DMI
В	34	30.8	1.3	4.1
С	60	37.2	1.7	4.5
D	40	29.6	1.3	4.5

^{*} mean dwarf mistletoe rating of all live trees

^{**} mean dwarf mistletoe rating of live, infected trees

However, trees that were infected were moderately to heavily so, with prevalence of DMIs 4 to 6 (table 2).

Scattergrams of basal area (BA) increment averaged over 29 years versus tree dbh in 1989 are shown for different DMRs in figure 4. The linear relationships between increment and dbh in 1989 are significant (p < .001), with dbh alone accounting for about 41% of the variation in BA increment across all DMR classes. BA increments, adjusted for dbh within each DMR class, were > 2.3 cm² in all but the most severely infected old pines, whereas it was $1.67~\rm cm^2$ for trees in DMR class 6, about a 30% reduction (table 3). This reduction was significant (Bonferroni p < .005 for all comparisons), and we conclude that depressed growth took place mostly among the severely parasitized old pines.

Dwarf mistletoe accelerates tree mortality. The overall mortality of old pines reported by Moir et al. (1992) in these plots was 0.54%/year. In our somewhat smaller sample of old pines from the 44 blocks, we calculated a mean mortality of 0.58%/year over the 29 year period. The mean mortalities of trees in uninfected versus infected blocks were respectively 0.43%/year and 0.75%/year. This 74% greater rate of mortality was highly significant (p < .01).

Table 3. Lodgepole pine mean basal area growth increments (cm²) from 1960 to 1989 adjusted for dbh in each dwarf mistletoe rating (DMR) class. DMR 0 = uninfected trees, DMR 6 = severely infected trees.

DMR	No. old Pines	SLOPE	INTERCEPT			
0	2783	.13	83			
1	84	.16	-1.37			
2	91	.19	-1.84			
3	160	.17	-1.53			
4	278	.13	70			
5	339	.14	-1.07			
6	384	.12	-1.19			

CONCLUSIONS

Dwarf mistletoe distribution patterns in oldgrowth pine stands differ markedly from those in nearby young stands. We found no isolated infection centers in the old stands. Perhaps past isolated centers had time to coalesce in old growth, or perhaps some characteristic of old growth may be less favorable habitat for birds (the vectors of dwarf mistletoe) in the remaining uninfected area. We are unsure about mistletoe seed production on old pines or whether the open canopies in old-growth stands presented a reduced target for projected seeds.

Surviving old lodgepole pines in this lodgepole pine environment are relatively endurant of dwarf mistletoe parasitism. The effects of dwarf mistletoe on growth rates of old lodgepole pines are much less than for younger trees (fig. 5). There have been no

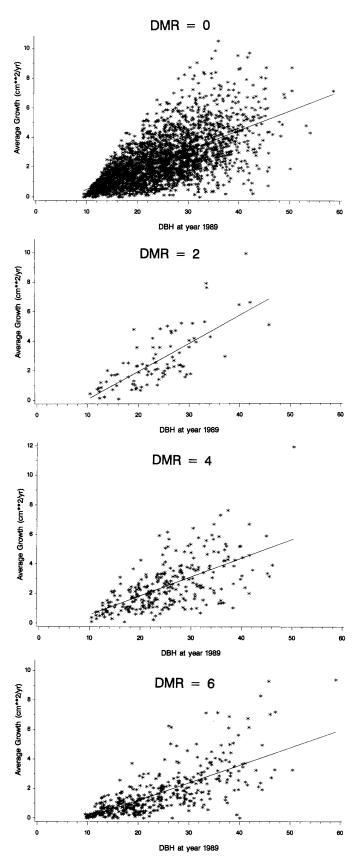
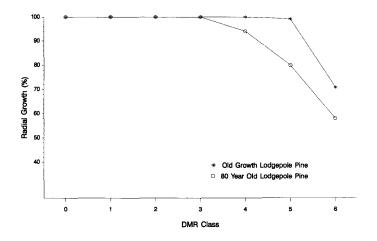


Figure 4. Scattergrams of old pine dbh (cm) and average basal area growth (cm²) from 1960-1989 for trees of different dwarf mistletoe infection (DMR classes). The regression line in each DMR class indicates growth rate related to tree size.



Radial growth rate expressed as a percentage of DMR class 0 for Old Growth and classes 0-3 for 80 Year Old Stands (Hawksworth and Johnson 1989)

Figure 5. Comparison of growth rates (as percent departure from trees without mistletoe) in relation to infection intensity (as DMR classes) for old-growth from this study versus 80-year-old stands. The old-growth data represent average basal area growth from 1960-1989. The 80-year-old stand data represent the last 10 years radial growth of more than 3000 trees in Colorado and Wyoming (Hawksworth and Hinds 1964, Hawksworth and Johnson 1989).

comparable studies in other host/parasite combinations where the effects of old versus young stands have been compared. However, studies of the effects of dwarf mistletoes in multi-aged stands show differing effects of smaller versus larger trees. For example, studies of Arceuthobium vaginatum on multi-aged ponderosa pine in Arizona (Hawksworth and Geils 1990) and Colorado (Maffei 1989) and A. douglasii on Douglas-fir in the Southwest (Mathiasen et al. 1990) all show that the effects of dwarf mistletoe are more pronounced in trees under 25 cm dbh than in larger trees.

Reasons for greater tolerance for dwarf mistletoe parasitism in surviving old lodgepole pines are unknown. The trees measured in 1990 are survivors of heightened mortalities that characterized infected stands during the last 29 years. Trees less tolerant of parasitism may have already died, and thus our sample yields more resistant old trees. But to confuse the issue, we do not know the initial degree of parasitism or its dynamics over the past 29 years, since our measurements were in 1990.

We do not know the physiological basis for this survivorship. The needle-bearing portion in old surviving pines (where infection takes place) is a smaller proportion of susceptible tissue in old trees than in younger trees. We speculate that dwarf mistletoe "taxes" less of the annual carbohydrate budget in these old survivors than in younger trees or older trees that already died. Mortality itself may contribute to survival of remaining trees. If surviving old pines are relatively free of tree-to-tree competition (Price 1990), they may have more tolerance to mistletoe. We know little about the biochemistry of senescence in lodgepole pine. Surviving old pines may support relatively larger loads of mistletoe if the parasite itself adjusts to the changes taking place in the host tree.

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Old-Growth Mixed-Conifer and Western Spruce Budworm in the Southern Rocky Mountains¹

Ann M. Lynch and Thomas W. Swetnam²

Abstract.—Thirty-one mixed-conifer stands 98 to 694 years old in the southern Rocky Mountains revealed a history of multiple western spruce budworm outbreaks. Outbreaks were neither more nor less frequent in older stands, nor did outbreaks appear to start in older stands. Western spruce budworm does not appear to directly threaten old growth stands, but management policies that repress natural disturbance regimes and promote budworm-prone forests may result in remnant old growth stands being less likely to survive severe insect outbreaks and potential catastrophic wildfires. Outbreaks may persist longer in older stands, but data from different areas and age groups are inconsistent. The appearance and structure of some stands are different from common perceptions of old growth mixed-conifer. Decadence and dead standing and down trees are probably not useful indicators of old growth in forest types subject to periodic mortality-causing insect outbreaks. Two exceptionally old stands in New Mexico, 494 and 694 years old, have tree densities exceeding 1000 trees per ha, have old trees smaller in size than the main canopy trees, and had fewer outbreaks in the last 120 years than most of the stands sampled in northern New Mexico.

INTRODUCTION

We have studied 31 mixed-conifer stands in the southern Rocky Mountains to reconstruct the history of western spruce budworm, *Choristoneura occidentalis* Freeman, outbreaks from tree-rings, and to make comparisons between habitat types and host species (Swetnam 1987a,b, 1989; Swetnam and Lynch 1989). Because older stands present the best opportunities for reconstructing lengthy insect outbreak histories, the stands selected for study consist of the oldest mixed-conifer stands we could find. In this paper we characterize these old-growth stands, and evaluate outbreak initiation, duration, and frequency with respect to stand age. We also discuss indirect factors through which western spruce budworm may affect old growth.

Western Spruce Budworm Ecology

The western spruce budworm is the most damaging forest insect pest in the Southwest (Linnane 1984). Throughout its distribution, western spruce budworm populations periodically increase to outbreak levels, causing extensive defoliation, reducing tree growth, killing trees, and altering successional dynamics. There have been 8 or 9 outbreaks in Colorado and New Mexico since 1700, with average return intervals of 30 to 40 years (Swetnam and

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Lynch 1989). The hosts in the Southwest are Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), white fir (Abies concolor (Gord. and Glend.) Lindl. ex Hildebr), subalpine fir (Abies lasiocarpa (Hook.) Nutt.). corkbark fir (Abies lasiocarpa var. arizonica (Merriam) Lemm.), Engelmann spruce (Picea engelmannii Parry ex Engelm.), and Colorado blue spruce (Picea pungens Engelm). Research in the northern Rocky Mountains indicates that these species' susceptibility should be, in decreasing order, white fir, subalpine fir and corkbark fir, Douglas-fir, and Engelmann spruce (Carolin and Honing 1972, Hermann 1987). Colorado blue spruce is considered an occasional host, or even a nonhost (Hermann 1987), but we have observed budworm-caused mortality on it. Western spruce budworm causes damage in the southern Rocky Mountains in Douglas-fir and mixed-conifer stands, as well as in stands of ponderosa pine (Pinus ponderosa Laws.) where Douglasfir or white fir are abundant.

Larvae feed on cones, seeds, vegetative and reproductive buds, and expanding new foliage. Older foliage is consumed when the current year's foliage is depleted. Defoliation reduces radial and height growth, reduces regeneration, and kills tops and entire trees (Carlson *et al.* 1983, MacLean 1985, Van Sickle 1987). Loss of reproductive organs and mortality of understory saplings and seedlings alter vegetation dynamics.

Generally, susceptible and vulnerable stands are mature, multi-storied stands with high proportions of shade-tolerant species on warm, dry sites (Carlson 1989; Carlson et al. 1983, 1985; Stoszek and Mika 1985; and Wulf and Cates 1987). Western spruce budworm infests stands with a variety of ecological

conditions: pure and mixed stands, low and high productivity sites, a variety of topographic, climatic, and elevation gradients, and many different habitat types (Fellin et al. 1983, Moir and Ludwig 1979). The insect is best adapted to the Douglas-fir, spruce, and lower subalpine Habitat Types, and is seldom found in the limber pine, ponderosa pine, lodgepole pine, upper subalpine, and timberline Habitat Types (Carlson et al. 1983, Fellin et al. 1983). The extent and severity of damage from western spruce budworm are affected by factors that influence both insect population dynamics and the ability of the tree, stand, or forest to resist, withstand, or recuperate from damage. Proximity to an ongoing outbreak is an extraneous factor that also affects risk (Wulf and Cates 1987).

Foliage in uneven-aged, multi-storied stands is exposed to more sunlight and is therefore warmer, providing acceptable budworm habitat and food resources. Suitable foliage is most abundant on crowns of mature, shade-tolerant trees that are exposed to sun. Multiple crown stories within a stand greatly increase the chance that dispersing larvae

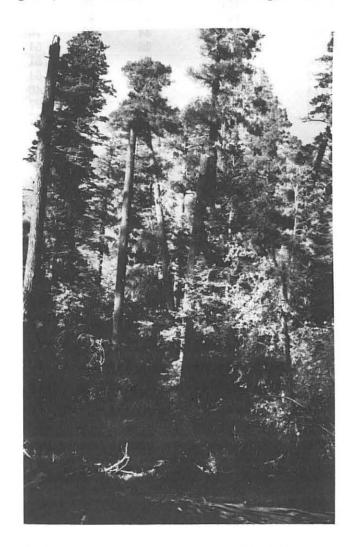


Fig. 1. Typical old growth mixed-conifer stand in New Mexico.

will land on suitable foliage. The incidence of defoliation increases in stands with multiple crown layers and greater crown closure.

Western spruce budworm's adaptation to shadetolerant species is well documented (Carlson et al. 1983, 1985; Carolin and Coulter 1975; Fellin et al. 1983; Heller and Anderson 1982; Hermann 1987; Wulf and Cates 1987), but the underlying mechanisms are not clear. Tree species' susceptibility related to shade tolerance has been associated with the timing of bud break with respect to spring larval activity (Carlson et al. 1985, Greenbank 1963, Kemp 1985), foliage nutrients (Clancy et al. 1988, Greenbank 1963), defensive secondary compounds (Carlson et al. 1985, Wagg 1958, Wulf and Cates 1987), flowering phenology (Schmidt and Lotan 1980), and climate zones (Kemp 1985, Stoszek and Mika 1985). Budworm adaptation to shade-tolerant, climax species coincides with those species' adaptation to site, climate, and successionary dynamics.

In some stands, trees weakened by the western spruce budworm may be predisposed to bark beetles (Collis and Van Sickle 1978), especially Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, and the fir engraver beetle, *Scolytus ventralis* LeConte. Bark beetle outbreaks may follow western spruce budworm outbreaks (Johnson *et al.* 1988, Pasek and Anqwin 1990).

Most research on factors affecting stand susceptibility and vulnerability to western spruce budworm has been conducted in the northern Rocky Mountains, the Pacific Northwest, and western Canada (Brookes *et al.* 1987a,b; Sanders *et al.* 1985). It is generally assumed that tendencies are similar in the southern Rocky Mountains (Larson *et al.* 1984). The experiences of Region 2 and 3 forest pest managers indicate that these assumptions should be applied with caution.

Little if any published research on western spruce budworm specifically addresses old growth issues. The most common questions asked about pest insect populations in old growth stands are (a) Do old growth stands harbor endemic populations, later serving as foci for outbreaks, and (b) Will current and future pest outbreaks threaten remnant old growth stands? Although our research was not originally designed to address these questions, we propose that our data can provide some insight into these issues.

STUDY AREAS

Since 1983 our investigations have included 6 stands in Colorado and 25 in northern New Mexico (Table 1). The Colorado stands, plus 5 in New Mexico (BRN, CPN, GAR, OSH, OAK, OCR and OSH) were sampled in 1983 in our original efforts to reconstruct western spruce budworm history from tree rings (Swetnam 1987a,b; Swetnam and Lynch 1989). They were selected to be representative of older mixed-conifer stands defoliated by budworm during the

Table 1. Stand inventory and site information for sampled stands. Diameters are for the stand *mean*, *large*st 5 host trees, and *old*est 5 host trees.

Stand	Habitat	Aspect	Density	Oldest	Mean age	DBH (cm) ²		
Type	Туре		(no/ha)	tree	oldest 5 trees	Mean	Large	Old
Front Ran	1ges							
BEM	n.d.	N	626	1812	166	19	47	n.d.
DGU	n.d.	NW	608	1733	249	19	38	n.d.
ICK	n.d.	varies	662	1694	279	22	54	n.d.
OPK	n.d.	varies	647	1761	231	20	38	n.d.
Wet Moun	ntains							
OAK	n.d.	N	435	1893	98	23	47	n.d.
OCR	n.d.	NW	444	1780	209	25	51	n.d.
Tusas Mo	untains							
BRN	n.d.	W	501	1790	202	22	42	n.d.
Jemez Mo	ountains							
BAR	Abco/Quga	flat	216	1714	217	28	65	39
EFK	Pipu/Libo	N	791	1701	224	26	76	37
FNL	Abco/Acgl	N	834	1830	147	23	49	32
FRC	Abco/Quga	SW	1052	1701	214	34	102	75
LEF	Pipu/Erex	N	715	1679	236	25	92	54
LGR	Abco/Acgl	NW	783	1696	211	25	56	51
LOG	Abco/Acgl	NW	597	1717	245	21	62	64
PEH	Abco/Vamy	N	649	1614	271	31	87	40
PEW	Abco/Acgl	N	629	1735	245	33	89	37
WVA	Abco/Quga	NE	602	1767	203	20	73	47
Sangre de	e Cristo Mts., Qu	ıesta						
BON	Abla/Vamy	NW	1052	1331/	494 (5)/	20	74	34
	_			1528	452 (4)		_	
CAB	n.d.	N	379	1871	116	20	n.d.	n.d.
FWN	Abco/Aruv	N	449	1839	143	23	50	35
RED	Abco/Aruv	N	932	1745	227	19	63	34
RTC	Abco/Aruv	S-SE	1074	1220	694	17	70	38
SRR	Abco/Syor	NW-NE	947	1748	241	19	45	32
	Cristo Mts., Ca						0.5	
ALA	Abco/Vamy	N-NW	467	1602	367	39	86	40
ALW	Abla/Vamy	NE	537	1622	275	30	94	95
CPN	n.d.	E	176	1790	188	28	39	n.d.
FLE	Abco/Vamy	SE	665	1689	261	22	67	51
GAR	n.d.	S-SW	599	1700	287	21	54+	n.d.
LAJ	Abco/Quga	S-SE	143	1685	221	40	91	70
OSH	n.d.	E	538	1696	281	20	52+	n.d.
POL	Pipu/Erex	S	396	1644	287	31	82	56

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1950s and the most recent outbreak, which began in the 1970s. The subsequent 20 stands were selected primarily on the basis of maximum age, preferably containing both Douglas-fir and white fir, and with minimal history of logging.

The Colorado stands are distributed along the Front Range in the upper Big Thompson drainage in Estes-Poudre Ranger District (R.D.) of the Roosevelt National Forest (N.F.) (BEM, DGU), in the Rampart Range in the Pikes Peak R.D. of the Pike N.F. (ICK, OPK), and in the Wet Mountains of the San Isabel N.F. (OAK, OCR). Although granite and gneiss are the most common parent materials in the complex geography of this faulted anticline region, a variety of igneous, metamorphic, sedimentary, and glacial till soils occur (Chronic 1980, Hunt 1967). Stands are mixed-conifer with varying amounts of Douglas-fir, white fir, ponderosa pine, lodgepole pine (Pinus contorta Dougl.), Engelmann spruce, Colorado blue spruce, and aspen (*Populus tremuloides Michx.*). Subalpine fir and Rocky Mountain juniper (Juniperus scopulorum Sarg.) are also found. Density ranged from 435 to 662 trees/ha (Table 1), and stocking from 20 to almost 30 sq m/ha.

The New Mexico stands are located in three general areas in the Santa Fe and Carson N.Fs. in the northern part of the State. Jemez stands: The Santa Fe stands are scattered in the Jemez R.D. of the Santa Fe N.F. in the Jemez Mountains, mostly in the Rio Cebolla, Jemez River, and East Fork of the Jemez River watersheds (BAR, EFK, FNL, FRC, LEF, LGR, LOG, PEH, PEW, WVA). Questa stands: Over half of the Carson stands are in the Questa R.D. in the Cabresto drainage (BON, CAB, RTC, SRR) and Red River drainage (FWN, RED) of the Taos Range of the Sangre de Cristo Mts. Camino Real stands: The remaining Carson stands are in the Camino Real R.D., in the Rio Pueblo watershed (ALA, ALW, FLE, LAJ, POL), Rio de Taos watershed (CAP, GAR), and adjacent Coyote Creek watershed (OSH) of the Sangre de Cristo Mountains. Stand BRN is in the Tusas Mountains northwest of the Rio Grande rift, 60 km west of the Questa stands.

Parent materials are entirely volcanic (rhyolite, tuff, pumice) in the Jemez Mts., and primarily sandstones, shales, and limestones in the Sangre de Cristo Mts. (Chronic 1987, Hunt 1967). Topographic position of sampled stands varies from steep slopes to flat ridge tops, most with north and north-east aspects (Table 1). Habitat Types, identified according to Moir and Ludwig (1979), are white fir, Colorado blue spruce, and subalpine fir series, and vary from cold, moist to warm, dry. Density ranges from 140 to 1100 trees/ha (Table 1), and stocking from 15 to 65 sq m/ha.

Dendrochronologic Procedures

Western spruce budworm leaves a record of its passage in the tree rings through defoliation-caused fluctuations in radial growth of surviving trees. The dendrochronologic procedures used for analyzing radial growth in budworm-damaged trees were described and illustrated by Swetnam et al. (1985). Their utility was demonstrated by Swetnam (1987a) and Swetnam and Lynch (1989), where we described and interpreted the chronologies developed from the first 10 stands we sampled. Briefly, the procedure is as follows: In each host stand, bole discs or 2 increment cores are taken from 10 dominant or codominant trees 20 cm or larger for each host species (Douglas-fir, white fir, subalpine fir) present within fixed- or variable-radius inventory plots. An additional 10 to 20 of the oldest appearing host trees are also sampled. At least 10 nonhost pines (ponderosa, limber, or piñon (*Pinus edulis* Engelm.) are similarly sampled in nearby fairly pure stands on severe sites and crossdated. Ring widths of both host and nonhost species are measured on a sliding-stage micrometer to the nearest 0.01 mm (Robinson and Evans 1980) and transformed to growth indices by fitting curves to the ring series and dividing the ring widths by the values of the fitted curves (Fritts 1976, Graybill 1979, Cook and Peters 1981). Nonhost tree-ring series are used to subtract climatic and other nonbudworm environmental signals from the host series, resulting in a corrected chronology for each stand (Swetnam et al. 1985, Nash et al. 1975). Individual tree chronologies and mean stand chronologies are examined in subsequent analyses.

The procedures and their assumptions and limitations for analyzing the effect of insect outbreaks on radial growth, and for distinguishing western spruce budworm outbreaks from other biotic and abiotic phenomena, are described in detail by Swetnam (1987a), Swetnam et al. (1985), and Swetnam and Lynch (1989). The procedures were validated by comparison of constructed chronologies with U.S. Forest Service Forest Pest Management and Ranger District records. Moderate to severe intensity outbreaks reliably show up in the chronologies, although light intensity outbreaks may not. Our conservative interpretation of the chronologies probably further eliminates some potential outbreaks, as fairly rigorous criteria are used for classifying a period of reduced growth as a budworm outbreak. Also, reduction in tree-ring growth indicates the time at which defoliation significantly impacts tree health, not necessarily the time when the insect population increases dramatically. Likewise, reduced ring growth may persist a year or more after the insect population has collapsed.

When looking for relationships with the duration of different outbreaks, we computed the standard deviate, $(\mathbf{x}_i, \dot{\mathbf{x}}_j)/s_j$, for each stand i and outbreak j, adjusting for the variability in relative lengths of the outbreaks (i.e., the duration of the 1880's outbreak averaged 15 years, but the 1910's outbreak averaged only 11). A significant positive correlation between stand age and the standard deviate of outbreak duration would indicate that outbreak duration increases with stand age. Not included in the analysis are: observations for the current outbreak, because its duration is not known for most stands;

observations of zero years for stands that didn't exhibit a particular outbreak; and observations for stands less than 80 years old in 1870.

RESULTS

Character of Old-Growth Stands Sampled

Most of the sampled stands are typical southwestern mixed-conifer, except that they are older (Table 1) and, in New Mexico, may have less white fir than is common today. Habitat Types range from warm Abco/Aruv to cool, moist Abla/Vamy. The only stands typed in the Psme series are in northern Colorado. Although the majority of the stands are on Abcoseries Habitat Types, white fir density greatly exceeded Douglas-fir density in only two stands, FRC in the Jemez Mountains and SRR in the Sangre de Cristos. Topographic positions range from flat to very steep. Most stands have northerly-facing slopes, but a few are southerly. Four stands, CAB, FNL, FWN, and OAK, are less than 150 years old, and are excluded from some of the analyses.

Mean stand diameters are between 17 and 40 cm, and mean diameter of the largest trees ranged from 39 to 102 cm (Table 1). Older trees were not necessarily the larger trees in the stands. In 12 of the 20 stands for which diameter and age data were available, the mean diameter of the 5 oldest trees was closer to the mean stand diameter than to the diameter of the 5 largest host trees. And the mean diameters of the two oldest stands, RTC and BON, are among the smallest sampled. Here and throughout our discussion, 'stand age' refers to the mean age of the oldest 5 host trees in the stand, computed from the inner-most ring dates, and using 1992 as the base year, regardless of sampling date.

Figure 2 shows the species and diameter distributions of the Sangre de Cristo stands. The Questa stands are all mixed-conifer with high proportions of Douglas-fir, except for SRR, which is only 11% Douglas-fir by density. Two stands, SRR and RTC, have an abundance of white fir. Although 2 stands, CAB and FWN, have low to average densities, the other 4, BON, RED, RTC, and SRR, have exceptionally high densities of over 900 trees per ha. The youngest stand, CAB, is the least dense, and the oldest stands have the highest densities (BON, RTC). In all stands, the maximum Douglas-fir DBH meets or exceeds the maximum white fir DBH. Only one stand, RTC, has particularly large trees. Age of the stands sampled at Questa varied considerably, from 116 to 694 years.

Stands at Camino Real are all mixed-conifer, composed of Douglas-fir and varying amounts of other species (Fig. 2). All have Douglas-fir with diameters greater than 70 cm. There are significant amounts of white fir in FLE, OSH, and CPN. Two stands, CPN and LAJ, have densities below 200 trees per ha, while other stands range between 400 and

700. Small subalpine fir is common in ALW, and small Engelmann spruce in OSH. Bristlecone pine was found in POL and LAJ.

Stands in the Jemez Mts. are mixed-conifer, usually with Douglas-fir predominant (Fig. 3). Most stands contain at least 5 species, with 7 species in PEH and PEW in the Peralta area. White fir is fairly dense in several stands. Spruce and sometimes pine are also significant components. There is substantial variability in DBH between stands, although trees with diameters larger than 70 cm were found in most. Density is between 400 and 850 trees per ha, except for BAR and FRC which have 216 and 1052 trees per ha, respectively. The Jemez stands were very uniform in age, with all but 1 (FNL) between 200 and 275 years.

The Colorado stands are more variable in species composition (Fig. 3), which is not surprising considering their distance from each other. One stand is almost pure Douglas-fir (DGU), and 3 are composed primarily of Douglas-fir and ponderosa pine (BEM, ICK, OAK). The 2 Wet Mts. stands contain small portions of white fir. Densities were very uniform, 608 to 662 trees/ha in the Front Ranges, and 435 to 444 trees/ha in the Wet Mountains. The mean diameters, and the diameters of the 5 largest host trees, are noticeably smaller in Colorado than in New Mexico (Table 1).

Exceptionally Old Stands

Two host stands, Bonita Canyon (BON) and Rito Claro (RTC) in Cabresto Canyon in the Taos Range of the Sangre de Cristos, are unusually old. The oldest Douglas-firs sampled at these sites are 652 and 772, respectively. Tree densities in these stands are the highest of all sampled stands (Table 1), almost twice that of most stands. Bonita Canyon is an Abla/Vamy site, with Douglas-fir, Engelmann spruce, aspen, subalpine fir, Colorado blue spruce, and a small amount of white fir (Fig. 2). It appears typical of commonly accepted concepts of old growth Douglas-fir, and the larger trees are, indeed, old. However, the oldest trees are not the largest, and have a mean diameter of only 34 cm (Table 1).

Rito Claro is a warm, dry Abco/Aruv site, with a high proportion of Douglas-fir mixed with a minor amount of white fir, plus small lodgepole pine, Engelmann spruce, and aspen (Fig. 2). Although 86 Douglas-fir and white fir per ha are greater than 50 cm DBH, and 20 exceed 60 cm, the stand doesn't visually appear to be exceptionally old. Indeed, the largest trees are relatively young, 300 years. But the stand is ancient, with many trees over 700 years. The oldest trees are in the lower and middle canopy layers, having been overtopped by later cohorts of Douglas-fir and white fir (Fig. 4). The mean DBH of the oldest 5 trees is 38 cm, but there are 90 trees per ha larger than 40 cm. A few snags and logs are present, but the general appearance of the stand is not typical old growth.

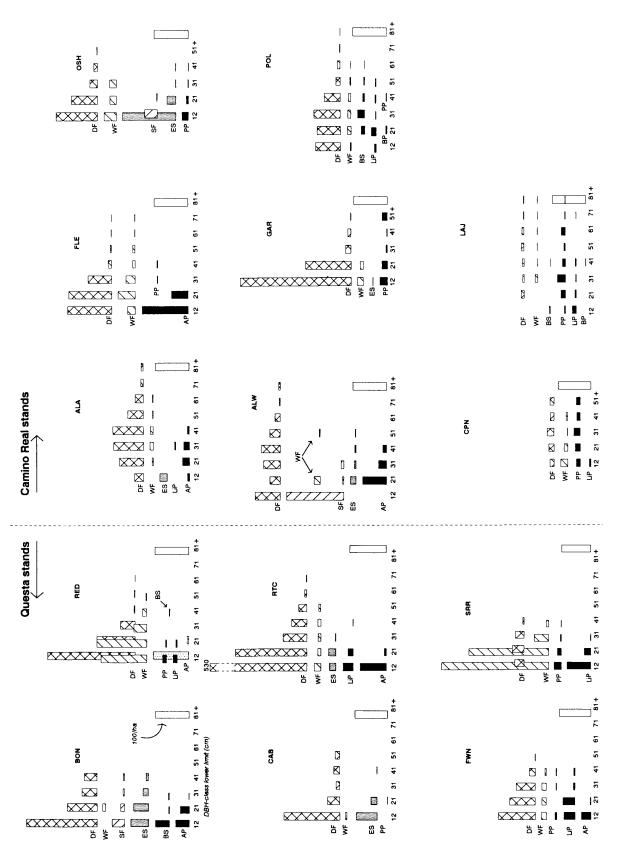


Fig. 2. Diameter and species distributions of stands in the Sangre de Cristo Mountains. Histograms are similarly scaled, and empty bars in the lower right of each histogram denote 100 trees per ha. Species are: AP-trembling aspen, BP-bristlecone pine (Pinus aristata), BS-Colorado blue spruce, CF-corkbark fir, DF-Douglas-fir, ES-Engelmann spruce, LiP-limber pine, SF-subalpine fir, WF-white fir.

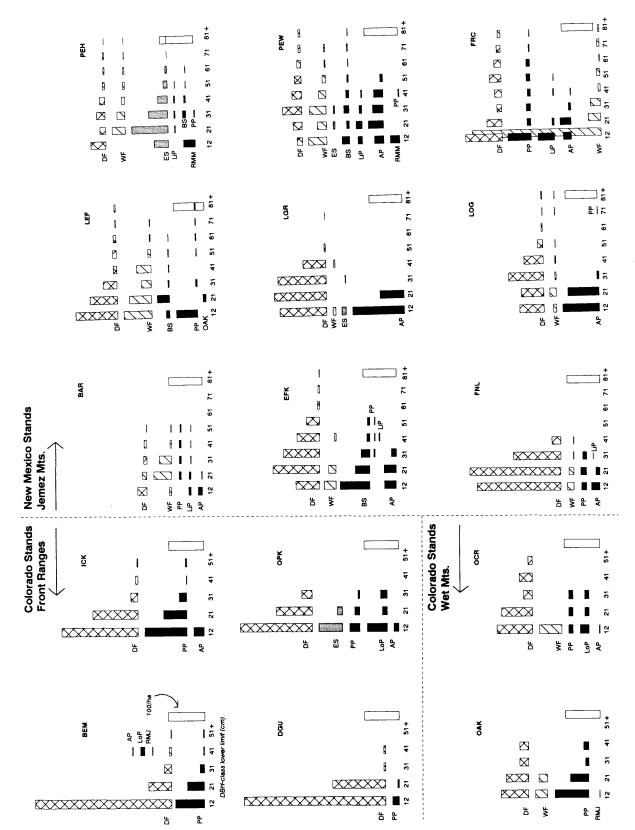


Fig. 3. Diameter and species distributions of stands in Colorado and in the Jemez Mountains of New Mexico. Histograms are similarly scaled, and empty bars in the lower right of each histogram denote 100 trees per ha. Species are: AP-trembling aspen, BP-bristlecone pine, BS-Colorado blue spruce, CF-corkbark fir, DF-Douglas-fir, ES-Engelmann spruce, LiP-limber pine, LoP-lodgepole pine, RMJ-Rocky Mt. juniper, RMM-Rocky Mt. maple (Acer glabrum), SF-subalpine fir, WF-white fir.



Fig. 4. This stand at Rito Claro (RTC) in the Taos Range of the Sangre de Cristo Mountains is almost 700 years old. Its density exceeds 1000 trees per ha, and the oldest cohort has been overtopped by younger Douglas-fir and white fir. The inner-most ring date of the center tree with the forked stem is A.D. 1210.

Of further note is a long-dead tree suspended above the forest floor, leaning against a large living tree. The outer ring of this snag dated to 1771, indicating that snags can persist under dry conditions for considerable periods of time.

Similarly, the nonhost pine site used to crossdate and define climatic variation for the RTC and BON sites was also unique (Swetnam and Brown, this proceedings). ERE is a limber pine site in nearby Red River canyon, and appears greatly different from the classic images of old growth stands commonly portrayed (Fig. 5). The trees grow at very low densities on sharp ridges and spines on a very steep, exposed south-facing slope. The slope endures constant wind erosion, and scree material falls from the slopes, frequently burying dead and living trees. Several trees over 800 years old were sampled, and the oldest living tree sampled on this site was over 1,600 years old. Younger trees were present but not sampled.

Chronologies

The chronologies extend back almost three centuries for most stands (Fig. 6 and 7). Periods of reduced growth attributed to western spruce budworm defoliation are interspersed with periods of no budworm activity. Note two relatively long periods in the 20th century that are budworm-free, before and after an outbreak which started in the 1940's in Colorado and the Jemez Mountains (Fig. 6), and the Camino Real area of the Sangre de Cristos (Fig. 7). The 1940's outbreak is not observed in the Tusas BRN stand or in the Taos Range at Questa, except at RED, where we indicate an outbreak that marginally met our classification criteria (Fig. 7). At Camino Real, the 1940's outbreak appears as either two outbreaks or an outbreak followed by a collapse and subsequent resurgent outbreak. The budworm-free periods before and after the 1940's outbreak (which at Tusas and Questa is one extended period), are longer than earlier periods between outbreaks. These 2 budwormfree periods are consistently recorded by all stands, which is unusual. Also unusual is the most recent outbreak, which we refer to as the 1980's outbreak. This outbreak is evident in each stand, a rare concurrence. These observations are discussed in detail in Swetnam and Lynch (1989), and are consistent with our earlier conclusions that there was a relatively long period of reduced budworm activity in the early 20th century, and that since that time outbreaks have been markedly more synchronous.

Some past outbreaks were quite long. These periods were frequently followed by extended periods without budworm, as seen at BON, LAJ, and RED, but not always, as at ALA and POL.

Questa appears to have had fewer and somewhat longer outbreaks than either Camino Real or the Jemez Mts. The Jemez stands consistently recorded budworm outbreaks, usually with every stand recording the outbreak. This is a different pattern than observed in the Sangre de Cristos.



Fig. 5. This limber pine site at Elephant Rock near Red River NM was used to crossdate and define climate variation for RTC and BON. Some live trees are older than 1600 years, but the stand differs greatly from classic images of old growth stands.

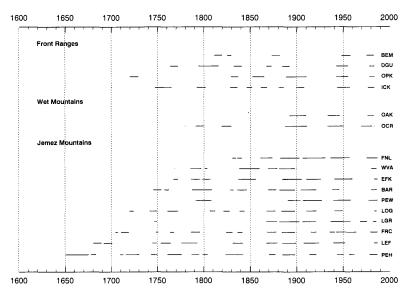


Fig. 6. Timing and duration of budworm outbreaks of stands in Colorado and the Jemez Mountains of New Mexico. Dotted lines denote the length of the chronology, solid lines denote periods of growth reduction caused by western spruce budworm.

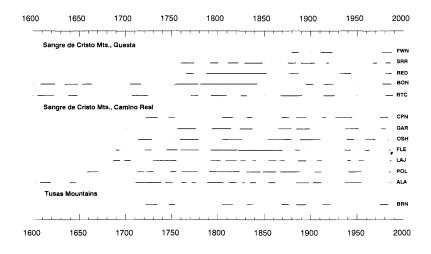


Fig. 7. Timing and duration of budworm outbreaks of stands in the Sangre de Cristo Mountains and Tusas Mountains in New Mexico. Dotted lines denote the length of the chronology, solid lines denote periods of growth reduction caused by western spruce budworm.

Western Spruce Budworm Outbreaks and Old-Growth Stands

Frequency: The number of outbreaks occurring since 1870, relative to stand age in 1870, is shown in Fig. 8. Earlier outbreaks are excluded to ensure that most of the stands were "old" at the time of the relevant outbreak. No age-related patterns are distinct. Most stands have had 4 or 5 outbreaks since the late 1800's, regardless of stand age, although the two oldest stands (BON and RTC at Questa) had only 3. Within the range of stand age between 80 and 250 years, there is no discernable relationship. Other factors, such as the history of previous outbreaks, grazing, fire, and logging, are probably more significant at Questa than stand age.

The only distinct pattern appears to be a difference between Colorado and New Mexico (Fig. 8). Either the 1870's or the 1910's outbreak is not evident in Colorado stands, with the first budworm-free period occurring earlier and lasting longer (Fig. 6).

Initiation: It is commonly speculated, or even stated as fact, that old growth stands serve as foci for pest outbreaks. The supposition is that old-growth of "over-mature" stands are of poor vigor and constantly susceptible to pest populations, and that these populations "break out" when conditions favor either dispersal or increases in population densities.

We tested this by comparing outbreak timing to stand age. Fig. 9 shows the initial years of the last 4 outbreaks against the age of the stand in year 1 (year

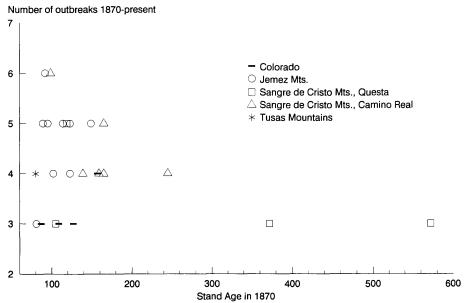


Fig. 8. Number of outbreaks occurring between 1870 and the present by stand age. Only stands 80 years or older in 1870 are included.

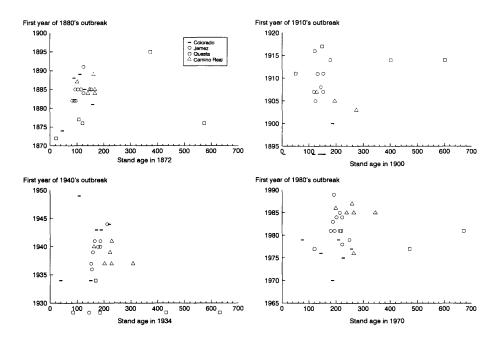


Fig. 9. Year in which growth reduction was first evident in each stand for the 1880's, 1910's, 1940's and 1980's outbreaks.

1 being the 1st year the outbreak was evident in any stand). The 1950/60's outbreak is not shown, as it occurred in a minority of the stands. If outbreaks initiated in old growth, then the outbreaks should be clustered in the lower right portion of each graph in Fig. 8. This is obviously not the case, especially considering the ages of the Questa stands not showing the 1940's outbreak, displayed below the x-axis. If anything, any trends are the opposite, with younger stands manifesting outbreaks first. Of course, the first year that the tree-ring index series show growth reduction may not be the first year that the insect population density reached outbreak levels. However,

it is likely that stands showing early growth reduction probably did have earlier high insect densities.

Duration: The period of growth reduction associated with western spruce budworm persists longer in older stands in the Sangre de Cristo Mountains for outbreaks starting between 1870 and 1960 (Table 2). Outbreaks were shorter in older stands in the Jemez Mountains. The range of stand age is much narrower in the Jemez Mountains than in the Sangre de Cristos (Table 1), representing only stands 200 to 270 years old. In the analysis, Sangre de Cristo stands were anywhere from 112 to 616 years old. The young-

Table 2: Correlation between stand age and the standard deviate of outbreak duration ((x -)/ for each outbreak), for the 1880's, 1910's, 1940's, and 1950/60's outbreaks, using all stands 80 years or older in 1870.

Area	\mathbb{R}^2	F	Sig.	-coef
Colorado	0.19	0.27	0.62	
Jemez	0.37	4.24	0.05	-8.72
Questa	0.48	6.46	0.04	3.25
Camino Real	0.12	2.29	0.15	4.84

est stand included was 112 when the 1880's outbreak started, and the oldest stand did not experience an outbreak in the 1950/60's and was 616 years old when the 1910's outbreak started. The Jemez stands, similarly, were anywhere from 93 to 235 years old in the analysis. The relationship in the Sangre de Cristos is not biased due to the extreme age of BON and RTC, since neither stand exhibited the 1940's or 1950/60's outbreaks, and the regression is significant without them (0.04).

DISCUSSION AND CONCLUSIONS

The Co-Existence of Old Growth and Western Spruce Budworm

Multiple western spruce budworm attacks are evident in 600 years of dendrochronologic records presented here for the Colorado Front Range, and the Jemez Mountains and Sangre de Cristo Mountains of New Mexico. Outbreaks occur neither more or less frequently in older stands, nor do they appear to originate in the oldest stands in our sample.

Lack of evidence of earlier budworm-induced growth reduction in older stands does not irrefutably establish that old growth stands are not outbreak foci. It is not completely implausible that older stands nurture endemic budworm populations, or that expansive endemic populations build up first in older stands but quickly disperse to more vigorous younger stands. Also, nearly all of our stands are old, so we are not making a comparison between immature, mature, and old growth stands. None-the-less, the evidence indicates that old growth mixed-conifer stands do not serve as foci for western spruce budworm outbreaks. At least with this pest, our data indicate that the presence of old growth is not hazardous to other stands. There may be pests where this is the case, however, because different types of pests behave very differently. Foliage rusts should not be casually compared to, or grouped with, defoliators, nor defoliators with bark beetles.

On the other hand, does western spruce budworm threaten old growth? The existence of 500- to 800-year old stands demonstrates very clearly that stands can survive many western spruce budworm outbreaks. These stands have survived not only the most recent outbreak, and the one before that, but many prior to those. And though outbreaks may persist

longer in old growth, the large majority of trees in the old growth stands have survived these events.

We conclude that western spruce budworm does not directly threaten old growth per se. However, western spruce budworm does contribute greatly to fuel loading and to fire risk and hazard (Flieger 1970, Stocks 1985). Fire exclusion favors multi-storied stands of shade-tolerant species preferred by budworm (Fellin et al. 1983), and therefore has contributed to increased extent, severity, and sychroneity of recent outbreaks (Swetnam and Lynch 1989). If western spruce budworm outbreaks are indeed more severe in the surrounding forest, then old growth is threatened by proximity alone. In the event of large, catastrophic wildfires occurring after extensive budworm or bark beetle outbreaks (Flieger 1970), remnant pockets of old growth are less likely to survive than under pre-historic fire regimes. Indirectly, then, western spruce budworm does appear to threaten old growth stands, especially under current management policies that modify natural disturbance regimes and promote budworm-prone forests.

Outbreak Duration

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Growth reductions induced during the 4 outbreaks preceding the most recent one persisted longer in older stands in the Sangre de Cristo Mountains, but were diminished in the Jemez Mountains. Do these conflicting results indicate differences between mountain ranges, or between stages of stand development? During the period from 1870 to the late 1960's, outbreaks persisted longer in the Sangre de Cristos than in the Jemez Mountains (Table 2), but the opposite was true in the previous 100 years (Figs 6 and 7). The two areas are represented by very different ranges in stand age, very broad in the Sangre de Cristos (470 years) and very narrow in the Jemez Mountains (70 years). We believe that these ostensibly conflicting results indicate that outbreaks generally persist longer in older stands, that different stages of stand development may differ greatly in habitat suitability for budworm, and that other factors are important, particularly local weather patterns.

Two explanations for longer periods of growth reduction are possible, the first being that the insect outbreak persisted longer, and the second being that older trees and/or stands are slower to recover from foliage loss and other physiologic damage. Either possibility is interesting and worthy of further investigation with dendrochronologic and other approaches. The variability in the relationship indicates that other factors besides stand structure and age are important. Further investigations should focus on stand structural development stages (especially species and size class distributions as they affect budworm habitat and natural enemy populations), Habitat Type, local weather patterns, and disturbance history. Such investigations should not be limited to old growth stands. Outbreak severity should be considered as well as duration when

evaluating the effects that temporal changes in stand structure have on budworm population dynamics. Our methodologies provide insufficient insight into tree mortality effects.

Typical Old Growth?

The stands we sampled cover a range in stand character, old growth characteristics, and continuity along stand development or successional gradients, as discussed by other authors in this volume. They do not represent a random sample from either mixed-conifer or old growth, although they probably are fairly representative of old growth mixed-conifer stands in New Mexico and Colorado today. The range of sampled Habitat Types is limited, and the proportion of white fir relative to Douglas-fir might be less than in the surrounding younger forest.

These stands do not represent a random sample of old growth that would occur naturally. The vast majority of mixed-conifer forests in Colorado and New Mexico have been logged at least once. These stands, or the older trees in them, are remnants of logging and fire disturbances. They are less accessible than most stands, usually by virtue of rugged terrain, or they had less desirable timber qualities, such as low densities or small diameters. Fire risk and hazard are low for some stands, because of their location in either moist canyons or on rocky ridges. Therefore, these stands do not represent the full range of site conditions possible for mixed-conifer, and are probably biased towards low site quality.

Most of the stands sampled meet the minimum criteria for old growth for Regions 2 and 3 (Bassett, this proceedings; Lowry, this proceedings; Mehl, this proceedings), but the appearance and structure of some stands are different from common perceptions of old growth mixed-conifer stands. Stands where the largest trees are not very big can be quite old, and the oldest trees are often not even close to being the largest of their species in the stand. This difference is dramatically demonstrated in the 2 oldest stands, BON and RTC. These stands are 494 and 694 years old, respectively, with mean diameters of the largest 5 host trees of 74 and 70 cm. However, the mean diameter of the 5 oldest trees is 34 cm at BON and 38 cm at RTC. The upper canopy and the older component of these and many other stands do not match closely.

Aside from the issue regarding characterization of old-growth stands, the disparity between size of old and large trees within a stand has interesting implications regarding tree resistance to western spruce budworm defoliation. At least in some cases, very slow-growing trees are surviving budworm outbreaks when faster-growing neighbors are not, e.g., RTC (Fig. 4). These old trees have survived centuries of climate variability, stand conditions, and insect numbers, while more vigorous neighbors have perished.

Density and stocking vary greatly, from less than 150 to almost 1100 trees/ha and from 15 to 65 sq m/

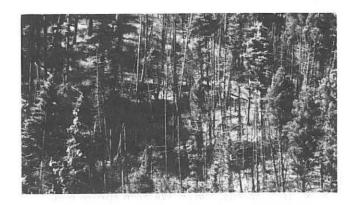


Fig. 10. This stand in Red River Canyon in New Mexico has suffered high mortality in the most recent western spruce budworm outbreak, but some trees have survived. It is typical of many mixed-conifer stands in Colorado and New Mexico.

ha. Mean diameters are 30 cm or larger in only 7 of 31 stands. The mean diameter of the largest 5 trees in 2 New Mexico stands does not meet the low diameter limit for Region 3 minimum criteria for structural attributes used to determine mixed-conifer oldgrowth (Bassett, this proceedings). Since our diameter data are for the largest 5 host trees in the stand, they over-estimate main canopy diameters. More of our stands may not meet the diameter minimum criteria. The mean diameter of the oldest 5 trees meets the minimum criteria in only 40% of the New Mexico stands. Diameter distributions of stands at least 250-years old vary from distinctly reverse-Jshaped (e.g., BON, ICK, FRC) to normal (e.g., ALA, PEH). Two stands with almost uniform diameter distributions, CPN and LAJ, are fairly young, 188 and 221 years, respectively. Except for CPN, diameter distributions of the stands younger than 200 years are weakly reverse-J-shaped (OAK, FNL, FWN) or strongly reverse-J-shaped (BEM, CAB).

Most of the stands have high numbers of dead trees, both snags and down trees. However, the majority of this mortality was caused by western spruce budworm or subsequent bark beetle attack. These insects regularly cause mortality in host stands. Mortality can be extreme, but seldom, if ever, kills all trees in the stand (Fig. 10). Most stands have been subjected to 4 or 5 western spruce budworm outbreaks in the last 120 years, some as many as 6. Large numbers of standing and down dead trees are to be expected under these circumstances. The usefulness of decadence and numbers of dead trees as criteria for old growth are probably limited in forest types subject to recurrent insect attacks that cause mortality.

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Postsettlement Changes in Natural Fire Regimes: Implications for Restoration of Old-Growth Ponderosa Pine Forests¹

W. W. Covington and M. M. Moore²

Heavy livestock grazing and fire suppression associated with Euro-American settlement has brought about substantial changes in forest conditions in western forests. Thus old-growth definitions based on current forest conditions may not be compatible with the natural conditions prevalent throughout the evolutionary history of western forest types. Detailed analysis of data from two study areas in the southwestern ponderosa pine type suggests that average tree densities have increased from as few as 23 trees per acre in presettlement times to as many as 851 trees per acre today. Associated with these increases in tree density are increases in canopy closure, vertical fuel continuity, and surface fuel loadings resulting in fire hazards over large areas never reached before settlement. In addition, fire exclusion and increased tree density has likely decreased tree vigor (increasing mortality from disease, insect, drought, etc.), decreased herbaceous and shrub production, decreased aesthetic values, decreased water availability and runoff, decreased nutrient availability, changed soil characteristics and altered wildlife habitat. To remedy these problems and restore these forest ecosystems to more nearly natural conditions, and maintain a viable cohort of old age-class trees, it may well be necessary to thin out most of the postsettlement trees, manually remove heavy fuels from the base of large, old trees, and reintroduce periodic burning.

"Between the two extremes of passively following nature on the one hand, and open revolt against her on the other, is a wide area for applying the basic philosophy of working in harmony with natural tendencies" (H. J. Lutz 1959).

INTRODUCTION

¹Paper presented at the Old-growth Forests in the Southwest and Rocky Mountain Regions, Portal, AZ, March 9-13, 1992.

²Professor and Assistant Professor, School of Forestry, Northern Arizona University, Flagstaff, AZ 86011. Understanding natural ecological conditions and processes, before significant impact by Euro-American settlement (Kilgore 1985), is central to developing ecologically coherent forest management programs (e.g., see Vogl 1974, Franklin 1978, Harris 1984, Kilgore 1985, Forman

and Godron 1986). This is particularly true for management of landscape diversity with remnant natural patches of old-growth forests (Bonnicksen and Stone 1985, Parsons et al. 1986, Moir and Dieterich 1988, Forman and Godron 1986, Booth 1991) or managing for the development of old-growth and other stages of forest development (Thomas 1979, Hoover and Wills 1984, Moir and Dieterich 1988). However, heavy livestock grazing, logging, and fire suppression associated with Euro-American settlement have brought about substantial changes in forest conditions in western forests, so much so that current conditions may be decidedly "unnatural." In particular, the exclusion of natural fires has led to increased tree densities and associated shifts in forest structure, fire hazard, and wildlife habitat in some western forest types. Thus oldgrowth definitions based on current forest structure may not be compatible with the natural conditions prevalent throughout the evolutionary history of the organisms living in western forests. For these reasons, we believe that planning and management for an old-growth component of ponderosa pine and other forest types in the Southwest and Rockies must include an understanding of past (presettlement), present, and future conditions. An attitude of "that was then and this is now" may lead to less than desirable forest conditions in the future.

In this paper we present a general discussion of changes in natural fire regimes, then examine in more detail the evidence for such changes in the southwestern ponderosa pine type and how these changes have affected overall ecological conditions. Finally, we close with a brief discussion of possible methods for remedying some of the problems

associated with postsettlement changes in western forests.

NATURAL FIRE REGIMES

Understanding the natural disturbance regimes under which a particular species evolved is central to predicting the ecological consequences of management activities (e.g., see Bormann 1981, White 1979). Periodic wildfire has played a central role in the evolution of forest and woodland ecosystems throughout the western United States (Parsons 1981, Kilgore 1981). In fact many species and forest types worldwide appear to be dependent upon a particular frequency and intensity of fire for their survival (Mooney 1981, Parsons 1981).

Fire regimes have been classified according to frequency, intensity, size, and type (Heinselman 1981, Kilgore 1981, Sando 1978). Frequency, or burning interval, has been defined as the average return period for fire burning through a particular vegetation type. Sando defined frequent fires as fires which occur at intervals of 1-10 years; infrequent fires by his definition are fires occurring at intervals greater than 10 years, often as infrequently as once every 20-300 years. Kilgore (1981) separated frequent from infrequent fires at 25 years.

Although fire intensity has been used as a qualitative term (e.g., light surface fire vs severe crown fire, see below), some authors argued for a quantitative definition such as fire line intensity (Sando 1978, Kilgore 1981). Specifically, they recommended Byram's fire line intensity, a product of heat yield per unit area (BTU per square foot) and the rate of fire spread (feet per second). The resulting units are BTU's per foot per second. To avoid

confusing qualitative and quantitative definitions, we recommend that qualitative differences be referred to as fire severity, and that the term fire intensity be reserved for a more quantitative measure.

Fire regimes have also been characterized according to size. For example, Heinselman (1981) classified fire size into four classes: small (100 acres and less), medium (101-1,000 acres), large 1,001 - 10,000 acres), and very large (>10,000 acres). On the other hand, the USDA Forest Service reported wildfire data in seven classes: A (<0.25 acres), B (0.26-9 acres), C (10-99 acres), D (100-299 acres), E (300-999 acres), F (1,000-4,999 acres), and G (5,000 acres and larger).

Fire type has been classified into as few as two (surface vs. crown) to six or more categories. For example, Heinselman (1981) differentiated fire type into light surface fires, severe surface fires, crown fires, and combinations of the three. Kilgore (1981) used the terms low intensity surface fire, high intensity surface fire, stand replacement fire, and combinations of these three categories. Several authors have related fire severity to fire intensity (Byram 1959, Van Wagner 1973, Albini 1976, and Sando 1978). Integrating these views on intensity:severity relationships, Sando (1978) concluded that at low to moderate (0-1200 BTU/ft/sec) fire line intensity, complete mortality of overstory vegetation would not occur. At levels above 1200 BTU/ft/sec nearly complete overstory mortality would be expected.

For this discussion we will use Sando's (1978) classification of natural fire regimes. He described four types:

Type one -- frequent fires (1-10 yr) of low to moderate intensity (<1200 BTU/ft/sec) (e.g., ponderosa pine, lower elevation mixed conifer, giant sequoia, southern pine forests, short grass and mixed grass prairies, savannahs).

Type two -- infrequent fires (>10 yr) of high intensity (>1200 BTU/ft/sec)(e.g., boreal and subalpine spruce-fir, lower elevation mixed conifer forests, temperate rain forests).

Type three -- frequent fires of high intensity (e.g., tall grass prairie).

Type four -- infrequent fires of low to moderate intensity (e.g., deserts, tundra, mesic deciduous forests).

Fire exclusion affects each of these fire regimes differently. Fire exclusion has little impact on the fire regime of types three and four. Only small remnants of type three exist, virtually all of it having been converted to agriculture. However, under natural conditions, fire suppression would not have been practical in this type because of the extreme fire behavior which occurred in type three. Fire exclusion in type four has little effect on the fire regime because excess flammable organic matter rarely accumulates.

Fire exclusion in type two will have a greater impact because over time more patches will be in a condition which will support crown fire. For example, if we assume that 100 years are necessary for a particular vegetation type to accumulate sufficient fuel to support a crown fire, then after 100 years of successful fire exclusion, all of the area in that type would be capable of supporting crown fire (Figure 1). Thus, in type two, fires become larger over time.

Assume 100 years to accumulate fuel loads which support crown fires (*indicates crown fire potential)

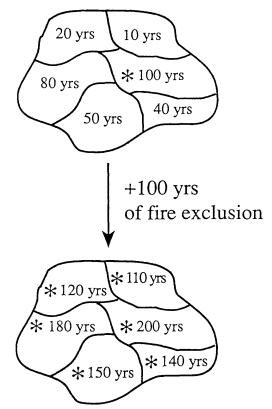


Figure 1. Effects of fire exclusion in landscapes with an infrequent, high intensity natural fire regime (Type II).

The greatest change in fire regime following fire suppression is in type one. Here the natural fire regime was frequent enough to keep surface fuel loads low and to thin out trees so that canopy fuels were separated both vertically and horizontally. With fire exclusion in this type, surface fuels accumulate and trees become established gradually providing a fuel ladder and increasing canopy closure. These changes in fuel structure lead to a shift from the light surface fires which maintain ecosystem characteristics to

intense stand replacement crown fires characteristic of the type two fire regime. As we will discuss below, continued fire suppression in this type might well lead to the same changes seen in type two fire regimes, i.e., the coalescing of patches into larger and larger areas capable of supporting crown fire (Figure 1). The classic example of a type one natural fire regime is ponderosa pine.

Now we will turn to a more detailed discussion of ecological consequences of shifts in fire regimes by examining postsettlement changes in southwestern ponderosa pine ecosystems.

POSTSETTLEMENT CHANGES IN SOUTHWESTERN PONDEROSA PINE FORESTS

It is widely acknowledged that fire exclusion and other factors associated with European settlement have greatly altered forest conditions in southwestern ponderosa pine (Cooper 1960, Weaver 1951, Covington and Sackett 1984, White 1985, Covington and Sackett 1986, Covington and Moore, accepted).

Reports from early travelers illustrate the changes in appearance of the ponderosa pine forest since settlement. E. F. Beale's 1858 report is quoted by C. F. Cooper (1960) as follows:

"We came to a glorious forest of lofty pines, through which we have travelled ten miles. The country was beautifully undulating, and although we usually associate the idea of barrenness with the pine regions, it was not so in this instance; every foot being covered with the finest grass, and beautiful broad grassy vales extending in every direction. The forest was perfectly open and unencumbered with brush wood, so that the travelling was excellent" (Beale 1858).

Cooper (1960) stated, "The overwhelming impression one gets from the older Indians and white pioneers of the Arizona pine forest is that the entire forest was once much more open and park-like than it is today."

Before European settlement of northern Arizona in the 1860's and 70's, periodic natural surface fires occurred in ponderosa pine forests at frequent intervals, perhaps every 2-12 years (Weaver 1951, Cooper 1960, Dieterich 1980). Extensive study of fire scars suggests that the natural fire size was approximately 3,000 acres (Swetnam and Dieterich 1985, Swetnam 1990).

Several factors associated with European settlement caused a reduction in natural fire frequency and size. Roads and trails broke up fuel continuity. Domestic livestock grazing, especially overgrazing and trampling by cattle and sheep in the 1880's and 1890's, greatly reduced herbaceous fuels. Active fire suppression, as early as 1908 in the Flagstaff area, was a principal duty of early foresters in the Southwest. A direct result of interrupting and suppressing these naturally occurring, periodic fires has been the development of overstocked forests.

Changes in the forest structure (e.g., tree density, cover, and age distributions) in southwestern ponderosa pine forests since European settlement have been blamed for many forest management problems (Biswell 1972, Cooper 1960, Weaver 1974, Covington and Sackett 1990, Covington and Moore, accepted). Forest management problems attributed to

fire exclusion and resulting increased tree density in ponderosa pine include:

- 1. overstocked sapling patches;
- 2. reduced tree growth;
- 3. stagnated nutrient cycles;
- 4. increased disease, insect infestation, and parasites (e.g., root rot, bark beetle, dwarf mistletoe);
- 5. decreased forage quality and quantity;
- 6. increased fuel loading;
- 7. increased vertical fuel continuity due to dense sapling patches;
- 8. increased severity and destructive potential of wildfires;
- 9. increased tree canopy closure;
- 10. decreased on-site water availability;
- 11. decreased stream-flow and ground water recharge; and
- 12. shifts in habitat quality for biota.

Evidence for the shift from a type one to a type two fire regime in ponderosa pine since settlement comes from a study by Barrows (1978) later updated by Swetnam (1990). Using USDA Forest Service wildfire statistics they determined that lightning caused crown fires had increased from 10,127 acres per year in the 1940's to 15,117 acres per year in the 1980's. In the 1970's an average of 33,801 acres per year were burned by wildfire in the Southwest. Both Barrows (1978) and Swetnam (1990) observed that lightning caused wildfires in the Southwest are getting larger and larger over time, with some fires reaching 10,000-20,000 acres, in contrast to the 3,000 acre surface fires of presettlement times (Swetnam and Dieterich 1985, Swetnam 1990). This represents a three- to six-fold increase in average fire size. Thus, we may be witnessing in the ponderosa pine type the kind of shift in size observed in the type two fire regimes, i.e., the coalescing of

patches into larger and larger areas capable of supporting very large (>10,000 acres) crown fires.

The Southwest has little quantitative information on the nature of its presettlement forest ecosystems. The major writings and research have been in the ponderosa pine type and deal only with tree densities. As mentioned earlier, Cooper (1960) cited the writings of early expedition leaders, Whipple (1856) and Beale (1958). They reported that the condition of the southwestern ponderosa pine forest "...was open and park-like with a dense grass cover." These early descriptions of the open nature of presettlement ponderosa pine forests are in agreement with results of recent research which found that canopy coverage by trees of presettlement origin range from 17% (Covington and Sackett 1986), to 22% (White 1985), to 2-31% (Moore unpublished) of the surface area for unharvested sites near Flagstaff, AZ. In addition, Pearson (1923) noted that "rarely does [ponderosa pine] crown cover reach more than 30% and usually not over 25%."

Cooper (1960) stated that the structure of the southwestern ponderosa pine type in the White Mountains of east-central Arizona is actually that of an all-aged forest composed of even-aged groups. He noted great variation in diameter within a single age class. Using contiguous quadrat analysis (Grieg-Smith 1952) in two stands, Cooper determined that the presettlement trees aggregated into areas ranging from 0.16 to 0.32 acres. White (1985), in a study conducted on the Pearson Natural Area near Flagstaff, noted that successful establishment of ponderosa pine in presettlement times was infrequent (as much as four decades between

regeneration events). White also quantified the strong aggregation of ponderosa pine stems. Using the nearest neighbor method (Clark and Evans 1954), White demonstrated that the aggregation ranged from 3 to 44 stems within a group, with a group occupying an area that ranged from 0.05-0.70 acres. "Ages of stems within a group were also variable with the most homogeneous group having a range of 33 years and the least having a range of 268 years (White 1985)." White's findings of a pattern of unevenaged groups near Flagstaff are in contrast to the results of Cooper (1960) for the White Mountains. However, White conducted a 100% dendrochronological analysis on all of the presettlement trees in his study area, while Cooper used a double sampling approach and developed a regression using age as a function of dbh, then applied this regression to extensive timber inventory data. In southwestern ponderosa pine, however, the age:dbh relationship is imprecise and therefore its use for determining simultaneity of presettlement regeneration events is questionable. For the southwestern ponderosa pine type, therefore, the data suggests that at the group-level the trees are basically all-aged and have sporadic regeneration events. (White 1985, Covington and Moore, accepted). At the landscape level (square miles in size), however, several studies have shown simultaneous regeneration events that were correlated with simultaneous surface fires, and favorable climatic oscillations (e.g. La Niña—opposite pattern of El Niño—Kerr 1980, Swetnam 1990, Savage 1989). Thus, we believe the confusion of whether the southwestern presettlement pine forests were all-aged or even-aged is a matter of scale and is a landscape issue. At the

patch level (or fine scale) the pine groups are all-aged, yet across a landscape (or coarse scale) where many surface fires may have burned at the same time, there are regeneration events that produced trees of the same age over large areas.

Madany and West (1983) discussed the effects that many years of heavy grazing and fire suppression have had on ponderosa pine regeneration in southern Utah (Zion National Park). They suggested that ponderosa pine seedling survival was probably greater in the early 1900's than in the presettlement days due to reduced competition of grasses (through grazing) with pine seedlings, and the reduced thinning effect that fires once had on seedlings in presettlement times.

Moir and Dieterich (1988) pointed out the importance of understanding the role of the natural, presettlement fire regime in directing successional processes toward ponderosa pine old-growth development and in keeping fuel loading low enough for large trees to survive wildfires. They stated that most of the old-growth in southwestern ponderosa pine forests has deteriorated because recurrent natural fires have been suppressed. Finally, they present an eleven stage model of succession from open meadow through sapling, pole, yellow pine, and dead snag dominated landscape units.

Postsettlement changes in the ponderosa pine type are not unique to the Southwest. In fact, studies in Utah (Madany and West 1983, Stein 1987), Montana (Gruell et al. 1982), Idaho (Barrett 1988, Steele et al. 1988), Washington (Weaver 1959), and California (Laudenslayer et al. 1989) suggested that increased tree density, fuel loading, and crown fire occurrence are common consequences of fire exclusion throughout the ponderosa pine type (Kilgore 1981). Simulation studies (van

Wagtendonk 1985, Keane 1990) indicated that this phenomenon may occur not only in the pure ponderosa pine type, but also in ponderosa pine/Douglas-fir and mixed conifer forests as well. Thus, although many questions remain regarding the ecological and multiresource implications of postsettlement changes in ponderosa pine forests, there is a wide consensus that today's forests are radically different from those present before European settlement.

DETAILED ANALYSIS OF TWO STUDY AREAS IN ARIZONA PONDEROSA PINE

To better understand postsettlement changes in southwestern ponderosa pine, we studied changes in forest conditions for two areas in northern Arizona. One, the Bar-M study area, has soils of volcanic origin and is on the Mormon Lake Ranger District of the Coconino National Forest. The other has soils of limestone origin and is on the North Kaibab Ranger District of the Kaibab National Forest. More detailed descriptions of the study area and methods used are available in Covington and Moore (1992 accepted) and Covington and Moore (in preparation).

Study Areas -- The Bar-M Canyon study area is located approximately 25 miles south of Flagstaff. The Bar-M watershed is part of the Mogollon Rim Plateau. It is a gently rolling landscape, dissected by many steep canyons. Elevations range from 6360-7710 feet. Our plots were located between 6800 and 7200 feet. The bedrock underlying the area consists of igneous rocks of volcanic origin. The soils, developed on basalt and cinders, are mostly silty clays and silty clay loams less than 2.6 feet deep (Brown et al. 1974)

The average annual precipitation for the area is 25.0 inches. There are two major precipitation seasons. Sixty-four percent of the precipitation falls during the winter—October through April. Thirty-two percent falls during the summer—particularly July and August (Brown et al. 1974).

The North Kaibab study area is located on the Kaibab Plateau of north central Arizona, approximately 100-120 miles north of Flagstaff. Like Bar-M canyon it is a gently rolling landscape, dissected by steep canyons. The elevation of our plots ranged from 6800-7800 feet. The bedrock underlying the area consists primarily of Kaibab limestone. The soils, developed from limestone, are mostly sandy and gravelly loams and loams. Average annual precipitation for the North Kaibab ponderosa type is 22 inches (Brewer et al. 1991).

The forests of both study areas are predominantly ponderosa pine (Pinus ponderosa Laws.), with a mixture of Gambel oak (Quercus gambelii Nutt.) and juniper (Juniperus spp). In the cooler, moist portions of the study areas quaking aspen (Populus tremuloides Michx.)., and small amounts of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), spruce (Picea spp.), and fir (Abies spp.) regeneration may be found (although all of these species were found in much greater proportions on the North Kaibab study site). The understory grasses consist primarily of mutton bluegrass (Poa fendleriana (Steud.) Vasey), pine dropseed (Blepharoneuron tricholepis (Torr.) Nash.), black dropseed (Sporobolus interruptus Vasey), blue grama (Bouteloua gracilis H.B.K. Lag.), bottlebrush squirreltail (Sitanion hysterix Nutt); and forbs such as showy aster (Aster commutatus Torr. and Gray), spreading fleabane (Erigeron divergens

Torr. and Gray), showy goldeneye (Viguiera multiflora Nutt.), western ragweed (Ambrosia psilostachya DC.), and snakeweed (Gutierrezia spp.). The shrubs are primarily New Mexican locust (Robinia neomexicana Gray), Gambel oak sprouts, buckbrush (Ceonothus fendlerii Steud.), and Oregon grape (Berberis repens Lindl.) (Brown et al. 1974, Brewer et al. 1991). Notable differences include large components of long-tongue mutton bluegrass (Poa longiligula (Scribn. and Williams) and lupine (Lupinus spp.) at the North Kaibab that was not found at Bar-M. A peculiarity was that only a small amount of Arizona fescue (Festuca arizonica Vasey) was found at either of the study sites. Plant nomenclature follows Kearney and Peebles (1964).

Field Procedures -- On both sites we used a stratified systematic sampling procedure. The areas were stratified by soil type and topography using the U.S. Forest Service Terrestrial Ecosystem Survey (TES) (Anon. 1987, Brewer et al. 1991). At Bar-M, map unit #582 was the most common soil-slope-vegetation unit (Typic Argiboroll and Mollic Eutroboralf; Low Sun Cold, with ponderosa pine and Gambel oak as the dominant trees, 0-15% slope). Within the North Kaibab study area, map units #293 and #294 were the most common (Mollic Eutroboralf; Low Sun Cold, with ponderosa pine and Gambel oak as the dominant trees, 0-15% slope (#293) the most common and 14-40% slope (#294) also represented).

At the Bar-M study area, seventy 0.62 acre (one-quarter hectare) plots were systematically located within map unit #582. The large plot size was chosen to incorporate the patchy nature of ponderosa pine old-growth and for spatial analysis in the future. Sixty-two of these plots were

extensive; only the presettlement trees were sampled on these plots. All presettlement trees (live, snags, stumps, and down) were stem-mapped (exact x,y location recorded on the plot). In addition to location, presettlement tree species and dbh were recorded.

An additional eight 0.62 acre plots were sampled more intensively at Bar-M. Information on all trees was gathered on these plots. In addition to location, the species (live, snags, stumps, and down), size class (e.g., seedling, sapling, etc.), dbh, and density (number per acre and basal area) were also recorded. A ten percent sample of all trees less than 14.6 and greater than 3.9 inches dbh was selected to determine an age distribution and approximate date of postsettlement tree establishment. All trees greater than or equal to 14.6 inches were aged as was any pine tree with yellow bark. Our logic for these dbh and bark criteria was similar to that of White (1985) who determined statistically that the majority of presettlement ponderosa pine would be > 14.6 in., and that those which were not would have yellow bark. This latter criterion is based on the observation that in the Southwest ponderosa pine bark changes color from "black" to "yellow" as the tree ages (Pearson 1950).

At the North Kaibab study site we made our plot locations compatible with an earlier inventory (Lang and Stewart 1910). Our sample plots were located in the center of systematically selected quarter sections. Forty-six 0.62 acre (0.25 ha) plots were located in TES #293 and #294. Presettlement trees were sampled on all plots, while additional information on postsettlement trees was gathered on 36 of these plots. Data collected and sampling techniques used were the same as described above for the Bar-M study site.

The results for only 16 intensive plots (data on all trees) from the North Kaibab are presented in this paper because we are still analyzing the remainder.

The tree rings of all presettlement trees from both study sites were used to determine total age. We also counted and measured the rings from present to time of European settlement (1867 - Bar-M; 1881 - North Kaibab) to determine the diameter of each tree at that presettlement date, and to determine average annual growth since settlement. If the tree was a stump, snag, or down material then the year of death was estimated (Thomas 1979, Maser et al. 1979, Cunningham et al. 1980, Rogers et al. 1984), and the presettlement diameter determined.

Simulation Models -- To understand how forest structure and patterns changed over time we linked the spatial data from the stem-mapped intensive plots (8 from Bar-M and 16 from North Kaibab) to the ECOSIM multiresource forest growth and yield simulation model (Rogers et al. 1984). The tree growth and yield model used in ECOSIM is based on the FREP/STEMS model (Belcher et al. 1985, Brand 1981) calibrated with continuous forest inventory data from Arizona and New Mexico. The water yield model is based on the "Baker-Kovner" model (Brown et al. 1974) in which streamflow is a function of winter precipitation, aspect, slope, and tree density. For herbage production, a modification of Clary's (1978) model was used, where herbage is a function of annual precipitation, tree density, and range site class. Forest floor accumulation is estimated as the difference between litterfall (calculated from tree density and canopy biomass) and decomposition using Fogel and Cromack's (1977) estimates for ponderosa pine

decomposition rates. Near view scenic beauty is estimated using equations developed by Daniel and Boster (1976) and Schroeder and Daniel (1981). An index of scenic beauty is calculated as a function of number of large (> 16 inch dbh) trees, number of mid-sized trees (5-16 inches dbh), amount of logging slash, amount of herbage, and amount of shrubs. For more detail on the simulation techniques the reader is referred to Rogers et al. (1984).

Each simulation run consisted of entering the dbh of all presettlement trees (live trees, snags, downed trees and stumps) by diameter class as stand conditions in 1867 for Bar-M and 1881 for the North Kaibab. Settlement of the Flagstaff area preceded that of the North Kaibab area, thus grazing and hence fire exclusion began earlier at the Bar-M study area. Then, based on the regeneration events inferred from the age distribution of the postsettlement trees, we entered trees into the stand at appropriate intervals in simulated time. The output from these computer runs was a series of tables (from 1867 or 1881 through 2030) which quantitatively estimate the changes in forest density in southwestern ponderosa pine since European settlement. This information on forest density was used to run fuel loading, herbage, water yield, and esthetics models (Rogers et al. 1984). We used the model results to draw inferences about temporal changes in multiresource conditions since European settlement and to forecast future trends.

Results and Discussion -- Tree density at both study areas has increased greatly since the late 1800's (Table 1).

Presettlement tree density was higher by a factor of two on the North Kaibab study area than at the Bar-M study area.

Postsettlement tree density was much

greater at Bar-M than at North Kaibab. However, because of the small sample size (8), the postsettlement tree densities at Bar-M should be viewed with caution. Our estimates of presettlement tree density are consistent with estimates from other sources (Table 2).

Table 1. Changes in the tree density since settlement for two ponderosa pine study sites. Data are means (\bar{x}) based on varying sample size (n).

Study Area	Presett (ca. and	1880	Curr (ca. 1							
	trees/acre									
	\bar{x}	(n)	x	(n)						
North Kaibab (limestone)	55.9 ²	(36)	276.3 ²	(30)						
Bar-M Canyon (volcanic)	22.8	(70)	851.0	(8)						

¹includes stumps, snags, and down trees
²North Kaibab sampling and data analysis are in process; eventual sample size is 50, and data will be analyzed according to ecological strata (soil/slope/vegetation)

Table 2. Density of southwestern ponderosa pine presettlement or yellow pine trees reported in the literature and in this study.

Location	Trees/acre
Specific studies in the Southwest:	
Ft. Valley, Coconino N.F. ¹	13
Bar-M, Coconino N.F. ²	23
North Kaibab R.D., Kaibab N.F. ³	56
North Kaibab R.D., Kaibab N.F.4	40-45
White Mountains, Apache-Sitgreaves N.F.5	35-45
Southern Utah, Zion N.P.6	3-25
USFS Bulletin 101: ⁷ (some of the heavily stocked yellow pine stand	s)
Coconino N.F.	27
Kaibab (Tusayan) N.F.	35
Carson N.F.	26-47

¹White, 1985; ²Covington and Moore, 1991;

³Covington and Moore, this paper; ⁴Rasmussen, 1941;

⁵Cooper, 1960; ⁶Madany and West, 1983; ⁷Woolsey, 1911

The results from the simulation model analysis are presented in Tables 3 and 4. We initialized the simulation in 1867 for Bar-M and 1881 for North Kaibab as follows:

- 1. Tree density -- we entered the trees by dbh and species present in 1867 at Bar-M and 1881 at North Kaibab.
- 2. Site index = 75, the site index for Terrestrial Ecosystem Survey map unit #582, 293, and 294.
- 3. Soil rating factor = 9 for Bar-M and 12 for North Kaibab, based on the forage production potential for map unit #582, 293, and 294. Soil rating factor is an index varying from 0 for poor range sites to 12 for the best.
- 4. Fuel loading = 0.1 t/ac of fermentation + humus layers and 0.1 t/ac of litter layer of the forest floor. This is based on the fuel loading data from Covington and Sackett's (1986) 2-year interval prescribed burning plots in ponderosa pine with the assumption that tree canopy covered approximately 20% of the surface of the land (Covington and Sackett 1986, White 1985).
- 5. For Bar-M, average annual precipitation = 25"; average annual winter precipitation = 16.9". This is the 22 year average for the ponderosa pine watersheds in the Beaver Creek drainage (Campbell and Ryan 1982). Precipitation was held constant throughout the simulation. For North Kaibab, average annual precipitation = 22"; average annual winter precipitation = 12.1:, based on climatic data reported in the Terrestrial Ecosystem Survey for north Kaibab map units 293 and 294.

Table 3. Simulated changes since settlement for 8 plots on a volcanic site (Bar-M).

Simulated Date (year A.D.)	Tree Basal Area (ft²/ac)	Crown Closure (percent)	Fuel Loading (t/ac)	Herbage Production (lbs/ac)
1881	23	8.0	2.0	1000
1907	30	9.9	3.1	856
1927	38	12.4	4.0	571
1947	60	21.4	6.2	134
1967	85	33.6	11.5	124
1987	154	57.2	19.0	114
2007	234	80.9	30.1	112
2027	306	92.1	42.0	112
2030	315	93.1	43.7	112

Table 4. Simulated changes since settlement for 16 plots on a limestone site (NKRD).

Simulated Date (year A.D.)	Tree Basal Area (ft²/ac)	Crown Closure (percent)	Fuel Loading (t/ac)	Herbage Production (lbs/ac)
1881	44	15.6	0.2	589
1901	62	20.8	6.0	441
1921	81	25.9	9.3	308
1941	103	31.8	12.1	221
1961	132	38.9	15.0	154
1981	158	47.1	18.3	132
2001	192	56.1	22.1	124
2021	228	65.8	26.4	118
2030	245	70.2	28.4	117

To simulate the establishment of postsettlement trees we entered seedling density corresponding with the number of postsettlement trees for each species. Seedlings were entered beginning at the point in simulated time which represented the earliest establishment data observed on the plot. Similarly, the last date of seedling establishment was used as the last seedling establishment date in simulated time.

The results of the simulation model provide an estimate of how forest conditions have changed since European settlement in Arizona ponderosa pine type and how these trends might continue into the future (Tables 3 and 4). Increases in tree density through 1990 are estimated to have caused substantial declines in average herbage production (decreases of over 1,000 lbs/ac at Bar-M and 350 lbs/ac on the North Kaibab). This decreased herbage in conjunction with increased small diameter tree density has caused a striking decline in near view scenic beauty (Covington and Moore, accepted). At the same time, forest floor and fuel loading is estimated to have increased from less than 1 t/ac before settlement to an average of over 20 t/ac at both study areas. Vertical diversity, fuel ladder continuity (as estimated by diameter distribution of trees), and crown closure have also increased substantially (Tables 3 and 4).

To estimate changes in wildlife habitat characteristics since 1867, we used the simulation output for tree density by diameter class to classify the simulated stand into vegetation structural stages (Thomas et al. 1979) and then used the Forest Service Southwestern Region's forest planning wildlife report (Byford et al. 1984) to determine the change in relative habitat value from 1867 to the present. This analysis indicates that there

has been a shift away from the grass-forb structural stage common in the late 1800's to a seedling dominated structural stage after the turn of the century, and then to mature timber and finally old-growth trees growing over dense sapling and poles from the 1960's on.

These changes in vegetation since settlement indicate a shift in foraging habitat from one favoring grassland/savannah species (e.g., pronghorn antelope, grasshoppers, bluebirds, and turkeys) to one favoring species feeding in dense forests (Abert squirrel, porcupine, bark beetle, pygmy nuthatches and Mexican spotted owl). On the other hand, cover habitat may have increased for many wildlife species since settlement. In sum, the shift in tree density seems to have favored species dependent on closed forest conditions at the expense of those which require some portion of their habitat in grass/forb or savannah. Gruell et al. (1982) noted similar changes in wildlife habitats for ponderosa pine/Douglas-fir forests in western Montana.

Under the assumption that no substantial tree mortality occurs between 1987 and 2027, many of these trends are predicted to continue (Tables 3 and 4).

Undoubtedly, the increased tree density is a key factor contributing to the increased occurrence of large crown fires in southwestern ponderosa pine (Barrows 1978). Fire simulation studies of ponderosa pine and related forest types (van Wagtendonk 1985, Keane et al. 1990) are consistent with these conclusions.

Furthermore, increased density is responsible for decreased growth rates of presettlement trees (Sutherland 1983), and hence decreased vigor (Waring 1983), which increases susceptibility to bark beetle attack (Sartwell 1971, Sartwell and

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Stevens 1975) and other agents of mortality. Numerous studies have demonstrated that the mortality of ponderosa pine increases with both diameter and stand density (McTague 1990). A trend toward increasing rates of mortality, especially of the largest and oldest presettlement trees is supported by an analysis of the Pearson Natural Area data (Covington and Moore, accepted).

Thus, the increase in tree density following European settlement has resulted, on the one hand, in a major increase in forest canopy cover and vertical diversity within the tree canopies, and on the other hand striking decreases in herbage production. Our results are consistent with studies in Interior (Gruell et al. 1982, Keane et al. 1990) and California (van Wagtendonk 1985, Laudenslayer et al. 1989) ponderosa pine forests which describe changes in tree density, fuel loads, wildlife habitat, and aesthetics after fire exclusion. Of particular concern is the increased risk of mortality, especially for the oldest age classes of presettlement trees, from crown fire, bark beetles, and other agents and the implications for old-growth forest management in the ponderosa pine type.

IMPLICATIONS FOR OLD-GROWTH ECOLOGY AND MANAGEMENT

Disruptions of natural disturbance regimes coupled with postsettlement anthropogenic disturbances have led to forest and woodland conditions which may bear little resemblance to natural conditions. Thus, old-growth definitions and management objectives based only on current stand structure may not be compatible with the conservation biology goal of preserving species diversity by providing for the habitats in which species

have evolved. In fact, detailed analysis of tree density, size, and crown closures indicates that before settlement, none of the plots sampled at Bar-M nor at the North Kaibab would meet the current minimum criteria for old-growth used in the Southwest³ (Anon 1990). In addition, when we compared the current conditions of the 36 intensive plots on the North Kaibab (all were site index 70-80) to these same criteria for old-growth, only three plots met the old-growth trees/acre requirements; however, in all three cases only half of the dominant trees met the 180 year requirement, and only one of these plots met the snag, while none met the down log requirement.

Setting aside old-growth ponderosa pine stands which most closely meet current old-growth definitions may have unexpected consequences. These stands that have higher than normal canopy closures when compared to presettlement times, are likely to be the most susceptible to crown fire, low tree vigor, and mortality from drought, insects, and diseases.

Thus definitions of old-growth should take into account natural conditions before Euro-American settlement, particularly the natural fire regime and patchy nature of the forest. In managing toward natural (using presettlement conditions as the "yardstick") old-growth, it may well be necessary to design and apply treatments for restoring candidate stands (e.g., thinning from below, manual fuel treatments, prescribed burning).

³Tentative old-growth structural definition for the USFS Southwestern Region - for high sites (Minor site index > 55): large dominant/codominant trees - 20 trees/acre > = 18 inches dbh, and these trees average 180 years; with a total tree basal area of 90 ft²/acre, and a total canopy cover of 50%; and with a dead tree component of 1 snag/acre of 14 inches dbh and 25 feet in length, 2 down logs/acre of 12 inches dbh and 15 feet in length, and canopies single or multiple storied

RESTORATION OF SOUTHWESTERN PONDEROSA PINE

To summarize, numerous lines of evidence point to striking postsettlement changes in southwestern ponderosa pine forests. A combination of livestock grazing and fire exclusion has resulted in increases in tree density, canopy closure, vertical diversity, aerial fuel continuity, and surface fuel loads. At the same time, herbaceous and shrub production have likely declined. As a consequence, the forests of today differ substantially from the natural conditions before Euro-American settlement. These changes in ecosystem structure imply changes in wildlife habitat, water relations, nutrient cycling, soils, forest health, and other resource characteristics.

Furthermore, these changes in ponderosa pine structure have led to a shift away from the natural fire regime of frequent, low intensity surface fires to high intensity crown fires. Most recently, the occurrence of larger and larger crown fires in the ponderosa pine type may indicate a further shift to a regime characterized by very large (>10,000 acre) crown fires.

To remedy these problems and restore these forests to more natural conditions, it may well be necessary to thin out (either mechanically or with fire) most of the postsettlement trees, manually remove heavy fuels from the base of large, old trees (or larger replacement postsettlement trees in the absence of old-growth) and reintroduce periodic burning.

However, before embarking on widescale restoration treatments it is necessary to determine postsettlement changes in ecological conditions (Bonnickson and Stone 1985) for a broader range (e.g., a variety of soil types, topographies, and vegetation types) of

forest and woodland types in the Rocky Mountain and Southwest regions. Then a combination of an adaptive resource management approach (Walters 1986), and process oriented simulation modeling (e.g., van Wagtendonk 1985, Keane 1990, Covington and Moore accepted) could be used to design restoration management regimes appropriate for each set of conditions. Simultaneously, small (10-20 acre) plot studies could be established to examine the ecological effects and practicality of various restoration treatment scenarios. Using such an integration of historical studies, simulation modeling, and management experiment approaches should ensure that we address our wildland management issues in a more coherent and ecologically sound manner.

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Old-Growth Concepts from Habitat Type Data in the Southwest¹

John B. Popp, Patrick D. Jackson, and Richard L. Bassett²

Abstract:—Tree data collected from plant association field plots was viewed to develop an old-growth data base to help determine an inventory definition for old-growth in the Southwestern Region. The plant association field plots were helpful in establishing the minimum criteria for the live tree, dead tree, and basal area structural attributes used to identify potential old-growth.

INTRODUCTION

There has been an effort to determine an inventory definition for old-growth in the Southwest. An old-growth core team was established in 1989 to develop definitions for the pinyon-juniper, ponderosa pine, mixed-species group (includes Douglas-fir, white fir, blue spruce, bristlecone pine, and limber pine) and

Engelmann spruce-subalpine fir forest cover types in the Southwestern Region.

Seven structural attributes were identified to inventory candidate old-growth stands. The attributes are shown in table 1. The first five attributes were designated as National required standards for all Regions; the remaining two were additional attributes considered important for the Southwest.

Table 1. The minimum criteria for the structural attributes used to determine old-growth.

Forest Cover Type, Name	Pinyon-J	uniper		erior osa Pine	į.	-Species oup		nn Spruce- pine Fir	
Forest Cover Type, SAF Code	239	9	2	37	209,210,2	211,216,219	2	206	
Site Capability Potential					50 Dou	glas-Fir	50 Engeln	nann Spruce	
Break Between Low and High Site			55 N	linor	Edminst	er & Jump	Alexander		
Site	Low	High	Low	High	Low	High	Low	High	
1. LIVE TREES IN MAIN CANOPY									
TREES/ACRE	12	30	20 12 @ or @	20 14 @ or @	12	16	20 15 @ or @	30 25 @ or @	
DBH/DRC	9"	12"	14" 18"	20" 24"	18"	20"	10" 12"	14" 16"	
AGE (YEARS) 2. VARIATION IN TREE DIAMETERS	150	200	180	180	150	150	140*/170**	140*/170**	
(YES OR NO) 3. DEAD TREES	ND	ND	ND	ND	ND	ND	ND	ND	
STANDING							_		
TREES/ACRE	0.5*	1	1	1	2.5	2.5	3	4	
SIZE, DBH/DRC	9"	10"	14"	14"	14"	16"	12"	16"	
HEIGHT (FEET) DOWN	8'	10'	15'	25'	20'	25'	20'	30'	
PIECES/ACRE	2	2**	. 2	2	4	4	5	5	
SIZE (DIAMETER)	9"	10"	12"	12"	12"	12"	12"	12"	
LENGTH (FEET)	8'	10'	15'	15'	16'	16'	16'	16'	
4. TREE DECADENCE									
TREES/ACRE	ND	ND	ND	ND	ND	ND	ND	ND	
5. NUMBER OF TREE CANOPIES	SS/MS	SS/MS	SS/MS	SS/MS	SS/MS	SS/MS	SS/MS	SS/MS	
6. TOTAL BA, SQUARE FEET/ACRE	5	23	70	90	80	100	120	140	
7. TOTAL CANOPY COVER, PERCENT	20	35	40	50	50	60	60	70	

PINYON-PINE * Dead limbs help make up dead material deficit. ** Unless removed for firewood or fire burning activities. SPRUCE-FIR * In mixed corkbark fir and Engelmann spruce stands where Engelmann spruce is less than 50 percent composition in the stand.

ND is not determined; SS is single-storied; MS is multi-storied

^{**} In mixed corkbark fir and Engelmann spruce stands where Engelmann spruce is 50 or more percent composition in the stand.

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The purpose of this study was to develop an old-growth data base that would help establish the minimum criteria for the structural attributes used to inventory old-growth (table 1). Tree data from over 2,000 forest and woodland habitat type (plant association) field plots was viewed and 1,585 plots had complete, usable data that could be used to develop the old-growth data base. A simple comparison procedure was then used to help establish the minimum live trees, dead trees, and basal area per acre minimum old-growth structural attributes.

METHODS

Data Collection

Several researchers, contractors and others collected plant species information during the late 1970s and early 1980s to develop forest habitat type (plant association) classifications for the southwestern United States (Arizona, New Mexico, and southern Colorado). The information was collected from temporary sample plots that were purposely located in undisturbed, forest climax communities. This biased sampling method provided the greatest amount of information for a selected habitat type with the least number of plots. Since old-growth forests are ecosystems distinguished by old trees and related structural features that are in the later stages of stand development, the habitat type classification data could be used to establish an old-growth inventory data base.

The original plant association field plot data and a computerized comprehensive habitat type data base developed by Muldvin *et al.*, were archived at the Forestry Sciences Laboratory, Rocky Mountain Forest and Range Experiment Station, Albuquerque, New Mexico (Muldvin *et al.*, 1990). The archived,

noncomputerized, field plot data included information on stand structure, site productivity, soil analysis, plus descriptive materials such as photographs and maps. The computerized habitat type data base included information about floristic diversity, environmental characteristics, stand productivity, and other descriptive information on the forest communities.

Data Analysis

Although there were 2009 plant association plots, a total of 1585 plots were used for the new old-growth data base. Many of the original field plots were not useable because there was no tree data recorded, the data was lumped in the field, or because of questionable plot sizes which would yield unreliable results when expanded. There were also a number of plots with the field data cards missing.

The tree data from the 1585 useable plots were organized in the new old-growth data base that was compatible with the VARGEN stand data processing program. The data base included the species, diameter of each tree, and site tree data, when available. The VARGEN program was able to determine forest cover type and site productivity (site index) as well as generate two-inch diameter class stand tables by each species and a summary for all species on a plot.

The next step was to combine the VARGEN stand table information into three tables for comparison purposes. Tables were generated for the mean number of live trees per acre, mean number of dead standing trees per acre and mean square foot basal area per acre.

The mean number of live trees per acre is shown in table 2 by 2-inch diameter classes, by no, low, high, and all sites, and each forest cover type. The number of plots for each forest cover type and site is shown on

Table 2. Summary Data in 2-inch Diameter Classes for Live Trees Per Acre.

	DIAMETER, DBH/DRC																		
	0-	2-	4-	6-	8-	10-	12-	14-	16-	18-	20-	22-	24-	26-	28-	30-		Total	Number
	1.9	3.9	5.9	7.9	9.9	11.9	13.9	15.9 1	17.9	19.9	21.9	23.9	25.9	27.9	29.9	31.9	32+	Trees	of Plots
PINYON-JU	JNIPE	R																	
NO SI	988	77	50	31	20	15	10	6	7	6	2	3	2	2	0	0	1	1220	52
LOW SI	607	81	57	36	32	13	10	6	8	5	3	5	2	3	1	1	1	871	23
HI SI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ALL SI	871	78	52	33	24	14	10	6	7	6	2	4	2	2	0	0	1	1113	75
PONDEROS	SA PIN	VΕ																	
NO SI	943	74	53	38	22	18	15	12	9	7	4	6	3	2	1	1	1	1209	137
LOW SI	237	37	24	17	13	11	10	9	7	6	5	3	2	1	1	0	1	384	219
HISI	316	45	29	20	14	12	10	8	7	6	6	8	3	2	1	0	1	488	384
ALL SI	409	48	32	22	15	13	11	9	7	6	5	6	3	2	1	0	1	591	740
MIXED-SPI	ECIES																		
NO SI	741	94	60	43	27	24	18	13	9	8	6	5	3	2	1	2	4	1060	126
LOW SI	399	84	56	38	31	21	16	14	8	8	6	4	2	2	1	1	2	693	72
HISI		103	66	40	25	21	18	13	10	8	7	10	2	1	1	1	1	837	289
ALL SI	553	98	63	4 0	26	22	18	13	9	8	7	8	2	1	1	1	2	873	487
SPRUCE-FI	R																		
NO SI	806	114	76	52	51	44	32	22	13	11	7	4	2	2	0	0	0	1236	31
LOW SI	850	136	89	61	45	36	29	19	14	8	8	4	3	2	1	1	1	1307	99
HI SI	854		77	56	38	32	31	22	14	10	7	5	2	1	1	1	1	1277	143
ALL SI	847	128	81	57	42	35	30	21	14	9	7	5	2	1	1	1	1	1283	273

Table 3. Summary Data in 2-inch Diameter Classes for Dead Trees Per Acre.

DIAMETER	DRH/DRC
DIAMETER	, DBII/DIC

											, _									
	0- 1.9	2- 3.9	4- 5.9	6- 7.9	8- 9.9	10- 11.9		14- 15.9		18- 19.9		22- 23.9	24- 25.9	26- 27.9	28- 29.9	30- 31.9	32+	Total Trees	Number of Plots	
PINYON-JU	NIPE	\mathbf{R}																		
NO SI	29	9	4	2	2	1	0	1	1	0	0	0	0	0	0	0	0	49	52	
LOW SI	36	15	7	2	2	0	0	0	0	0	0	0	0	0	0	0	0	62	23	
HI SI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
ALL SI	31	11	5	2	2	1	0	1	1	0	0	0	0	0	0	0	0	53	75	
PONDEROS	A PIN	1E																		
NO SI	9	9	4	2	1	1	1	1	0	0	1	1	1	0	0	0	0	31	137	
LOW SI	5	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8	219	
HI SI	5	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	10	384	
ALL SI	6	3	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	13	740	
MIXED-SPE																				
NO SI	12	8	7	5	2	2	2	1	1	1	0	1	0	0	0	0	0	42	126	
LOW SI	31	20	7	6	3	2	1	1	1	0	0	0	0	0	0	0	0	72	72	
HI SI	12	13	8	4	3	2	2	1	1	1	0	1	0	0	0	0	0	48	289	
ALL SI	_ 15	13	8	5	3	2	2	1	1	1	0	1	0	0	0	- 0	0	50	487	
SPRUCE-FI																				
NO SI	17	20	13	12	10	9	_	10	3	3	2	1	0	0	0	0	0	103	31	
LOW SI	30	21	16	9	8	7	5	4	2	2	2	0	1	0	0	0	0	107	99	
HI SI	22	19	14	10	7	7	5	4	2	2	1	1	1	0	0	0	0	95	143	
ALL SI	24	20	15	10	8	7	5	5	2	2	1	1	1	0	0	0	0	100	273	

the right side of the table. The all site plot number represents the total of no, low, and high site plots. No site means that the site tree data was not calculated because site tree information was not complete.

The mean number of dead standing trees per acre is shown in table 3 by 2-inch diameter classes, by no, low, high, and all sites, and each forest cover type. The number of plots for each forest cover type and site is shown on the right side of the table. The all site plot number represents the total of no, low, and high site plots.

The mean square foot basal area per acre is shown in table 4 by 2-inch diameter classes, by no, low, high, and all sites and each forest cover type. The number of plots for each forest cover type and site is shown on the right side of the table. The all site plot

number represents the total of no, low, and high site plots.

The data were then used to compare the number and diameter of live trees per acre, number and diameter of standing dead trees per acre, and total basal area per acre to the proposed guidelines for each forest cover type and site capability potential in table 1. Data were not collected for tree age, down dead trees, height of standing dead trees or total canopy cover so these attributes could not be tested. Since there is no established break in site capability potential for pinyon-juniper the same plots were tested using both high and low standards.

Because tree diameter data was collected by 2-inch size classes it was not possible to calculate the exact number of plots meeting or exceeding the minimum

Table 4. Summary Data in 2-inch Diameter Classes for Basal Area Per Acre.

	DIAMETER, DBH/DRC																		
	0-	2-	4-	6-	8-	10-	12-	14-	16-	18-	20-	22-	24-	26-	28-	30-		Total	Number
	1.9	3.9	5.9	7.9	9.9	11.9	13.9	15.9	17.9	19.9	21.9	23.9	25.9	27.9	29.9	31.9	32+	BA	of Plots
PINYON-JUI	NIPE	R																	
NO SI	0	1	7	8	9	10	9	8	12	12	5	9	8	7	1	1	10	117	52
LOW SI	0	1	8	10	14	8	9	7	12	10	8	13	8	11	4	5	12	140	23
HI SI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ALL SI	0	1	7	9	11	9	9	8	12	11	6	10	8	8	2	2	11	124	75
PONDEROSA	A PIN	\mathbf{IE}																	
NO SI	0	1	7	10	10	12	13	15	15	14	11	17	9	9	4	5	9	161	137
LOW SI	0	0	3	5	6	7	9	11	11	13	12	8	6	6	2	3	5	107	219
HI SI	0	0	4	5	6	8	9	10	12	13	15	22	10	7	6	2	7	136	384
ALL SI	0	0	4	6	7	8	10	11	12	13	13	17	9	7	4	3	7	132	74 0
MIXED-SPE	CIES																		
NO SI	0	0	8	11	12	16	17	16	14	15	14	13	9	8	7	8	32	200	126
LOW SI	0	0	8	10	14	14	15	18	13	16	16	12	7	9	4	5	17	178	72
HI SI	0	0	9	11	11	14	17	16	16	15	17	28	6	5	3	4	11	183	289
ALL SI	0	0	9	11	12	15	17	16	15	15	16	22	7	6	4	5	17	187	487
SPRUCE-FIR	2																		
NO SI	0	0	10	14	23	29	30	26	21	22	16	12	6	7	2	2	0	220	31
LOW SI	0	0	12	16	20	24	27	24	22	15	18	13	9	6	5	3	9	223	99
HI SI	0	0	11	15	17	21	29	27	22	19	17	15	5	5	3	3	5	214	143
ALL SI	0	0	11	15	19	23	28	26	22	18	17	14	7	6	4	3	6	218	273

diameter criteria when the proposed value fell in the middle of a size class. Consequently, it was necessary to run some tests using all data within the size class of the proposed value.

Tests were conducted to determine the number and percent of plots in each forest cover type and site potential that met or exceeded the proposed minimums in table 1. This testing method was useful in identifying attributes that have a low proportion of plots satisfying the proposed standards, which would suggest that the minimum criteria are set too high. This method, displayed in table 5, could not provide further analysis of the attributes which had 100 percent of the plots meeting or exceeding the proposed minimum guidelines. A second test was therefore conducted to find out how far they exceed the proposed minimum standards. The test compared the mean values for each attribute in the summary tables 3, 4, and 5, to the proposed guidelines in table 1. This provided a partial analysis of the relationships between plot averages and the proposed guidelines and is displayed in table 6.

RESULTS

The percent of plots concurring with (meeting or exceeding) the proposed minimum guidelines for each

attribute are shown by forest cover type in table 5. With one exception (ponderosa pine basal area) low site attributes had levels of concurrence that were equal to or higher than their high site counterparts.

Comparisons of proposed minimum attributes to the mean plot values are displayed in table 6. In general, attributes with a level of concurrence at or near 100% have mean values which are much higher than the proposed minimum standards. Pinyonjuniper plots showed the greatest difference between mean values and proposed minimum guidelines.

Comparison of the plot data to the proposed guidelines for each attribute yielded the following results:

Basal Area - With two exceptions (low site spruce-fir and ponderosa pine), basal area had the highest level of concurrence for any forest type and site group (table 5). Low and high site indexes usually had similar levels of concurrence. Mean plot values in all forest types exceeded proposed minimum guidelines by at least 51% in all cases (table 6).

Dead Trees - This attribute always had the lowest level of concurrence of any variable. The level of concurrence among low site plots was always equal to or higher than high site plots (table 5).

Live Trees - In general, low site plots had a higher level of concurrence for this attribute than high site plots (table 5). Where two sets of values

Table 5. Test Results of Individual Attributes by Forest Type.

PINYON-ITINIPER

			PINTON-JUNIPER		
LOW SI	NUMBER	PERCENT	HIGH SI	NUMBER	PERCENT
	OF PLOTS	CONCUR		OF PLOTS	CONCUR
Total	23	100	Total	23	100
BA 5 sq. ft.+	23	100	BA 23 sq.ft.+	23	100
Dead Trees 8"+	5	22	Dead Trees 8"+	5	22
Live Trees 8"+	23	100	Live Trees 12"+	21	91
Live Trees 10"+	23	100			
			PONDEROSA PINE		
LOW SI	NUMBER	PERCENT	HIGH SI	NUMBER	PERCENT
	OF PLOTS	CONCUR		OF PLOTS	CONCUR
Total	219	100	Total	384	100
BA 70 sq.ft.+	155	71	BA 90 sq.ft.+	304	79
Dead Trees 12"+	31	14	Dead Trees 12"+	51	13
Live Trees 14"+	171	78	Live Trees 20"+	210	55
Live Trees 18"+	107	49	Live Trees 24"+	62	16
			MIXED-SPECIES		
LOW SI	NUMBER	PERCENT	HIGH SI	NUMBER	PERCENT
	OF PLOTS	CONCUR		OF PLOTS	CONCUR
Total	72	100	Total	289	100
BA 80 sq.ft.+	67	93	BA 100 sq.ft.+	264	91
Dead Trees 12"+	20	28	Dead Trees 16"+	55	19
Live Trees 18"+	47	65	Live Trees 20"+	168	58
			SPRUCE-FIR		
LOW SI	NUMBER	PERCENT	HIGH SI	NUMBER	PERCENT
	OF PLOTS	CONCUR		OF PLOTS	CONCUR
Total	99	100	Total	143	100
BA 120 sq.ft.+	95	96	BA 140 sq.ft.+	134	94
Dead Trees 12"+	67	68	Dead Trees 16"+	54	38
Live Trees 10"+	99	100	Live Trees 14"+	117	82
Live Trees 12"+	98	99	Live Trees 16"+	93	65

Table 6. Comparison of proposed minimum attributes and averages by forest cover type.

BAS	SAL AREA		
	Proposed	Average	Pct. of
	Miminum	Value	Minimum
Pinyon-juniper, Low SI	5	140	2,800
Pinyon-juniper, High SI	23	140	609
Ponderosa Pine, Low SI	70	107	153
Ponderosa Pine, High SI	90	136	151
Mixed-species, Low SI	80	178	223
Mixed-species, High SI	100	183	183
Spruce-fir, Low SI	120	223	186
Spruce-fir, High SI	140	214	153
DEAD TR	EES PER A	CRE	

	Proposea	Average	Pct. oi
	Miminum	Value	Minimum
Pinyon-juniper, Low SI	0.5	2	400
Pinyon-juniper, High SI	1	0	0
Ponderosa Pine, Low SI	1	0	0
Ponderosa Pine, High SI	1	0	0
Mixed-species, Low SI	2.5	2	80
Mixed-species, High SI	2.5	3	120
Spruce-fir, Low SI	3	16	533
Spruce-fir, High SI	4	7	175

LIVE TREES PER ACRE

Proposed	Average	Pct. of
Miminum	Value	Minimum
12	90	750
30	90	300
20/12	35/19	175/158
20/14	21/7	105/50
12	26	217
16	23	144
20/15	126/90	630/600
30/25	64/42	213/168
	Miminum 12 30 20/12 20/14 12 16 20/15	30 90 20/12 35/19 20/14 21/7 12 26 16 23 20/15 126/90

were proposed, the smaller tree diameter had a higher level of concurrence than the larger tree

Comparison of the plot data to the proposed guidelines yielded the following results for each forest cover type:

Pinyon-Juniper - All live tree attributes had over 90% concurrence (table 5). There was no difference in results between the 8+ and 10+ inch diameters for low site live trees. Mean basal area values were extremely high relative to the proposed minimum values (table 6).

Ponderosa Pine - Levels of concurrence were higher for the density of live trees on low site plots than high site plots, and also higher with the smaller of the two diameter limits (table 5). Levels of concurrence for dead trees were almost the same for both high and low site plots. These values were lower than for any other forest cover type, and both had mean values of zero (table 6).

Mixed-Species - Over 90% of both high and low site plots met or exceeded the proposed minimum standards for basal area (table 5). The level or concurrence for live tree attributes was similar for both high and low sites.

Spruce-Fir - Over 90% of both high and low site plots met or exceeded the proposed minimum standards for basal area (table 5). Low site plots were tested for both 10+ and 12+ inch diameter live trees. yielding similar results for each, with both having over 90% concurrence. The test results of the two high site live tree diameter variables (14+ and 16+ inches) were quite different, as were the results for high and low site dead trees.

DISCUSSIONS AND RECOMMENDATIONS

There is always a chance that the habitat type data used for the old-growth data base is biased towards heavier than normal tree densities. Prior to fire suppression in the early 1900s, forests in the southwest were burned by low intensity ground fires at 2 to 15 year intervals, ponderosa pine), 5 to 22 year intervals, mixed-conifer, and lesser frequencies to stand replacement fires in the spruce-fir (Cooper 1960, White 1985, Swetnam 1988, Covington and Moore 1991)

The small number of pinyon-juniper plots limits the reliability of the results from this forest cover type. Additional plot data which was collected in pinyon-juniper habitat types is needed to increase the accuracy of the summary data and subsequent analysis.

Attributes with low levels of concurrence may have minimum standards which are set too high. Since the plot data represents the best available example of what old-growth is, there should be a strong correlation between the plot data and the proposed guidelines. Adjusting the minimum standards to obtain a high level of concurrence would seem to be justified.

The number and size of dead trees consistently had the lowest level of concurrence of any attribute tested. It is possible however, that the proposed minimum guidelines for this attribute are set appropriately. Past management practices may have reduced the number of standing snags to unnaturally low levels throughout the Region. Rather than lowering the proposed minimum standards, management practices need to recruit new snags.

Attributes which have concurrence at or near 100% also need to be examined. Table 5 suggests which guidelines may be set too low by displaying mean values that greatly exceed the proposed minimum standards. Basal area should be looked at especially carefully. Not only was it the attribute which had the highest level of concurrence most often but the calculated value for basal area was probably too low in many instances. Due to the variable cut-off point and subsequent lumping of data when recording diameters, the number of 20-inch and 22-inch trees is overestimated while the number of trees over 22 inches is underestimated. Because basal area is a function of tree diameter, the total basal area may be to low on any plot containing lumped diameter data, and therefore to low in the plot summary data.

When considering adjustment of site capability potential, special considerations may be in order. The site indexes calculated for many of the plots are too low due to the use of the largest, oldest trees near the plot for site trees. The mean annual increment for

these trees is significantly less than that of young, vigorous trees which are more appropriate for measuring site indexes. Therefore, certain plots belonging in the high site category may have been shifted to the low site category. This could result in artificially raised mean values and percent concurrence of live tree attributes for both high and low site categories.

This work is not meant to be a final analysis of the validity of the proposed old-growth guidelines. It is only a preliminary evaluation meant to provide suggestions to the Regional old-growth team while they fine-tune the minimum structural attributes for ecological old-growth by forest cover type. An alternative use of the data base would be to develop a set of guidelines based on the plot data itself. The mean value minus one (or more) standard deviation could be the minimum guideline. This method would allow the data to set the standards, rather than using it to merely evaluate proposed guidelines.

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Old-Growth Descriptions for the Major Forest Cover Types in the Rocky Mountain Region¹

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Abstract.—Old-growth descriptions have been developed for each of the major forest cover types in the Rocky Mountain Region of the Forest Service. Included with each description is a minimum list of tree and stand variables that characterize old growth. Additional attributes are listed that affect the quality of old growth. These descriptions will be used to locate, map, and inventory old-growth forests for forest planning.

INTRODUCTION

This document describes the old-growth forest conditions for the major forest cover types in the Rocky Mountain Region (Region 2) of the Forest Service. Region 2 covers the states of Colorado, Wyoming, South Dakota, Kansas and Nebraska.

These old-growth descriptions are not precise definitions. There is a certain amount of subjectivity in defining old growth. Old growth is conceptual and difficult to define precisely. For that reason the term "description" was chosen instead of "definition." They describe the ecologically important structural features of old-growth forest ecosystems. They include a list of attributes measurable from stand-level inventories that characterize old-growth ecosystems. There are intangible elements, various functions and interactions occurring in old-growth ecosystems and the composition of the understory vegetation that are not part of these descriptions.

The following descriptions are the first attempt to describe old growth structurally by major forest cover type for Region 2. They form the collective knowledge of what is thought to describe old growth. These descriptions will be dynamic and will be modified as we learn more about the dynamics of old-growth ecosystems and its need and influence on the landscape.

Descriptions have been developed for the Engelmann spruce/subalpine fir, Douglas-fir, lodgepole pine, ponderosa pine, aspen and pin-yon-juniper forest cover types. Ponderosa pine grows in 3 distinct topographical areas in Region 2: the Black Hills, front range of the Rocky Mountains, and southwest Colorado, each with different stand characteristics. Separate old-growth descriptions have been developed for each area.

The forest cover types are defined in the Society of American Foresters (SAF) handbook Forest Cover Types of the United State and Canada, 1980. These cover types are those by which most inventory and management is done. Descriptions for the minor forest types such as limber pine or white pine will be added in the future.

These descriptions and associated attributes will be used to map and inventory old growth in the Region for Forest planning. They are general. For project level work detailed site specific analyses may be needed.

The descriptions follow a format developed by the National Old-Growth Task Group.

Description

Old-growth forests are unique ecosystems that are an important component of biological diversity. Old growth occurs at some point in the later stages of the development of a stand (fig. 1).

A stand that has reached an old-growth condition has developed a diversity of functions and interactions that did not exist in earlier stages. The later stages of development also differ from earlier stages by structure such as tree size, standing and down dead trees, number of canopy levels, age and the composition of the understory species.

The age at which old growth develops and the structural attributes that characterize old growth will vary by forest cover type, climate, site conditions and past disturbances. However, old growth is typically distinguished from younger growth by several of the following stand attributes:

- large trees for species and site.
- variation in tree sizes and spacing.
- standing and down dead trees.
- decadence in the form of broken or deformed tops or bole and root decay.
 - multiple canopy layers.
- gaps in the tree canopy and understory patchiness.

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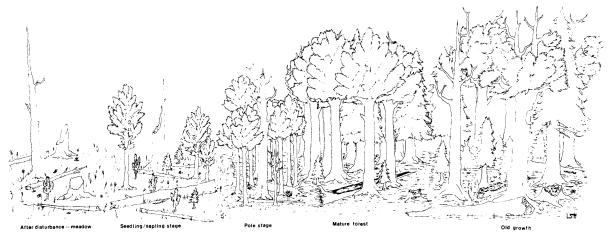


Figure 1. Developmental stages of a stand to an old-growth condition.

A stand may contain some trees that meet the criteria for old growth but the stand as a whole could lack the functions and interactions of an old-growth ecosystem and would not be considered old growth.

Old growth encompasses both older forests dominated by fire-dependent species and forests dominated by shade tolerant species. Different stages or qualities of old growth will be recognizable in many forest cover types. Sporadic, low to moderate severity disturbances are an integral part of the internal dynamics of many old-growth ecosystems. Canopy openings resulting from the death of overstory trees often give rise to patches of small trees, shrubs, and herbs in the understory. Frequent, low intensity fires are important for some species to maintain their dominance on a site.

Old growth is not necessarily "virgin" or "primeval". It could develop following human disturbances. It could also develop from man's indirect influence on the landscape by the control of fire.

Attributes

There are many attributes that could be used to characterize old growth, but these descriptions use attributes that are tree and stand-level characteristics such as diameter, canopy layers or patchiness. While there may be some attributes that seem applicable to all cover types, there is not one universal set of attributes that can adequately describe old growth for all cover types.

Each Region, as directed by the National Old-Growth Task Group, was to use a basic set of attributes to describe old growth. These are referred to as the "standard" attributes. Where necessary each Region had the option to include "additional" attributes to more fully describe old growth. In combination they provide the minimum requirements for determining if a stand is old growth.

A special set of attributes called "quality attributes" have been added. These are items

that further enhance the value of an old-growth stand once it has been determined to be old growth based on the above minimums. They are not required for old growth, but provide higher quality old growth if present. These criteria would be useful for deciding which old-growth stands are the most important for retention.

These attributes are tree and stand characteristics that are normally used in stand inventories. Table 1 summarizes the attributes by forest cover type. The glossary at the end of this paper defines each attribute. They are readily identifiable and measurable in a consistent manner. In addition the standard attributes are generally obtainable from remote sensing sources such as aerial photography. The additional and quality attributes may require some field work to collect.

The minimum stand size required for a stand to be old growth was not considered in these descriptions. Managers will decide the appropriate size as configuration, location and position in the landscape are also important in determining the value of a stand as old growth.

Old growth may have evidence of past treatment including stumps, slash, down logs, roads, fences and other improvements. However, this may affect the quality of old growth.

Development of Descriptions

During the summer of 1990, workshops were held in various locations throughout the Region (fig 2).

The purpose was to visit old-growth sites and discuss the tree and stand related attributes that could describe these old-growth sites. Attendees at the workshops included District, Forest and Regional staff and scientists from the Rocky Mountain Research Station. Each workshop was focused on a specific forest cover type. From the workshops a list of tree and stand attributes by each forest cover type was developed descriptive of old growth. The description and list of attributes for the pinyon-juniper cover type were adapted from Region 3.



Figure 2. Workshop on the Arapaho/Roosevelt NF looking at lodge pole pine old growth.

The descriptions and lists were then sent out for review and comments to additional Regional and Rocky Mountain Station staff and interested publics.

SPRUCE-FIR - SAF COVER TYPE 206

Narrative

Engelmann spruce (*Pica engelmannii*) and subalpine fir (*Abies lasiocarpa*) comprise the spruce/fir forest cover type in the subalpine zone in the Rocky Mountain Region. Spruce-fir occupies the highest and coldest forest area in the Region and is generally found from 9,000 to 11,000 feet but may grow as low as 8,000 feet and as high as 12,000 feet or timberline.

Engelmann spruce and subalpine fir are extremely shade tolerant compared to the other major forest species. By being shade tolerant they can reproduce under themselves and barring any major disturbance, perpetuate the stand. Subalpine fir is more shade tolerant than Engelmann spruce and may reproduce vegetatively by layering. In younger stands subalpine fir may be the major component of the forest type. However, it is shorter lived than Engelmann spruce. Consequently, most of the overstory in a spruce-fir oldgrowth stand is Engelmann spruce. The under-

Table 1.—The minimum criteria for the structural attributes used to determine old growth and those that add a quality attachment. Attributes with an "X" or a numerical value are considered "must" criteria. Those with a "Q" are quality criteria. The quality attributes are not required for old growth, but provide for higher quality old growth if present. Any of the "must" criteria in excess of the minimums could also indicate a higher quality of old growth.

Forest Cover Type, Name	Spruce/ Fir	Douglas- Fir	Lodgepole Pine	Front Rng	onderosa Pi Blk Hills	ne So. West	Aspen	Pinyon- Juniper
20 (10 (10 (10 (10 (10 (10 (10 (10 (10 (1		. 70, 172	00.150000					
Forest Cover Type, SAF Code	206	210	218	237	237	237	217	239
STANDARD ATTRIBUTES			C.					
LIVE TREES:								
Upper Canopy		-						
DBH/DRC	16	18	10	16	16	18	14	12
TREES/ACRE	10	10	10	10	10	10	20	30
AGE	200	200	150	200	160	160	100	200
VARIATION IN DIAMETER	X	X		X	Q	X	Q	X
DECADENCE	X	x	X	x	X	X	X	x
MULTIPLE CANOPY LAYERS	X	Q	Q				Q	
DEAD TREES:								
Standing								
DBH/DRC	10	10	8	10	10	10	10	10
TREES/ACRE	2	2	2	2	2	2	Q	1
Down								
PIECES/ACRE	X	X	X	Q	Q	Q	Q	2
ADDITIONAL/QUALITY ATTRIBUTES								
SLOW GROWING (MAIN CANOPY)	X	X	X	X	X	X	X	
CANOPY CLOSURE 50% PLUS							X	
CANOPY CLOSURE 35% PLUS								X
WIDE RANGE OF VIGOR	Q	X		X	1.1.	1 1		
NET GROWTH NEAR ZERO	X		Q	15,041		Q		1
PATCHINESS	X	Q	Q					
MANY STAGES OF DECOMPOSITION	X		Q Q			X		
MULTIPLE TREE SPECIES			Q				Q	1
DISTINCTIVE BARK	Q			Q	Q	Q		
DISTINCTIVE CROWNS	1		Q	Q	Q	Q		1

story may still have an abundance subalpine fir due to it's high tolerance to shade and vegetative layering. Engelmann spruce life span averages 350 to 400 years with 500-year-old or more trees not uncommon. Trees over 250 years are not uncommon for subalpine fir but most are 150 to 200 years old. It is quite susceptible to heart rot and generally dies at an earlier age than Engelmann spruce.

Spruce-fir is climax in the range that it occupies. No other tree species will replace it. The only time the stand would be replaced by another species is when a major disturbance like fire would occur, opening up the stand to sunlight. Less shade tolerant species then could occupy the site. Over time, up to 300 years or so, the more shade tolerant Engelmann spruce and subalpine fir would re-dominate the site.

After a stand replacing event such as fire or clear felling, lodgepole pine or aspen will be the replacing species at the lower elevational range of spruce-fir. If there is a sufficient seed source, spruce-fir will begin to develop in the understory and the lodgepole will begin to break apart with the stand reverting back to spruce-fir. Where there is not a sufficient spruce-fir seed source the stand will remain in lodgepole pine or aspen.

When at climax the stands are usually quite stable and will remain on the site indefinitely until replaced because of fire, logging, insect, disease, windstorm or other major disturbance.

Description

Spruce-fir old-growth stands are at climax and generally have a high number of large, old trees with an understory of shrubs and small subalpine firs. The percentage of canopy closure can vary. There is usually a considerable amount of stand-



Figure 3. Down trees in an old-growth spruce-fir stand on the Arapaho/ Roosevelt NF.

ing dead and down trees making it quite difficult at times to walk through the stand (fig. 3).

There can be lichens hanging from the tree branches and on the stems of the trees. It usually contains a mixture of different tree sizes providing a variety of structure within the stand. The upper canopy would consist of a cohort of older trees that are slow growing. These older trees can be characterized as having dead or broken tops, having flattened and open crowns, containing rot and possibly having bark that is reddish in color. Other tree species could be present such as lodgepole pine or aspen but generally would be scattered within the stand and at the lower elevations.

Attributes

Table 2 lists the tree attributes that are being used to describe spruce-fir old growth.

Table 2–Summary of Old-Growth Attributes for Spruce Fir – SAF Cover Type Code 206

STANDARD ATTRIBUTES
LIVE TREES:
Upper Canopy - Older Component
Minimum DBH (inches)16
Minimum Number of Trees Per Acre 10
Minimum Age 200
Variation in Tree Diameter Yes
Decadence - dead, broken or deformed
tops and/or bole or root rot Yes
Multiple Tree Canopy Layers Yes
DEAD TREES:
Standing
Minimum DBH (inches) 10
Number of Trees Per Acre2
Down
Minimum Pieces Per AcreSome
ADDITIONAL ATTRIBUTES:
Trees in Upper Canopy Are Slow
Growing Yes
Net Growth Near ZeroYes
Patchiness Yes
Many Stages of Decomposition Yes
QUALITY ATTRIBUTES:
Above Attributes in Excess of
Minimums Yes
Wide Range of Tree Vigor Yes
Distinctive Bark Yes

INTERIOR DOUGLAS-FIR -SAF COVER TYPE 210

Narrative

The interior Douglas-fir (*Pseudotsuga menziesii* var. glauca) cover type occurs throughout Region

2 from 6,000 to 10,000 feet in elevation. It occurs as pure stands or in association with other species such as Engelmann spruce and subalpine fir at higher elevations to lodgepole pine and aspen at its mid-elevational range and to ponderosa pine in its lower elevational range. In southwest Colorado, it grows with white fir and ponderosa pine were it is also referred to as mixed conifer.

Interior Douglas-fir is much different than the coastal variety of the Pacific Northwest. It grows in a drier climate and does not attain the growth, size or age of the Douglas-fir (Pseudotsuga menziesii var. menziesii) of the Pacific coast.

Douglas-fir is more shade tolerant than pine and aspen but less tolerant than Engelmann spruce or subalpine fir. When growing in association with spruce-fir it will be seral giving way eventually to the more shade tolerant spruce-fir. When growing in association with ponderosa pine, lodgepole pine or aspen it often dominates these species becoming the climax species if succession is not interrupted by a major disturbance such as fire.

Since Douglas-fir is shade tolerant, it can reproduce under its own canopy. This results in old stands of pure Douglas-fir that tend to be uneven-aged rather than single-aged. These pure stands most likely originated from fire. They remain over time because of Douglas-fir's ability to survive successive fires due to rapid growth, thick corky bark, ability to form adventitious roots and the longer fire interval on cool and moist north facing slopes. These stands generally reach a maximum age of 400 years old although some have reached an age of 700 years.

Where Douglas-fir grows in pure stands, it is usually on cooler and damper north facing slopes. Along the front range of Colorado, these stands have been heavily damaged by a spruce budworm infestation that began in the mid 1980's.

Insects often modify the structure of older Douglas-fir stands, creating large gaps or patches and groups of dead trees. This produces a patchy stand of large trees with Douglas-fir seedlings and saplings growing in the gaps giving the stand more vertical structure and an uneven aged composition.

At its lower elevational range, it has been easily accessible and influenced by post settlement activities. It has been heavily utilized for mining timbers and lumber and for recreation. Consequently few stands of old-growth Douglasfir exist at lower elevations. However, its area is increasing in the lower elevations as it is replacing ponderosa pine especially on the cooler more moist north facing slopes. The frequent low intensity fires that kept Douglas-fir from becoming established in the ponderosa pine type have been reduced, allowing Douglas-fir to become established under the ponderosa pine.

Description

An old-growth Douglas-fir stand would consist of an overstory of trees that are predominately or entirely Douglas-fir. On the cooler, more moist, north facing slopes it may be growing in association with spruce-fir or white fir. On drier sites old-growth Douglas-fir could be associated with ponderosa pine, lodgepole pine and aspen. Where the site is dry, the stand would be more opengrown compared to a cooler, more moist site such as a north facing slope or drainage bottom. Some dead standing trees and down dead trees would be present. Some of the overstory trees would have large and open branched, flattened or dead tops and contain some rot.

Attributes

The following table lists the tree attributes that are being used to describe Douglas-fir old-growth.

Table 3–Summary of Old-Growth Attributes Interior Douglas-Fir – SAF Cover Type 210

STANDARD ATTRIBUTES LIVE TREES:
Upper Canopy - Older Component
Minimum DBH (inches)
Minimum Number of Trees Per Acre 10
Minimum Age200
Variation in Tree Diameter Yes
Decadence - dead, broken or deformed
tops and/or bole or root rot Yes
Multiple Tree Canopy Layers No DEAD TREES:
Standing Ni in a DRII (in above)
Minimum DBH (inches)
Minimum Number of Trees Per Acre 2
Down
Minimum Pieces Per AcreSome
ADDITIONAL ATTRIBUTES:
Trees in Upper Canopy Are Slow
Growing Yes
Wide Range of Tree Vigor Yes
_
QUALITY ATTRIBUTES:
Above Attributes in Excess of
Minimums
Multiple Tree Canopy Layers Yes
Patchiness Yes

LODGEPOLE PINE - SAF COVER TYPE 218 Narrative

The lodgepole pine (*Pinus contorta* var. latifolia) cover type in Region 2 consists of extensive stands of pure lodgepole pine or, to a lesser extent, stands in association with other species such as Engelmann spruce, subalpine fir, or aspen. It occurs between 7,500 feet and 11,500

feet elevation but reaches maximum development in the upper montane and lower subalpine zones on south and west facing slopes between 9,000 and 10,000 feet elevation.

In contrast to the shade tolerant Engelmann spruce and subalpine fir, lodgepole pine is shade intolerant and is an aggressive pioneer developing on sites recently opened up due to fire, insects and disease, windstorms, clearcutting or other major stand removing disturbance. Lodgepole pine stands that are 350 to 400 years old exist but they are uncommon. The average life span of lodgepole pine is probably closer to 250 years or less because of the frequency of stand replacing disturbances such as fire. Fires are more frequent in lodgepole pine than spruce-fir as they occur in a warmer and dryer environment.

Lodgepole pine is generally considered a seral species. That is, it will be replaced by the more shade tolerant Engelmann spruce and subalpine fir. Most lodgepole pine stands become established after stand replacing events such as fire. As the lodgepole pine matures Engelmann spruce and subalpine fir will appear as the understory eventually replacing the overstory lodgepole pine. The stand will remain as spruce-fir until another stand replacing event occurs.

There are instances when lodgepole pine can be considered climax. In areas where a seed source of more shade tolerant trees species does not exist or the site is marginal for other tree

source of more shade tolerant trees species does not exist or the site is marginal for other tree species, the lodgepole pine stand will not be replaced. If there is a stand replacing occurrence like fire the stand will re-seed with lodgepole pine. If not disturbed the stand will begin to develop gaps in the tree canopy as trees die. These gaps will allow sunlight to reach seedlings, renewing the stand but a stand with a more varied structure. Over successive generations the stand would develop a structure more consistent of old growth in shade tolerant species. When fire was more prevalent few stands would have had the opportunity to reach this structure.

When the overstory trees in a lodgepole pine stand begin to die and fall, the overstory probably will not persist for more than 50 years or so.

Description

Many people do not believe that lodgepole pine old growth really exists. Using a definition of old-growth where a stand must be climax would eliminate much of the Region's lodgepole pine as old growth. However, the seral lodgepole pine condition can exhibit old-growth characteristics albeit they may not last long in one place, but overall in a landscape this old-growth condition can exist for quite some time. Lodgepole pine is more dynamic in its landscape behavior than the more shade tolerant species such as Engelmann spruce or subalpine fir.

In a seral condition lodgepole pine old growth would be described as having an overstory of large old trees without lower limbs, with dead or dying tops and with crowns that are sparse, open branched and somewhat flattened (fig 4).

The stand would probably have mistletoe, rust or stem rot present contributing to the decadence of the overstory. The understory would consist of Engelmann spruce and subalpine fir. Depending on the age of the understory there could be a fair amount of structure and variation in tree diameters within the stand. Some down material would be present, increasing as the overstory continued to degenerate. It is important to note that when the older lodgepole pine is replaced by the understory, the stand is no longer old growth. The stand would be a young spruce-fir stand.

Where lodgepole pine is considered climax, old growth will again include large old trees lacking lower limbs and with dead or dying tops and crowns with sparse foliage, open branched, misshapened and somewhat flattened. It would probably have mistletoe, rust and/or stem rot present contributing to the decadence of the overstory. However, it will not have the spruce-fir understory. It will most likely have one canopy layer and thus not much structure. There probably would be very little variation in tree diameter. There may be a lot or little down dead material depending on how advanced the decline is of the overstory. In stands that are very old perhaps 300 or more years old, there may be a fair amount of stand structure developed due to trees developing in openings created by trees in the original overstory that had fallen.



Figure 4. Seral old-growth lodgepole pine stand.

Attributes

The following table lists the tree attributes that are being used to describe lodgepole pine old growth.

Table 4–Summary of Old-Growth Attributes
Lodgepole Pine – SAF Cover Type 218

I	STANDARD ATTRIBUTES
	LIVE TREES: Upper Canopy - Older Component Minimum DBH (inches)
	DEAD TREES: Standing Minimum DBH (inches)
	ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing
	QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Net Growth Near Zero Yes Multiple Tree Canopy Layers Yes Multiple Tree Species Yes Patchiness Yes Many Stages of Decomposition Yes Distinctive Crowns in the Upper Canopy Yes

INTERIOR PONDEROSA PINE -SAF COVER TYPE 237 (Front Range)

Narrative

Front Range ponderosa pine (*Pinus ponderosa* var. scopulorum) forests extend along the east slope of the Rocky Mountains from south of Pueblo on the Pike/San Isabel National Forest north to the Laramie Peak area on the Medicine Bow National Forest. It occurs at elevations between 6,000 and 8,000 feet, lower than the other Rocky Mountain conifers except for pinyon juniper and is well adapted to the warm dry sites

at these lower elevations. Although there are stands of pure ponderosa pine, it frequently occurs with Douglas-fir and is often referred to as mixed conifer.

Ponderosa pine is shade intolerant. It occurs in stands that are open-grown, often lower in stocking than other conifers and interspersed with meadows and parks. Fire has played a very important role in shaping ponderosa pine stands. In the past cool, light ground fires would burn through ponderosa pine stands every 8-15 years, removing competing understory vegetation, down dead material and young trees. This resulted in developing irregular shaped stands with evenaged groups of trees varying in size. Patchy distribution of clumps of trees varying in size, age and density are characteristic of naturally occurring ponderosa pine forests.

Where ponderosa pine is the sole species or fire is still part of the ecology, it can be considered the climax species. These stands develop into and remain as open-grown, irregular and unevenaged stands. Some stands with trees over 450 years do exist but 300 to 350 year old trees are more common.

Where fire has been excluded and the more shade tolerant Douglas-fir is present, ponderosa pine is generally considered seral. The opengrown stands develop an understory of more shade tolerant species such as Douglas-fir. These more shade tolerant species will replace the ponderosa pine if not removed whether by fire or some other means. On sites more marginal in growing conditions it can exist with other species and not be replaced by them.

The lower elevations where ponderosa pine grows are easily accessible and have been highly influenced by man's activities compared to conifers growing at higher elevations. Consequently, most ponderosa pine stands have been harvested for mining timber, lumber and railroad ties and used heavily for recreation. As a result few stands of ponderosa pine over 150 years old exist except in isolated areas that were difficult to access.

Description

Where ponderosa pine is climax and fire has been present, stands will contain clumps of large uneven-aged trees with little understory or down woody material and few if any standing dead trees (fig. 5).

Where fire has been controlled or less frequent there will be old large trees with smaller size trees in the understory giving the stand some structure. Dead down material will be present in varying amounts along with some standing dead trees. In both cases the large old trees will have irregular, open and large branched crowns and have lost their lower branches. The bark will also be thick, have large and somewhat concave

plates and have a lighter color compared to younger trees. Burls and other deformities may be present including fire scars that could be completely healed over.

Where ponderosa pine is seral due to the lack of frequent fires or the site is outside its normal range, stands will contain large trees with a multi-layer canopy and contain various amounts of standing and down dead trees (fig. 6).

It has an understory component of smaller trees including the more shade tolerant Douglasfir filling in the openings between the groups of older ponderosa pine.

Attributes

The following table lists the tree attributes that are being used to describe Front Range ponderosa pine old growth.

Table 5-Summary of Old-Growth Attributes Interior Ponderosa Pine - SAF Cover Type 237 (Front Range)

STANDARD ATTRIBUTES LIVE TREES: Upper Canopy - Older Component Minimum Number of Trees Per Acre 10 Minimum Age 200 Variation in Tree Diameter Yes Decadence - dead, broken or deformed tops and/or bole or root rot Yes Multiple Tree Canopy Layers No DEAD TREES: Standing Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing...... Yes Wide Range of Vigor...... Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes Distinctive Crowns in the Upper Canopy. Yes

INTERIOR PONDEROSA PINE -SAF COVER TYPE 237 (Black Hills)

Narrative

Black Hills ponderosa pine (*Pinus ponderosa* var. scopulorum) occurs in Region 2 in the Black Hills of South Dakota and Wyoming and the Bear Lodge Mountains of Wyoming. Here it forms a



Figure 5. Old-growth ponderosa pine on the Arapaho/Roosevelt NF with little understory.



Figure 6. Old-growth ponderosa pine on the Manitou Experimental Forest with some understory and down material.

unique and isolated ecotype of the interior ponderosa pine type. It usually grows in pure stands at 3,600 to 7,000 feet in elevation.

Old photographs show ponderosa pine growing in even-aged clumps or groups of trees apparently before the 1870's. These groups or clumps were separated by grassy areas or parks. This condition dominated the landscape and was similar to that of ponderosa pine in other parts of the Rocky Mountain Region where periodic low intensity fires removed competing vegetation and prevented large numbers of trees from maturing.

Where periodic, low intensity fires were not part of the ecosystem, ponderosa pine grew in a multi-storied and a more homogeneous and denser condition with standing dead and down trees.

A few old ponderosa pine stands, about 350 years old, remain in the Black Hills. Virtually all of the accessible areas have been cut over at least once since the mid 1870's. The open-grown clumps of ponderosa pine have been converted to stands with an older overstory and a young understory through harvesting and intensive management. The amount of stocking has been dramatically increased with the control of fire.

Ponderosa pine is considered a climax species in the Black Hills. After fire or other disturbances, the stand may temporarily be replaced by other plant species but will soon return to ponderosa pine.

Since little old-growth ponderosa pine remains in the Black Hills old growth will have to develop from existing stands. It will take active management to return existing stands to an old-growth condition similar to that which dominated the landscape at pre-settlement.

Where old-growth stands do exist a dense understory of younger trees has developed due to the absence of fire. This is dramatically different from what existed as old growth prior to the 1870's.

Description

Where periodic, low intensity fires have been part of the ecosystem, old-growth stands would consist of clumps or groups of trees with grasses in the openings between the clumps. They would contain large old trees with open branches, irregular and flattened crowns. The clumps or groups of trees would contain little down dead material and few small trees.

Where periodic, low intensity fires have not been part of the ecosystem, old-growth stands would contain large old trees with open branches and irregular crowns. The stands would have multiple canopy layers made up of various aged trees. They would be well stocked with trees and contain standing dead and down trees.

Attributes

The following table lists the tree attributes that are being used to describe Black Hills ponderosa pine old growth.

Table 6-Summary of Old-Growth Attributes Interior Ponderosa Pine - SAF Cover Type 237 (Black Hills) からのでは、100mmのでは、100mm

STANDARD ATTRIBUTES LIVE TREES:
Upper Canopy - Older Component
Minimum DBH(inches)16
Minimum Number of Trees Per Acre 10
Minimum Age
Variation in Tree Diameter No
Decadence - dead, broken or deformed
tops and/or bole or root rotYes
Multiple Tree Canopy Layers No
DEAD TREES:
Standing
Minimum DBH (inches) 10
Number of Trees Per Acre2
Down
Minimum Pieces Per Acre None
ADDITIONAL ATTRIBUTES:
Trees in Upper Canopy Are Slow
Growing Yes
QUALITY ATTRIBUTES: Above Attributes in Excess of
Minimums
Distinctive Bark Yes
Variation in Tree Diameter Yes
Down Dead Trees Yes

INTERIOR PONDEROSA PINE – SAF COVER TYPE 237 (Southwest)

Narrative

Southwest ponderosa pine (*Pinus ponderosa* var. scopulorum) occurs in Region 2 in the southwest portion of Colorado, but covers extensive areas of Arizona, New Mexico and southern Utah. As with ponderosa pine elsewhere, it occurs at the lower elevations between 6,000 and 8,000 feet. It reaches maximum development between 7,000 and 7,800 feet where it is a climax forest.

Southwestern ponderosa pine is shade intolerant. It occurs in stands that are open-grown, often poorly stocked and interspersed with meadows and parks. Fire has played a very important role in shaping ponderosa pine stands. In the past, low intensity fires would burn through ponderosa pine stands every 8-15 years, removing competing understory vegetation and down material. This resulted in irregular shaped stands of even-aged groups of trees varying in size, age and density. There is a greater variation in age groups than for ponderosa pine elsewhere as the occurrence of having good moisture, seed production and germination is quite infrequent.

At the lower elevation limits, pinyon-juniper may grow in association with ponderosa pine.

Where ponderosa pine is the sole species or low stocking and frequent fires are still part of the ecosystem, it can be considered a climax species. Some stands with trees over 450 years do exist but more commonly contain trees 300 to 350 years old.

Where periodic low intensity fires have been eliminated from the ecosystem, allowing more shade tolerant species such as Douglas-fir or white fir to survive, ponderosa pine is seral. It will eventually be replaced by more shade tolerant species. The existing open-grown stands are developing understories of Douglas-fir, white fir, and blue spruce with Gambel oak filling in the openings. These old-growth stands will eventually be replaced by these species if fire or some other low intensity disturbance is kept out of the ecosystem.

As with ponderosa pine elsewhere, it has been easy to access and has been heavily used since the mining days of the 1850's. It has been harvested for many things such as mine props, railroad ties, lumber, and firewood. Grasses growing in the open areas provided forage for livestock. Harvesting in the last 30 years or so has generally been by selection and has maintained the uneven-aged structure of old-growth stands. However, with the exclusion of fire, these stands are developing thick understories of Gambel oak, pine and Douglas-fir with a buildup of down dead material, providing excellent conditions for catastrophic fires that could completely eliminate the stands. Ponderosa pine will be replaced by the more shade tolerant species such as Douglas-fir. The dense Gambel oak understory is also difficult to remove, further complicating ponderosa pine being returned to a pre-settlement old-growth condition through management.

Description

Where fire has been present, stands will be climax and contain groups of large, old trees with little understory vegetation or down woody material and few standing dead trees. The age difference of the groups of trees would be large. Where fire is less frequent there will also be smaller size trees in the understory giving the stand some structure with various canopy layers. Dead, down material will be present in varying amounts along with some standing dead trees. In both cases the large old trees will have irregular open, large branched crowns (fig. 7). The bark will be lighter in color, almost yellow, thick and some will likely have basal fire scars.

Where ponderosa pine is seral, generally where fire has been controlled or outside of its optimum elevational range, stands will contain large trees with a multi-layer canopy with various amounts of down, dead material and standing dead trees



Figure 7. Large open-branched crown of an old ponderosa pine tree on the San Juan NF in southwestern Colorado.

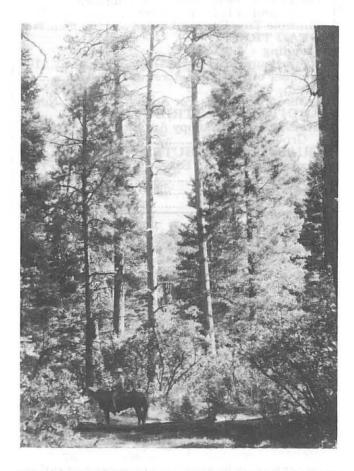


Figure 8. An old-growth ponderosa pine stand on the San Juan NF with Douglas-fir and Gambel oak in the understory. Note the horse and rider in the lower left foreground.

(fig. 8). It will have an understory component of smaller trees such as Douglas-fir, blue spruce, white fir and Gambel oak, filling in the openings between the groups of the large older ponderosa pine. Eventually these species will replace ponderosa pine. There would be varying amounts of dead, down material and some standing dead trees. The large old trees will have irregular open, large branched crowns. The bark will be lighter in color, almost yellow and thick or platy.

Attributes

The following table lists the tree attributes that are being used to describe southwest ponderosa pine old growth.

Table 7-Summary of Old-Growth Attributes Interior Ponderosa Pine - SAF Cover Type 237 (Southwest)

STANDARD ATTRIBUTES LIVE TREES: Upper Canopy - Older Component Minimum DBH (inches)	
Upper Canopy - Older Component Minimum DBH (inches)	
Minimum DBH (inches)	
Minimum Number of Trees Per Acre	Upper Canopy - Older Component
Minimum Age	Minimum DBH (inches)
Minimum Age	Minimum Number of Trees Per Acre 10
Variation in Tree Diameter Yes Decadence - dead, broken or deformed tops and/or bole or root rot Yes Multiple Tree Canopy Layers No DEAD TREES: Standing Minimum DBH (inches) 10 Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	
Decadence - dead, broken or deformed tops and/or bole or root rot Yes Multiple Tree Canopy Layers No DEAD TREES: Standing Minimum DBH (inches) 10 Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	Variation in Tree Diameter Var
tops and/or bole or root rot Yes Multiple Tree Canopy Layers No DEAD TREES: Standing Minimum DBH (inches) 10 Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	
Multiple Tree Canopy Layers	
DEAD TREES: Standing Minimum DBH (inches) 10 Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Yes Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	tops and/or bole or root rot Yes
Standing Minimum DBH (inches) 10 Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Yes Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	
Minimum DBH (inches) 10 Number of Trees Per Acre 2 Down Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	DEAD TREES:
Number of Trees Per Acre	Standing
Number of Trees Per Acre	Minimum DBH (inches)
Minimum Pieces Per Acre None ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing Yes QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	Number of Trees Per Acre 2
ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing	Down
ADDITIONAL ATTRIBUTES: Trees in Upper Canopy Are Slow Growing	Minimum Pieces Per AcreNone
Growing	
Growing	Trees in Upper Canopy Are Slow
QUALITY ATTRIBUTES: Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	
Above Attributes in Excess of Minimums Yes Distinctive Bark Yes Down Dead Trees Yes	QUALITY ATTRIBUTES:
Distinctive Bark Yes Down Dead Trees Yes	
Down Dead Trees Yes	
	Distinctive Crowns Yes

ASPEN - SAF COVER TYPE 217

Narrative

The aspen (*Populus tremuloides*) cover type occurs throughout Region 2 and is associated with both montane and subalpine vegetation. Aspen is found within a broad elevational and moisture gradient occurring on all aspects and slopes, with the most extensive aspen forests occurring between 8,500 and 10,000 feet elevation, similar in elevation to lodgepole pine.

Aspen is the most shade intolerant tree species in the Rocky Mountain Region. Unlike the other major tree species in the Region, most aspen regeneration is by sprouting or suckering rather than by seeding. Aspen does produce seed but requires a bare mineral soil with constant moisture to germinate. Rarely does this occur. Typically aspen regenerates after a major disturbance such as fire, abnormal wind or snow storms, or harvesting by clear felling. In conifer stands where aspen is a minor component, the majority of the regeneration after a stand replacing disturbance can be aspen. Aspen stands can reach an age of 160 or more years but the average life span is probably closer to 125 years.

Like lodgepole pine, aspen is generally considered a seral species. And like lodgepole pine, most aspen stands regenerate following some major stand replacing event such as fire. As the aspen matures, it will be usually replaced by the more shade tolerant Engelmann spruce and subalpine fir and in southwest Colorado also by white fir and Douglas-fir. The stand may still contain some scattered aspen.

In areas where no Engelmann spruce or subalpine fir seed source exists, the aspen stand will not be replaced by another species and can be considered climax. Two things could happen. The stand could reach its maximum life span and the overstory aspen trees rapidly fall with reproduction being sparse as aspen generally requires a major disturbance to initiate abundant sprouting. Or the overstory aspen trees could gradually fall. This path could have two possible results. The stand would not reproduce under itself. Or it would reproduce under itself, creating a multilevel canopy of various tree ages. This condition could continue for many generations. In any case it is difficult to predict which path the stand would take. Any down dead material would quickly decompose.

Description

Many people believe that aspen old growth does not exist. Using a definition of old growth where a stand must be climax to be old growth would eliminate much of the Region's aspen as old growth. However, the seral aspen condition can exhibit some old-growth characteristics. They may not last long in one place but overall in the landscape this old-growth condition can exist for quite sometime.

In a seral condition aspen old growth would be characterized as having a single canopy level of old trees. The aspen would be the overstory which would be closed with an understory of Engelmann spruce and subalpine fir. However, there could be instances where the conifers have become the overstory. Depending on the age of the understory could be a fair amount of structure and variation in tree diameters. There probably would not be much dead down material until the aspen stand began to degenerate. Then the amount of down dead material would accu-



Figure 9. An old-growth climax aspen stand on the Grand Mesa, Uncompander and Gunnison NF near Kebler Pass. Stand is approximately 100 years old.

mulate quickly as the aspen stand would degenerate rapidly. It is important to note that if the understory conifers are relatively young, the remaining stand may not be old growth.

Where aspen is considered climax, old growth will again include a canopy of old large aspen trees which would be closed. However, the stand would have little structure as there would be no understory conifers and little down trees or standing dead trees (fig. 9).

Once stand deterioration started, mature stems could die and fall rather quickly, or the process might take some time. An overstory of various levels with trees of various ages and some down dead trees would then exist. This condition might exist over successive generations. However, if no regeneration occurred when stems died, a single canopied, thinly stocked stand containing gaps in the canopy and down dead trees might persist until all the remaining trees had fallen.

Attributes

The following table lists the tree attributes that are being used to describe aspen old growth.

Table 8–Summary of Old-Growth Attributes Aspen – SAF COVER TYPE 217

77.50 • AUGUST 150 - AUGUST 150
STANDARD ATTRIBUTES LIVE TREES:
Upper Canopy - Older Component
Minimum DBH (inches)
Minimum Number of Trees Per Acre20
Minimum Age100
Variation in Tree Diameter No
Decadence - dead, broken or deformed
tops and/or bole or root rotYes
Multiple Tree Canopy Layers No
DEAD TREES:
Standing
Minimum DBH (inches)No
Minimum Number of Trees Per Acre No
Down
20111
Minimum Pieces Per AcreNo
ADDITIONAL ATTRIBUTES:
Trees in Upper Canopy Are Slow Growing Yes
Canopy Closure Greater Than 50%Yes
QUALITY ATTRIBUTES:
Above Attributes in Excess of Minimums Yes
Multiple Tree Canopy LayersYes
Multiple Tree SpeciesYes
Standing Dead Trees 10" plus DBHYes
Down Dead TreesYes
Variation in Tree DiametersYes

PINYON-JUNIPER - SAF COVER TYPE 239

Narrative

Pinyon pine (*Pinus edulis*) and juniper (*Juniperus scopulorum*) comprise the pinyon-juniper cover type. Pinyon-juniper occurs as a forest type but more often as woodland as the trees are generally shorter than 20 feet and the crowns rarely touch. Pinyon-juniper is found in the southern and western portions of Region 2 extending just into the southern portion of Wyoming. Although pinyon-juniper usually refers to a mixture of both species it may consist of just either one. It occupies the lower and warmest elevations growing from 4,500 to 9,000 feet growing in a semiarid climate. It grows best just below the lower elevational range of ponderosa pine and may also intermix with ponderosa pine.

The stands exhibit considerable diversity in

appearance and composition.

Stands may consist of all ages or one age. Dominant trees are often 400 years old. Trees 800 to 1000 years old have been recorded. The trees can be single stemmed or have a sprawling multi-stemmed character. A few stands may have closed canopies with single or both tree species, with little or no understory, but most stands are open-grown with widely scattered trees of one or both species with a wide variety of understory vegetation.

The pinyon-juniper woodland is shade intolerant. It is the climax cover type remaining on the

site until disturbed by fire. When disturbed by fire it will revert to grasses and eventually return to pinyon-juniper woodland.

The pinyon-juniper woodland has been used for grazing, firewood, building material and especially prized for its pine nuts for over 400 years. Few untouched natural stands probably exist. With the reduction in fire and possibly the reduction of competing grasses due to grazing, pinyon-juniper woodland is increasing its area and also tree densities within existing stands.

Description

An old-growth pinyon-juniper stand would be fairly open grown and contain a cohort of dominant old slow growing trees with little or no understory of grass or shrubs. The old trees would be single to multi-stemmed and shorter than the tree species at higher elevations. Being open grown it would be hard to distinguish if more than one tree canopy exists. The old trees would vary in diameter some would have dead branches/limbs including even part of the stem. There would be an occasional dead standing tree. Down dead material would exist and for quite awhile as the climate is semiarid. However a significant amount of the dead material would also exist on the live trees.

Attributes

The following table lists the tree attributes that are being used to describe pinyon-juniper old growth.

Table 9-Summary of Old-Growth Attributes
Pinyon-Juniper SAF COVER TYPE 239

STANDARD ATTRIBUTES
LIVE TREES:
Upper Canopy - Older Component
Minimum DRC (inches) 12
Minimum Number of Trees Per Acre 30
Minimum Age
Variation in Tree Diameter Yes
Decadence - dead, broken or deformed
tops and/or bole or root rot Yes
Multiple Tree Canopy Layers No
DEAD TREES:
Standing
Minimum DRC (inches) 10
Number of Trees Per Acre 1
Down
Minimum Pieces Per Acre 2
ADDITIONAL ATTRIBUTES:
Trees in Upper Canopy Are Slow
Growing Yes
Canopy Closure Greater Than 35% Yes

GLOSSARY OF OLD-GROWTH ATTRIBUTES

Forest Cover Type - a descriptive classification of forested land based on present occupancy of an area by tree species. Forest cover types are named after predominant tree species. Predominance is determined by basal area and the name is confined to one (ponderosa pine) or two (spruce-fir) species. The mixed-species/mixed conifer forest cover type is not a forest cover type in itself as defined by SAF but includes several forest cover types.

Attributes - The elements that are measured to determine the classification of a stand as oldgrowth. They are as follows:

Standard Attributes

1. Live trees:

Upper canopy - a grouping of the taller (dominant and codominant) trees in the stand. For live trees the following attributes of minimum DBH, number of trees per acre, and age refer to the upper canopy of the stand. There must be an upper canopy of trees meeting these minimums for the stand to be considered old growth.

Minimum DBH - this refers to trees in the upper canopy and not to average DBH for the stand which would generally be lower. It is the minimum DBH that would be required for the stand to be considered old growth. DBH is the diameter of a tree at 4.5 feet from the ground measured on the uphill side. It is generally outside bark. However, if the tree is dead and the bark has fallen then it would not include bark.

Minimum DRC - this is used for woodland species such as pinyon-juniper. DRC is the diameter at the root collar. The root collar is the region where the root and stem merge.

Minimum Number of Trees Per Acre - the minimum number of trees per acre in the upper canopy meeting or exceeding the above minimum DBH.

Minimum Age - the minimum mean age of the trees in the upper canopy meeting or exceeding the above DBH. This would be total tree age. Age is just one part of the equation for a stand to be old growth. A stand could meet the minimum age requirements and may still not be old growth. Age has been included as an attribute to give an idea of what age old growth is thought to begin. It is the attributes that develop with age such as stand structure, dead trees, down material, distinctive bark, net stand growth near zero and tree decadence that need to be considered. Some stands may meet the minimum age require-

ment but have not yet developed these other attributes.

Variation in Tree Diameters - there are trees of various diameters present in the stand. This would allude to an uneven aged stand and/or a stand with more than one tree species. All of which suggest a more structured stand. No diameter ranges have been suggested as little is known what they should be. However it was common consensus that such an attribute is an important characteristic of old growth.

Decadence - this refers to the trees in the upper canopy. The tops or crowns of some of the trees are broken, dead, deformed or have sparse foliage or the stems have rot and/or root rot. These are indicators that the stand could be past maturity and declining. Growth is being succeeded by mortality. The stand is not young and vigorously growing. It could also mean that the stand has been infected with some disease and that's all. But if the above attributes are present in a stand, decadence would be a further indicator of old growth. No values are listed as no data is available on how many trees should have reached senescence.

Multiple Tree Canopy Layers - more than one tree canopy layer or story is present. A canopy layer or story is roughly a horizontal stratum or layer formed by the crowns of trees. A stand can have one to many canopy layers. Generally trees of the same age or species tend to grow to the same height in a stand. This height or horizontal layer formed by the tree crowns would be a canopy layer. The tallest canopy layer representing the most crown cover in a stand would generally be the upper canopy layer.

Dead Trees

Standing - a tree, vertical or near vertical, that is supporting itself or leaning on another tree. A standing dead tree is also called a snag.

Minimum DBH - the minimum diameter at 4.5 feet that a dead tree would be considered for old growth.

Minimum Number of Trees Per Acre - the minimum number of dead trees per acre that are equal to or above the minimum DBH to be considered for old growth.

Down - tree that has fallen down, is dead and laying horizontal. May be a whole tree or section of one. All, part or none of the whole tree or section may be touching the forest floor.

Additional and Quality Attributes

Trees in Upper Canopy Are Slow Growing - trees are growing slower than in the past. This indicates the stand has reached maturity and/or may be over-mature, that is past it's peak of maximum growth. Generally the crowns are beginning to flatten and become broader and more open.

Canopy Closure Greater Than 50% - 50% or more of the ground is covered by foliage of the upper canopy in a vertical projection.

Wide Range of Tree Vigor - trees in the stand are growing at various rates from vigorous growth to almost no growth.

Net Growth Near Zero - this applies to the stand as a whole. Basically the amount of new growth is offset by trees dying.

Patchiness - a stand has breaks in the upper canopy level and/or has openings. An opening is defined as an area within the stand that contains vegetation different than the majority of the stand, such as grasses, forbs, shrubs and young trees.

Many Stages of Decomposition - this refers to the dead material either standing or down. The dead material is in various conditions of decay.

Multiple Tree Species - there is more than one tree species in the stand.

Distinctive Bark - some species of trees with age acquire bark characteristics that are much different (distinctive) than when younger and vigorously growing. The bark becomes platy that is it has large patches with deep furrows in between the patches. The bark may also be different in color for some species. Darker for lodgepole pine, reddish for spruce-fir and light tan or yellow for ponderosa pine.

Distinctive Crowns in the Upper Canopy - as they age some species of conifer trees acquire crown characteristics that are much different than when young. The crowns loose their conical shape as growth diminishes with the crowns flattening. Crowns develop holes, become misshapen and foliage develops dead areas. Branching is more open with large branches. Part or all of the crown can die. These characteristics are very evident in older ponderosa pine and lodgepole pine trees. These characteristics can also be attributable to insects or pathogens so the other attributes need to be considered as well.

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An Old-Growth Forest Inventory Procedure for the Arapaho and Roosevelt National Forests, Colorado¹

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Abstract:—Information on extent and nature of old-growth conifers has been generally unconfirmed. Field inventories were conducted in 1990 and 1991 to locate and assess old growth. Unvisited potential old-growth sites are being interpreted from aerial photos. With about half of the aerial photo interpretation accomplished, approximately 9 percent of the major forested types has been identified as old growth. A total of about 14 percent is predicted, once the inventory is complete. Most old growth occurs in high-elevation spruce and fir, less in mid-elevation lodgepole pine, and least in low-elevation Douglas-fir and ponderosa pine forests. Spatial and statistical analyses are planned. This effort is intended to contribute information necessary to manage existing and future old growth.

INTRODUCTION

Old growth was recognized as a unique forest structural stage prior to 1990 in the Arapaho and Roosevelt National Forests. What existed was generally unknown and how it functioned was only partially understood. It was apparent that development of this condition took centuries, and that parts of the Forests had very limited amounts or were devoid of these previously existing forested conditions. This led to development and adoption of an old growth policy that addressed definition, inventory, and interim management direction (USDA 1990).

Information on existing and future old growth is needed for day-to-day resource management, and in developing a revised Forest Plan. Prior to 1990, detailed definitions had not been developed and there was little consistency in identifying old-growth stands throughout the Forest. After definitions were developed in 1990, we realized that the data necessary to identify and classify old growth were not generally available in Forest data bases. Therefore, an inventory was necessary to collect this information.

Field surveys were conducted during 1990 and 1991 to inventory and classify the location, quality, and amount of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) old growth. Elevations range from 11000 feet to 6000 feet, respectively.

The study area is north-central Colorado along the Front Range between the Colorado-Wyoming border and the Mount Evans vicinity just west of Denver.

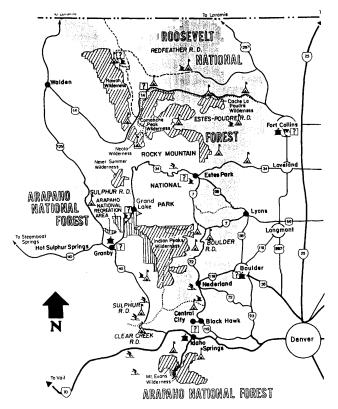


Figure 1. Study area.

Included are forests on both sides of the continental divide that essentially surround Rocky Mountain National Park (fig 1).

Throughout this text, the words site and stand are used synonymously to mean uniform vegetation within a variable-sized unit area. Also, the terms inventory and survey are used to describe the same general activity performed. Standing dead trees are referred to as snags.

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GOAL AND OBJECTIVES

Our goal was to locate and assess all stands of old growth to improve biodiversity management. The aim was to field-visit the majority (75 percent or more) of the potential old growth sites and collect necessary information for Forest resource planning and management. Remaining sites were to be interpreted from aerial photos, making comparisons with photo images of field-truthed sites. Both field and photo work were to be completed in time for incorporation into the revised Forest Plan.

The primary objective in meeting this goal was to inventory existing old growth throughout both National Forests and ascertain location, quality and amount by the end of the 1991 field season. This required an extensive field survey to collect information from a large number of forested stands.

The second objective was to obtain empirical data to better describe and define old growth from the field surveys. This required additional, more intensive effort to take limited measurements and to rate and categorize data. This information is important for three primary reasons: 1) to provide additional data for more complete biodiversity assessments, 2) to allow use of these same data in the future to reinventory old growth if definitions should change, thus avoiding the need for additional field efforts and 3) to contribute to the Rocky Mountain Regional effort to define or characterize old growth.

METHODS

Definitions

Definitions for old growth were developed for the Arapaho and Roosevelt National Forests in 1990. These are included in a Forest Service Manual supplement addressing old growth management policy. Definitions are based on structural characteristics that include indices for old trees.

Structural requirements are described but exacting, rigid definitions are avoided as evidenced by this statement which precedes old growth definitions in the Forest Policy: "All of the characteristics listed below are seldom found in individual old growth stands. The more conditions met, the better the quality of old growth habitat. Therefore, there are degrees of old growth habitat quality ranging from excellent to marginal (USDA 1990)."

Three definitions were developed for forested sites dominated by different conifer species. The following are *key old-growth characteristics* by major conifer zone.

In sites dominated by spruce or fir:

Presence of large live trees (14"+ dbh), including 15 or more trees per acre 12"+ dbh.

Presence of large snags (14"+ dbh), including 2 or more snags per acre 12"+ dbh.

Presence of large fallen trees (14"+ diam), including 3 or more per acre 12"+ diam.

Presence of multi-storied canopy. Overhead canopy closure >20%.

Presence of large, old, declining live trees.

In sites dominated by lodgepole pine:

Presence of 15 or more large live trees (10"+ dbh) per acre.

Presence of 2 or more large snags (10"+ dbh) per acre.

Presence of 3 or more large fallen trees (10"+ diam) per ac.

Overhead canopy closure >20%.

Presence of large, old, declining live trees.

In sites dominated by Douglas-fir or ponderosa pine:

Presence of large live trees (18"+ dbh), including 15 or more trees per acre 12"+ dbh.

Presence of large snags (14"+ dbh), including 2 or more snags per acre 12"+ dbh.

Presence of large fallen trees (14"+ diam), including 3 or more per acre 12"+ diam.

Presence of multi-storied canopy. Overhead canopy closure >20%.

Presence of large, old, declining live trees.

The following are other common old growth characteristics for all before mentioned forested sites.

Presence of more than one tree species. Presence of small openings with grasses, forbs, or shrubs.

Presence of seedlings, saplings, or poles.
Little or no evidence of logging.
Little or no evidence of fire, insect, or wind disturbance.

Potential Inventory Sites

Sites considered included those previously classified as mature or old growth structural stages in the Forest Resource Inventory System (RIS), a data base containing information by forest stand. This includes forested stands having Engelmann spruce, subalpine fir, Douglas-fir, ponderosa pine trees or lodgepole pine trees of at least 9 inches dbh.

Areas with past activities or treatments that had removed key characteristics of old growth were deleted from this long list of possible old-growth sites. Sites with detailed inventory data showing absence of key old growth characteristics were dropped. Silviculturists and foresters who had first-hand information on numerous areas excluded stands from consideration where old growth characteristics were known to be absent. In some cases, photo interpretation of latest aerial photos revealed where recent insect epidemics or forest fires occurred and potential for old growth was now lacking.

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The inventory crews assessed conditions within these previously defined RIS sites. For example, entire sites were called either old growth or non-old growth, even though areas of each occurred within individual sites. If a spruce-fir or lodgepole pine stand was estimated to be old growth over more than half of the area, it was rated as old growth, and visa versa. In Douglas-fir and ponderosa pine sites, where

conditions were clumpy and fragmented, less than half of the area could be old growth and still be rated as an old growth site. Often, percentage estimates of each were noted on the stand scoresheets, as well as where each occurred if apparent during the stand walk-through (e.g., "The top 1/3 of stand is old growth and the bottom 2/3 is not old growth").

Field Crews and Training

Field crews generally consisted of two person teams. Often individuals from a team would split and inventory sites independently for efficient use of time, but worked in close proximity knowing one another's location. Otherwise, single-person inventories were avoided for safety reasons.

In 1991, surveys were conducted mid-May through mid-October. Three teams of 2 people were employed. Two teams operated on the east side of the continental divide and one team on the west. Five people stayed with the survey start to finish. One member was replaced by July 1 by a person who stayed the rest of the season. In 1990, surveys were conducted mid-July through mid-November. Various teams of 2 people were employed. However, consistency of where teams operated, the individuals on teams, and the time each person participated in the survey varied more than in 1991. Two individuals on one team were present throughout both field seasons.

Crew members were trained for travel in remote, rugged terrain, interpretation of topographic maps and aerial photos, and orientation using maps and photos. Instruction also included identification of plants, classification of habitat types or plant associations, estimation of crown cover percentages, recognition of old-growth characteristics, assessment of old-growth quality, and prediction of time remaining as old growth or until sites might become old growth. Direction was provided in obtaining measurements of live and dead tree basal area, standing tree diameter, height, age, and fallen tree diameter, soundness, and number of trees per unit area.

Field work included the use of vehicles, portable radios, compasses, map/photo scales and protractors, prisms, angle gauges, diameter tapes, distance tapes, clinometers, increment borers, and cameras. Field references were used for identification of plants (Powell 1987), classification of habitat types (Hess and Alexander 1986) and rating of live, declining trees (Thomson 1940).

Two of the crew members from the 1991 field survey are, at the time of this writing, photo-interpreting the remaining potential spruce-fir and lodgepole pine old-growth sites that were not field visited. Few potential Douglas-fir/ponderosa pine oldgrowth sites remain unvisited in the field; available photos are too old to show areas of recent insect epidemics, and therefore, old growth in these areas is not being photo interpreted at this time. Old Delft Scanning Stereoscopes, ODSS III, are being used to interpret as much old growth information as possible. Sites field-rated as old growth are used as standards

in photo comparisons to evaluate potential sites that have not been field visited in the same vicinity.

The primary data rated from aerial photo interpretation are dominant tree cover; old growth or not; if old growth, the estimated quality condition; if lodgepole old growth, whether seral to spruce and fir; if not old growth, whether it will become such within 100 years; and presence or absence of small openings, streams, or seeps.

Inventory Sheets

Inventory sheets were developed for the 1990 season and refined slightly for 1991. One content change was made in adding "presence of old, declining live trees" to the list of key old growth characteristics on the 1991 stand scoresheets.

Stand scoresheets were used to record average conditions within a stand based on all walk-through observations, including plot measurements and estimates made within the site. Information was recorded prior to leaving each site. An example of the spruce-fir scoresheet is presented (table 1).

Plot data sheets were used to record measurements taken at one or more sample plots within each old growth site. Usually it was obvious early during the traverse whether the stand would rate as old growth. Most of the old-growth sites and few of the non-old-growth sites were measured.

Criteria for Assessment of Old Growth

When judging whether sites were old growth or not, primary consideration was given to the presence or absence of key old-growth characteristics. As a minimum rule, large live trees, some of which were old and declining; either snags or fallen trees; and greater than 20 percent overhead canopy closure were all prerequisites for a site to be called old growth.

Common old growth characteristics were not determinants of whether old growth existed but were qualifiers, in addition to key old growth characteristics, in assessing old-growth quality.

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Sites found to be old growth were rated as excellent, good, fair, or marginal quality. Primary consideration was given to the number of key old-growth characteristics present, and to the degree site conditions exceeded the described minimums in the definitions. The more categories met, the larger and more abundant the trees (live, old and declining, dead and fallen), the higher the vertical structure, and the denser the canopy, then the higher the quality rating. In arriving at which quality rating was appropriate, there were no set formulas or thresholds. The crew members, having seen the extremes of conditions from excellent to marginal, approximated where each old growth site fit within this four-part spectrum.

In sites found to be old growth, the length of time remaining as old growth was estimated. Sites would

Table 1. Spruce-fir old growth scoresheet. SPRUCE-FIR 2.22 5/8/91 OLD GROWTH INVENTORY

LOCATION	:				SITE:			
DATE:	(M	MDDYY) O	BSERVER		DISTRICT LEGAL: T	NG D	W SEC	
ELEVATION	N:	S	LOPE:		ASPECT:	No r_	_w sec	
POSITION:	RIDGE FLAT	UPPER 1/3 (WET)	UPPER 1/3 (DRY)	MIDSLOPE (WET)	MIDSLOPE (DRY)	LOV (WE	VER 1/3 LOWE (T) (DRY)	
	(WET)	FLAT(DRY)	BOTTOM	ROLLING	BROKEN			
SLOPE CON	NFIGURATIO	N: CONVEX	CONCA	AVE STRA	IGHT/FLAT	NOT I	DESCRIBABLE	
	Total Crown	Cover %	% of	% of Total Cov	er for Species			
TREES:	DID.1		Total Cover		MS US			
		NG. SPR. JB. FIR				100 100		
		DDGEPOLE						
		SPEN				100		
		MBER				100		
	0.	THER	100			100		
	%		97	,		%		%
SHRUBS	,-	over FORBS		o Cover FORBS (con't)	% Cover	GRASSES	70
Cover Juniperus con	nmunis	Arnica cordif	olia	Polemoniu	ım delicatum		CALAMAGROSTI	S
Lonicera invo	lucrata	Arenaria fen		Pyrola chl			canadensis	
Pachistima m	yrsinites	Caltha leptos	sepala _	Pyrola mi			CAREX geyeri	
Rosa woodsii Salix spp.		Epilobium an Equisetum a	_	Saxifraga Sedum ste	arguta enopetalum		Carex spp. Deschampsia	
Vaccinium my	rtillus	Haplopappus	parryi _	SENECIO) triangularis		caespitosa	
VACCINIUM	scoparium	Lathyrus leu Mitella penta	1	Smilacina	stellata UM dasyphyllum		Poa spp. Festuca spp.	
		Mertensia cil	iata _	Trifolium	parryi		Juncus spp.	
		Osmorhiza de			wormskjoldii		Trisetum spicatum	
		Penstemonw	• •				Luzula parviflora	
Habitat Typ	e (%): PIEN -	TRDA AB	LA - CAGE	_ ABLA -VAS	SC ABLA	- SETR _	ABLA - CAC	A
KEY OLD G								
Y N	Presence	of large live trees		in	cluding 15 or mo	re trees j	per acre 12"+ dbh	
Y N	Presence	of large snags (14	4"+ dbh)	in	cluding 2 or mor	e snags p	per acre 12"+ dbh	
Y N Y N		of large down wo of multi-storied o		14" + dbh) in	cluding 3 or mor	e logs pe	r acre 12 + dbh	
Ϋ́N		of >20% overhead		re				
Y N	Presence	of old, declining l	ive trees (d	ead tops, bi	roken tops, f	lat tops	, rounded tops)
OTHER CO	MMON OID	GROWTH CHARA			aly bark, pla	aty bark		
YN	-	of more than one	_					
Y N	Presence	of small openings	s with grasses,	forbs, shrubs				
Y N		of seedlings,		poles				
Y N Y N		no evidence of log no evidence of fire		disturbance				
ASSESSME		no evidence of fire	e, msect, wind	uistui bance				
Y N		and apparently O	ld Growth					
	If so, rate	ed as: Excellent _	, Good ,	Fair , Marg	inal			
		owth, how long re						
		rs , 26-50 l reason for less th						
Y N		owth, will it impr						
	Principal	reason for impro	vement?					
	If not Old	d Growth, how lor	ng until it beco	mes Old Growth	n?			
		rs , 26-50 , ts	31-100, 1	.00+				
Notos: V 1				· · · · · · · · · · · · · · · · · · ·				
		streams or seeps ation in stand; not	able character	ristics)				

be judged to remain longer where decadence was just beginning, in the form of large snags or fallen trees, and where most larger trees were healthy as compared to sites with high decadence and mostly old, declining live trees. Different average life spans by tree species were considered in making estimates. Years remaining as old growth were estimated assuming that catastrophic changes would not occur, such as from insects, fire, or wind.

Sites found to be old growth were judged as to whether quality would improve. In the examples of the previous paragraph, the former (healthy, large trees with little decadence) may improve in quality and the latter (declining, large trees with high decadence) probably would not. If the former example contained trees that would continue to grow larger, increase canopy closure and recruit more than minimum amounts of large snags or fallen trees, then we predicted that quality would improve.

Sites found to not be old growth were rated as to how long it may take to become old growth. Considerations from the previous four paragraphs were used in making this assessment. For example, is it possible for successional change from mature to old growth within a stand, barring unpredictable catastrophic changes? Is a site within 100 years of meeting the minimum old-growth characteristics described for live trees, decadence, and canopy closure?

RESULTS

Completed Work

Field data have been collected and aerial photo interpretation is partially completed. About half of the remaining potential old-growth sites has been photo interpreted. Field data and completed photo interpretation data were entered into Forest data bases.

With half of the aerial photo interpretation completed, findings show that almost 9 percent of all spruce-fir, lodgepole pine, Douglas-fir and ponderosa pine forests is old growth. Assuming that similar amounts will be found in the remaining photo inventory, about 14 percent may be the final total.

About 68 percent of the old growth identified so far is spruce-fir, 31 percent is lodgepole pine and less than 1 percent is Douglas-fir/ponderosa pine. This indicates that the most old growth exists at the highest elevations with least roads, and the least old growth exists at the lowest elevations with most roads.

Part of the tabular field collected data from sites rated as old growth have been statistically analyzed by Phil Robertson in the paper "Interpretations of Old-growth Forests from Inventory Data of the Arapaho and Roosevelt National Forests", which is included in this report.

Ongoing Work

Remaining potential old growth sites are now being photo interpreted. Photo-interpreted data are being entered into Forest data bases as they become available. Preparations are being made for the analysis of the current situation and the modeling of future possibilities for both existing and future old growth. Preparations for dealing with all old-growth data, from both field and photos, include spatial analyses and additional statistical analyses.

DISCUSSION

The procedures described were not fully developed at the beginning of the survey. Experience was a good teacher, however, and techniques were improved as the surveys progressed. Most adjustments to technique had been made by early in the second year.

Definitions

As mentioned in the Introduction, our definitions were developed prior to Regional definitions. However, they are consistent with subsequent Regional definitions described in the paper by Mel Mehl titled "Defining Old-growth Forests by Major Forest Types", which is included in this report.

The survey was for old growth forests of greatest concern; most affected in the past or likely to be affected in the future by management activities. Old growth dominated by other forest species such as aspen (*Populus tremuloides*), limber pine (*Pinus fexilis*), bristlecone pine (*Pinus aristata*), and Rocky Mountain juniper (*Juniperus scopulorum*) were not defined or inventoried.

Potential Inventory Sites

Variability in the quality of RIS site delineations is probably one determinant of the variability in old-growth assessment results. Examples include: sites with two or more aspect quadrants that contained different vegetative conditions; sites typed to greater detail outside of wilderness than within wilderness; and sites that have uniform vegetation only in the sense that vegetation is uniformly varied throughout. It is also likely that the more consistent makeup and operation of field crews in 1991 contributed to more consistent, reliable data, than that collected in the 1990 field season.

Because sites were not delineated by habitat type, often two or more habitat types were found in a site. The relative amounts of each were usually estimated and recorded on stand scoresheets. The location of different habitat types within sites was also recorded if apparent during the walk-through (e.g., "The upper 2/3 of the site is Abies lasiocarpa-Vaccinium scoparium (Abla-Vasc) and the lower 1/3 is Abies lasiocarpa-Senecio triangularis (Abla-Setr)," or "There is about 10 percent Abla-Setr scattered throughout this stand of predominating Abla-Vasc.").

Criteria for Assessment of Old Growth

Deciding if a site should be rated as old-growth, based on key old-growth characteristics, should probably be further explained. Decadence is a necessary criterion. Evidence of decadence is considered to be large snags, fallen trees and old, declining live trees (see Definitions in Methods Section). It is possible for old-growth stands to have either fallen trees or snags, but not both. There are locations where prevailing strong winds tend to topple most standing dead and other weakened live trees. In this example, snags are essentially absent but fallen trees are plentiful. In other old-growth sites, large tree mortality is just beginning, and here snags are present but have not fallen to the forest floor. Fallen trees are, therefore, essentially absent.

Large, declining live trees are considered a necessary part of all old growth stands. Crown and bark conditions helped to discern between healthy and declining large, live trees. The tendency toward round, flat, thin, dead, or broken tops helped to classify large live trees as older and declining from the younger, healthier trees with more pointed, full and vigorous tops. Thomson's (1940) age and vigor classes for ponderosa pine were considered relative and useful for rating other conifers as well. Tree bark that was platy in ponderosa pine, and scaly or thin in most other conifers was considered an indicator of old trees. These indicators were readily observed and contributed to time efficiency.

A multi-storied canopy is not always found in old growth, especially in lodgepole pine sites that do not contain spruce or fir. Here the canopy usually is one level. This condition would also be expected in pure ponderosa pine stands where recurring fire has kept most young Douglas-fir and ponderosa pine trees from establishing.

The characteristics of large live trees, some of which are old and declining, and greater than 20 percent canopy closure were considered necessary in rating a site to be old growth. Large, live trees are needed to produce large snags and large fallen trees. A decadent stand lacking large, live trees is likely the remnant of old growth that previously existed.

Presence of some large, old, declining live trees indicates sufficient age to produce large snags and fallen trees. This was especially helpful in deciding on the potential of non-old growth stands to become old growth, and how soon.

The greater than 20 percent canopy closure was an indicator that each site was more of a forest than an opening. Canopy closure of 20 percent is considered sufficiently open so as to not exclude possible old growth, such as dry-site Douglas-fir and ponderosa pine, which often have a relatively open canopy.

Rating of old growth quality into four categories is considered to be more objective than subjective in the following sense. Objectiveness was probably lowest before individuals gained appreciable field experience and during the start of each field season. However, once the extremes in old-growth conditions had been seen and measured, it became easier to estimate where in this spectrum old-growth sites fit. The few, simple categories of excellent, good, fair, and mar-

ginal allowed relatively easy approximation and differentiation.

The estimates of time for old growth to remain and for non-old-growth to develop into old growth are relative. In forest planning and resource allocation where choices between old-growth management areas and other resource objectives may be necessary, these estimates and indices of time are important. Relative differences of time periods amongst sites are of greater concern than the precision of the actual length of time estimates.

Completed Work and Ongoing Work

The time between end of field work and completion of data entry of field and photo information will likely be 6 months. The handling of collected field data required intensive, time-consuming effort to put into usable form within Forest data bases. The entire inventory and data entry are estimated to cost between \$85,000 and \$100,000 when finished.

Spatial analysis such as in a geographical information system is considered essential in obtaining the maximum useful benefit from the old-growth inventory data. Spatial analysis is needed to ascertain such things as which sites are adjacent to each other, thereby making larger blocks of old growth, and the location, size, and configuration of these blocks in relation to other blocks or isolated stands of old growth. Looking at areas where existing old growth, potential old growth, or neither exists will be essential for present and future old-growth management decisions.

Further analysis of tabular data should give insight into which types of areas may be most or least likely to allow development of old-growth conditions. This will be important in deciding which types of sites will be best choices for recruitment of future old growth.

PUBLIC PARTICIPATION

Volunteers from the Boulder County Nature Association were trained in a similar but abbreviated manner as were the Forest field crews. Limited time and equipment constrained the amount of inventory possible. They surveyed several sites in Boulder County that would otherwise not have been assessed in the field. Their interest and enthusiasm were important in gaining public understanding and support that extended beyond this group.

SUMMARY

Understanding the procedures of this old-growth inventory should assist in interpretation and understanding of the results. The first priority was to inventory presence or absence of defined old growth Forest-wide. The second priority was to collect estimated or measured attributes of old-growth and

non-old-growth sites. The survey was for major conifer types and general conditions, most affected or likely to be affected by forest management activities. This effort is intended to provide needed information for current management and planning, and to help identify future needs.

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Characteristics of Spruce-Fir and Lodgepole Pine Old-Growth Stands in the Arapaho-Roosevelt National Forest, Colorado¹

Philip A. Robertson²

Abstract.—During the summers of 1990 and 1991, over 1,700 forest stands in the Spruce-Fir and Lodgepole Pine cover types in the Arapaho-Roosevelt National Forest were surveyed for old-growth status. Most old-growth stands occurred in the *Abies lasiocarpa/Vaccinium scoparium* or *Pinus contorta/Vaccinium scoparium* habitat types. Old-growth Spruce-Fir stands were primarily located between 9,000 to 11,000 ft on north facing upper to lower midslope positions while old-growth Lodgepole pine stands occurred on similar topographic positions but at 8,500 to 10,000 ft. Discriminant analysis revealed that old-growth condition class rating was not strongly based upon measured structural characteristics. Based upon these analyses, it was concluded that the current model for analyzing old-growth forests is inadequate and a new model is proposed.

INTRODUCTION

This paper is the result of analyses of survey data taken during the summers of 1990 and 1991 in the Arapaho-Roosevelt National Forest, Colorado. Survey data were taken by field crews in three cover types, Douglas Fir/Ponderosa Pine, Lodgepole Pine and Spruce-Fir. Since so few old-growth Douglas-Fir/Ponderosa Pine Stands were found, only data from the Spruce-Fir and Lodgepole Pine types will be included. Methodology is described in the previous paper in this volume (Lowry, 1992).

Because of time limitations, not all data taken in the field were summarized or evaluated in this report. Little was done with estimates of stand composition made on the survey form; instead emphasis is placed on the environmental location of oldgrowth stands and their structural characteristics especially as the latter relate to old-growth designation and condition rating. When using variables with multiple entries on the field data forms, i.e., aspect, slope position, etc., only the assumed primary value (the first one entered) was used. The primary aspect was either converted to azimuth angle or linearly transformed using the following formula: Transformed aspect = COS(45 - aspect angle) + 1.0. Azimuth or transformed aspect was used depending on the analysis conducted. For brevity and simplicity, use of scientific names was kept to a minimum and standard abbreviations were used when referencing habitat types. The exception was the first mention of a given habitat type in which case the full scientific name was used.

GENERAL CHARACTERISTICS

Eighty-five percent of the Spruce-Fir stands occur in the Abla Vasc (Abies lasiocarpa/Vaccinium scoparium) habitat type with the remaining occurring in the Abies lasiocarpa/Calamagrostis canadensis, Abies lasiocarpa/Carex geyeri, Abies lasiocarpa/Senecio triangularis and Picea engelmannii/Trifolium dasyphyllum habitat types. Of the stands sampled, 605 were determined to be old-growth, 481 did not have old-growth characteristics and 8 stands were not rated for old-growth status.

There were over 560 Lodgepole Pine stands surveyed with most occurring in the Pico Vasc (Pinus contorta/Vaccinium scoparium) or Abla Vasc (Abies lasiocarpa/Vaccinium scoparium) habitat types. Of the stands sampled, 279 were determined to be oldgrowth, 234 were considered non old-growth and 46 stands were not rated. Seral Lodgepole pine stands were reclassified into their climax potential counterparts, i.e., Pinus contorta / Carex geyeri, Pinus contorta/Shepherdia canadensis, and Pinus contorta/Vaccinium scoparium were classified into the appropriate *Abies lasiocarpa* series. Of the stands sampled, 47.2% were considered to be seral and fifty six seral stands (21.3%) had a structure that was typical of Spruce Fir forests. Within the seral stands, 78% were determined to have a gap in time before the Spruce Fir old-growth would occur; in 65.4% of these stands the gap length was more than 100 years.

Analysis of old-growth condition was somewhat difficult as some stands were given more than one rating by the field crews. Stands that were rated in two or more condition classes were assigned the highest condition class rating given. Condition of the old-growth Spruce-Fir stands was generally interme-

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diate with about 65% of the stands occurring as either good or fair. Only 6.6% of the stands were classified as excellent. Of the time remaining in oldgrowth condition, 522 were more than 100 years, 21 were in the 50-100 year range, 6 were in the 25-50 year range and only 1 was in the 0-25 year range. The potential to improve in quality was positive in 466 or 81.2% of the old-growth stands. Condition of the Lodgepole Pine old-growth stands was also generally intermediate with about 77% of the stands occurring in the fair to marginal category. Only 3.3% of the stands were classified as excellent. Of the time remaining in old-growth condition, 203 were more than 100 years, 31 were in the 50-100 year range, 13 were in the 25-50 year range and only 3 were in the 0-25 year range. The potential to improve in quality occurred in 180 or 67.4% of the old-growth stands.

Acreage of old-growth Spruce Fir and Lodgepole Pine stands varied by more than one order of magnitude. Ninety percent of the 24,533 acres of Spruce-Fir old-growth is in the Abla Vasc (Abies lasiocarpa/Vaccinium scoparium) habitat type with minor acreage in the remaining habitat types. In the Lodgepole Pine type most of the 7,173 old-growth acres occur in the Abla/Vasc (58%) and the Pico Vasc (31%) habitat types. The acreage in the excellent category is less than 10% of that in the remaining classes, combined for both cover types. There is little difference in the acreage among the good, fair and marginal condition classes. The climax Lodgepole Pine old-growth will be expected to decline in acreage as the existing stands tend to break apart.

Of the 481 Spruce-Fir stands that were classified as non-old-growth, 90.9% (390) were considered to have the potential to become old-growth while 39 did not have old-growth potential (52 stands were not rated for their old-growth potential). Average time required to become old growth ranged from less than 25 to over 100 years. Four of the stands were rated at less than 25 years while 23, 79 and 283 were rated at 26-50, 51-100 and 100+ years to become old-growth, respectively. Ninety-two of the non old-growth stands were not rated with respect to the time required to become old-growth. Over 89% (217) of the non oldgrowth Lodgepole Pine stands were considered to have the potential to become old-growth while 25 did not have old-growth potential; (32 stands were not rated for their old-growth potential). Six of the stands were rated at less than 25 years while 13, 53 and 145 were rated at 26-50, 51-100 and 100+ years to become old-growth, respectively. Sixty-three percent of the non old-growth stands were climax that did not support old-growth structure. Fifty-seven non oldgrowth stands were not rated as to the time required to achieve old-growth status.

ENVIRONMENTAL LOCATION

Most of the Lodgepole Pine and Spruce-Fir oldgrowth stands occurred at a slope aspect between 270 and 90 degrees (west to east through north). The greatest number of Spruce-Fir stands occurred between 10,500 and 11,500 ft (fig. 1) while most of the Lodgepole Pine stands occurred between 9,500 and 10,500 ft (fig. 2). The majority of stands in both cover types occurred on upper or midslopes with only sporadic occurrences on bottom, flat or ridge top sites (table 1). The lack of old-growth stands on flat or bottom sites may be the result of past timber harvesting or other anthropogenic disturbance on these sites. Slope angle of sites supporting old-growth stands ranged from 0 to 90% with a mode of about 20 and a mean of 28.4 ± 16.05 . The low mode and mean indicate that most of the old-growth stands do not occur on very steep slopes. Most of the old-growth stands occurred on dry rather than wet sites, although many of the stands sampled (69.2%) had seeps or streams in them. There was little difference in slope angle between old-growth and non old-growth stands.

STRUCTURAL CHARACTERISTICS

Qualitative structure—. Of the various qualitative structural characteristics, including the presence of large trees, large snags, large down material, a multistory canopy, closed canopy and declining trees, evaluated for each stand, most showed clear relationships to old-growth status (Table 2). In the oldgrowth stands, all of the structural characters were present with a frequency of 80% or higher. In the instances where declining trees were scored as present, the crown characteristics were evaluated and scored according to Thomson's Growth Rate Classification Scheme (Thomson, 1940) or simply scored as present. The most prevalent growth rate classification values were 3C or 4D. Few stands were scored as Class 2, approximately 36% were scored as Class 3 and 60% were Class 4. It should be noted that there were many stands that were not rated in the field for these characteristics even though they were scored as old-growth. Given the scoring of these characteristics, it is clear that the stands rated as old-growth have tree crown characteristics or growth forms that indicate an "old" condition. This rating system was developed for Ponderosa Pine and should be applied with caution to other species.

Quantitative structure—. The discussion of structural characteristics of old-growth stands is based on

Table 1. Distribution of Spruce-Fir and Lodgepole Pine old-growth stands in relation to slope position and moisture regime.

Moisture Regime	Ridge	Upper Slope	Mid Slope	Lower Slope	Flat	Bottom
		SP	RUCE-FI	R		
Dry	8	102	133	46	11	11
Wet	0	20	62	40	4	-
		LODG	EPOLE I	PINE		
Dry	8	60	148	23	2	3
Wet	0	5	24	13	0	-

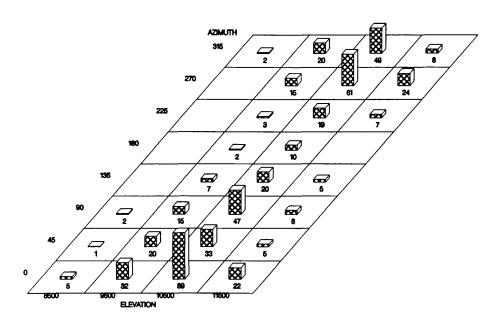


Figure 1. Distribution of old-growth Spruce-Fir stands in relation to elevation and aspect (azimuth).

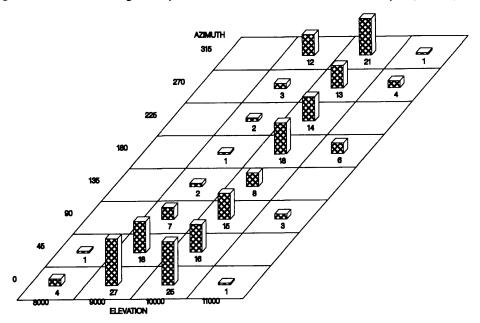


Figure 2. Frequency distribution of old-growth Lodgepole Pine stands in relation to elevation and aspect (azimuth).

only those stands that had plot or Stage II samples taken in them and therefore the sample size is less than the total number of stands surveyed. Structural comparisons between old-growth and non old-growth stands showed age, quadratic mean diameter (QMD) for all species, stand basal area, standing dead density and total canopy cover were higher and stand density was lower in old-growth stands. Total density of the old-growth Spruce-Fir stands ranged between 19.4 and 1186.9 stems per acre for trees greater than 5" dbh (diameter breast high) while stand basal area ranged between 60 and 240 ft²/acre (table 3). Mean

density and basal area was 322.0 ± 176.3 sd stems/acre and 240.3 ± 95.5 sd ft²/acre, respectively. Average dead tree density for all old-growth stands was 32.3 ± 38.8 sd stems/acre. Age varied from 196.9 ± 87.0 sd to 254.4 ± 100.6 sd years for non old-growth and old-growth stands, respectively. Maximum age was 556 years.

Density of the old-growth Lodgepole Pine stands ranged between 57.9 and 935.0 stems per acre for trees greater than 5" dbh (diameter breast high) while stand basal area ranged between 60 and 360 ft²/acre. Mean density and basal area was 335.2 ±

Table 2. Occurrence of various qualitative structural characteristics in both old-growth and non-old-growth Spruce-Fir and Lodgepole Pine (parentheses) stands. Declining trees were not evaluated in the 1990 sample and Multistory was not evaluated for Lodgepole Pine stands.

Response Large Trees		Large Snags			Canopy Closure	Declining Trees			
	OLD-GROWTH STANDS								
Present	601(273)	542(216)	549(236)	600	595(268)	303(223)			
Absent	4(3)	62(60)	55(39)	3	7(9)	77(34)			
Missing	0(3)	1(3)	1(4)	2	3(2)	225(22)			
	NON OLD-GROWTH STANDS								
Present	121(86)	101(65)	230(139)	422	384(238)	190(80)			
Absent	343(185)	363(206)	233(132)	422	384(36)	66(167)			
Missing	17(3)	17(3)	18(3)	17	18(0)	225(27)			

Table 3. Structural comparisons between old-growth and non old-growth Spruce-Fir and Lodgepole Pine stands. Values are means (upper) ± 1 sd (lower). Density values are stems/acre, basal area is in ft²/acre, QMD is in inches and Cover is percent.

Old Growth Status	Maxi- mum Age	Stand Density	Basal Area	Standing Dead Density	Quadratic Mean Diameter	Total Canopy Cover
			SPRU	CE-FIR		
Old	254.4	322.2	240.2	32.6	12.4	46.9
Growth	100.6	175.7	95.3	39.1	2.9	13.6
Non Old	196.6	459.5	266.2	25.4	10.5	37.7
Growth	87.0	216.3	132.6	37.8	2.3	16.9
		LO	DGEP	OLE PINE		
Old	148.9	336.9	184.3	20.7	10.5	44.3
Growth	87.1	165.9	63.4	33.2	1.9	15.2
Non Old	148.9	471.9	205.1	15.4	9.2	40.7
Growth	59.8	216.9	77.2	24.1	1.5	15.9

164.2 sd stems/acre and 184.0 ± 63.4 sd ft²/acre, respectively. Lodgepole Pine comprised most of the density and basal area in these stands while Fir and Spruce were subdominant in terms of density and basal area. Density of these three species was 251.6, 39.8 and 35.8 stems/acre while basal area was 140.8, 15.5 and 22.3 ft²/acre. Average dead tree density for all old-growth stands was 20.6 ± 33.3 sd stems/acre. Age of the largest trees in the stand averaged 177.0 ± 87.3 sd years. The maximum age of trees in the old-growth stands was 562 years (table 3). Coarse woody debris varied in terms of the amount of sound and rotten material on the ground but few differences were evident between old-growth and non old-growth stands in both cover types.

Generally most of the structural variables in the Spruce-Fir stands were highly intercorrelated (≤ 0.0001). For example, age was positively correlated with Spruce basal area and quadratic mean diameter, quadratic mean diameter of all species, and density of Fir and negatively correlated with Lodgepole Pine density, basal area and quadratic mean diameter.

Also, a number of significant correlations existed between the environmental variables and structural variables. For example, elevation was positively correlated (≤ 0.0001) with all structural variables except density, basal area and QMD of Lodgepole Pine. In the Lodgepole Pine stands, elevation was positively correlated with all structural variables but stand density and density of Lodgepole Pine which showed negative correlations. Likewise, there was a high degree of significant intercorrelation among the coarse woody debris variables, due in part because some of the variables such as total tons of coarse woody debris were calculated from other variables such as diameter and number of down woody stems, etc. Few coarse woody debris variables were significantly correlated with environmental characteristics.

All measured structural and coarse woody debris variables were included in a Stepwise Discriminant Analysis to determine which, if any, were important in discriminating the old-growth vs. non old-growth stands (table 4) in each of the cover types and, within old-growth stands, the condition classes. The variables that were important in distinguishing oldgrowth from non old-growth Spruce Fir stands were stand density, total cover, basal area of Lodgepole Pine, age, sound stem density, rotten stem density and diameter of rotten stems in order of decreasing importance. When only structural variables were used in the Discriminant Analysis, the classification accuracy improved for the old-growth stands and decreased the accuracy of the non old-growth stands. In the Lodgepole Pine stands only three structural variables were significantly related to the old-growth group structure (table 4). These variables include density of Spruce, quadratic mean diameter of Lodgepole Pine and basal area of Spruce, in order of decreasing significance. Quadratic mean diameter of all stems was the first variable in the model but was deleted because of its high correlation with other variables. Since there were no significant differences in the course woody debris between old-growth and non old-growth stands, these variables were not important in discriminating old-growth from non oldgrowth stands.

Of the total complement of structural variables, quadratic mean diameter of all species, age, total canopy cover, stand basal area, stand density, quadratic mean diameter of Lodgepole Pine and density of sound woody debris, in order of decreasing importance, were the only significant variables in discriminating the old-growth Spruce-Fir condition classes. Over 50% of the excellent category were classified correctly (table 5). However, substantial misclassification occurred in the good, fair, and marginal groups. It appears that adjacent groups in the lower three categories, i.e., good vs fair, are not easily distinguished on the basis of the measured structural variables. The important variables for distinguishing condition classes of old-growth Lodgepole Pine included, in order of decreasing importance, quadratic mean diameter of all species, Spruce basal area, age, Spruce density, Spruce quadratic mean

Table 4. Classification of old-growth vs non oldgrowth Spruce-Fir and Lodgepole Pine stands using Discriminant Analysis of structural and coarse woody debris attributes. Numbers in parentheses are percentages.

Status	Old-growth	Non Old-growth	
	SPRUCE-FIR		
Old-growth	427 (65.8)	114 (23.3)	
Non Old-growth	46 (29.9)	108 (70.1)	
	LODGEPOLE PIN	E	
Old-growth	200 (81.6)	6) 45 (18.4)	
Non Old-growth	19 (76.0)	9 (36.0)	

Table 5. Classification success of the condition classes Spruce-Fir (left) and Lodgepole Pine (right) old-growth stands using measured structural and coarse woody debris variables as discriminators. Values are number of stands (upper) and percentage of stands (lower) correctly classified in the group.

	Excellent	Good	Fair	Marginal
Excellent	15/2	8/0	0/2	4/0
n=27/4	55.6/50	29.6/0	0/50.0	15.0/0
Good	38/1	37/8	34/40	23/41
n=132/48	28.8/2.1	28.0/8.8	25.8/44.0	17.2/45.1
Fair	30/2	38/3	56/33	63/11
n=187/91	16.0/2.0	20.3/6.3	29.9/68.8	33.7/22.3
Marginal	10/2	19/13	28/101	94/121
n=151/98	6.6/2.9	12.6/5.4	18.5/41.7	62.3/50.0

diameter and total cover. Apparently the amount and size of Spruce are important in determining the condition class of the old-growth Lodgepole Pine. When variables associated with dead and down material on the forest floor were added to the structural variables in Discriminant Analysis, there was a reduction in classification accuracy. Apparently coarse woody debris attributes had little bearing on how field crews rated the condition of old-growth stands.

The Discriminant Analysis model showed little discrimination among the condition classes. Clearly, the measured structural variables were not the major criteria upon which the condition of the old-growth stands was based since the model that incorporated these variables did not account for much of the variance in the condition class data or show strong differentiation among class means. For condition class to be a useful variable, any further study of old-growth condition should be based on quantifiable attributes.

Unlike Spruce-Fir stands, Lodgepole Pine stands were rated as to their successional status with respect to a Spruce-Fir climax. There were 129 and 112 old-growth stands that were rated seral and climax, respectively. Twenty-eight stands were not rated for seral status. Some differences in structure were observed between seral and non seral categories

for old-growth stands. Age, standing dead density, and QMD, basal area, and density of Spruce and Fir were all significantly higher in seral stands. Density, basal area and QMD of Lodgepole Pine were significantly higher in climax stands. The higher density of standing dead in seral stands is primarily due to mortality of Lodgepole Pine. In the climax stands Lodgepole Pine is the dominant species while in Spruce-fir stands Spruce is dominant. Stand basal area, quadratic mean diameter of all species, quadratic mean diameter of Lodgepole Pine and sound coarse woody debris showed no difference between seral and non seral stands. Mean elevation of seral stands was almost 500 ft higher than climax stands. In the Abla Vasc habitat type, which is comprised of seral stands, 87% of the stands were determined to have a time gap between the current old-growth condition and the time when the old-growth Spruce-Fir would again occur. Of the 103 stands for which the gap length was estimated, 88% had a time estimate of more than 100 years.

SYNTHESIS

The present survey is an excellent first-step toward inventorying and understanding old-growth forests in Colorado. However, a thorough analysis of old-growth forests is lacking given concepts and methodology used here. Presently a set of minimum criteria are given for the definition and description of old-growth Lodgepole Pine and Spruce-Fir stands. These criteria are applied to the full range of environments over which a particular cover type occurs (see Model I, fig. 4). The minimum criteria do not allow for evaluation of old growth on harsh or unproductive sites (See area A, Model I) and condition class criteria are then applied to the range of environments in area B above the minimum criteria. Given this approach, the old-growth stands on the best and most productive sites will have the highest condition rating and those near the minima will have the lowest rating.

It is a well known ecological principle that vegetation composition and structure vary continuously across the landscape (Whittaker, 1970). Therefore, it is reasonable to expect that composition and structure of old-growth stands will vary in similar fashion. Given this, old-growth definitions should be based on the capabilities of a given site and condition-class rating should be based on spatial and temporal variation of structure and composition within that site type. One approach for dealing with the spatial variation in old-growth structure and composition would be to use the habitat type framework for defining old-growth forests. To account for temporal variation, successional relationships must be included in the model. In Model II the successional trajectory for vegetation development on each site type is presented along with the old-growth threshold (age) (fig. 5). Note that the model allows for succes-

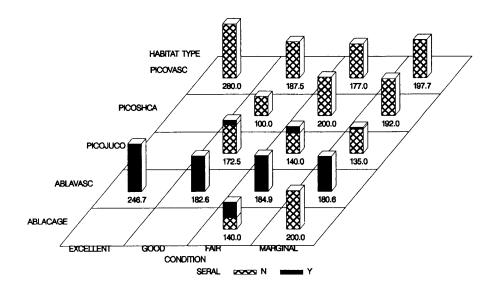


Figure 3. Stand basal area by habitat type, condition class and seral stage for old-growth Lodgepole Pine stands.

sional species forming temporary old-growth structure along the temporal gradient and that the oldgrowth threshold may not be the same on each site. Within each site or habitat type (including phase if necessary) and stage (age) of development the criteria for condition classes would be defined. While the model suggests 4 condition classes, it may be that 2 or 3 would suffice. Only by working with the concepts presented in Model II, can the full range of oldgrowth forests be truly evaluated. For example, low density, short statured stands on very harsh, dry sites can be evaluated for old growth in their own right and not compared to majestic old-growth stands on very mesic, productive sites. Habeck (1988) proposed that "an assortment of old-growth vegetation types, in all elevation zones, should be protected in perpetuity for their own sake" and that "old-growth forests have their own intrinsic value, that is, that the composite of living forms exhibiting mature

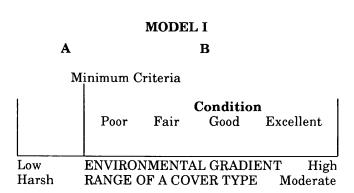


Figure 4. Current model used in defining old-growth forests. This model does not take into account variation in site potential and does not address the temporal variation that occurs in forest development.

stages of interaction with each other and their environment should be recognized and accepted as valued pieces of the landscape's total biotic diversity." Model II is a more complete conceptual framework within which to study old-growth forests and will

MODEL II

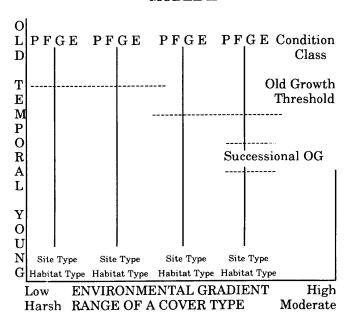


Figure 5. Proposed model of old-growth definition. This model incorporates variation in site potential and temporal variation in forest stands. Minimum criteria are developed for stands occurring on each site or habitat type along with temporal or successional threshold criteria. As seen on the right, successional species may form old-growth stands at points along any given trajectory.

permit a more comprehensive approach than is presently being used.

RECOMMENDATIONS FOR STUDY OF OLD-GROWTH FORESTS

The following comments are intended to be constructive in nature to improve future investigations of old-growth forests.

- 1. Stands selected for old-growth analysis should be homogeneous with respect to environmental characteristics, structure and composition. It becomes difficult, if not impossible, to assign meaning to relationships among biological variables and between biological and environmental variables when dealing with heterogeneous stands. For example, often in this study, stands would be assigned aspects that encompassed the entire azimuth range and/or up to four slope positions. In this situation relationships between stand characteristics and aspect or slope position are difficult to establish. Often stands would be so large as to include several habitat types and more than one cover type. In this situation, assignment of old-growth status or condition cannot be made with any degree of certainty. Also, determination of areal extent of old-growth stands is impossible. If the analysis of old-growth forests is to be placed in the context of habitat types, then the habitat typing skills of the field crews should be well honed. Homogenizing several habitat types in a given sample area results in substantial environmental heterogeneity which obscures true relationships with respect to distribution of old-growth conditions and with various environmental characteristics.
- 2. The fact that it was difficult to distinguish among the condition classes suggests that the methods of determining condition of old-growth stands needs refining. Perhaps four condition classes is too many. The analysis of the quantitative data taken in this survey suggests that the quantitative

- variables were not the major consideration in determining old-growth condition. The question arises as to the basis for the determining condition within the old-growth stands evaluated in this study. Determination of condition class should be soundly based on measurable criteria in the field rather than relying on subjective criteria.
- 3. The amount and extent of disturbance in old-growth stands should be evaluated and quantified. Invariably when discussing old-growth forests, the question of allowable disturbance arises. Since natural and anthropogenic disturbance is common in our forests, attempts should be made to quantify it for purposes of determining threshold limits for defining old-growth forests. In the case of past logging, the number of stumps/acre could be tallied. For fire, fire scars and dead and down burned logs could be quantified. Similar considerations could be given wind throw or insect disturbances.

Hopefully this report will provide some useful information for management or in developing further investigations into the nature of old-growth forests in Region 2. Only through careful and thoughtful investigative efforts can we develop sound inventory and classification methods for our diminishing old-growth forest resources.

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The Use of Digital Image Processing Techniques in Old-Growth Inventories¹

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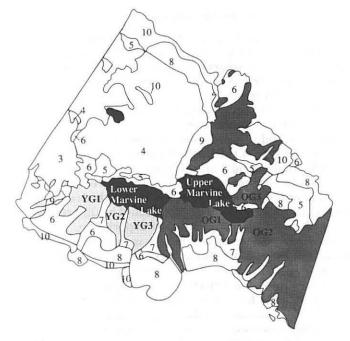
Abstract.—This paper describes a rapid, efficient and relatively inexpensive method of surveying large areas of spruce-fir forest in the Rocky Mountains in order to locate sites likely to consist of old-growth. Image processing techniques such as texture analysis, color-ratioing and vegetation indices successfully identified old-growth. The success of old-growth classification was evaluated in a geographic information system (GIS). Because of the high variance in spectral reflectance, old-growth cannot be classified on a pixel-by-pixel basis.

INTRODUCTION

The use of multispectral remote sensing techniques in the detection of old-growth forests is limited and has been largely concentrated in the Pacific Northwest. Intensive cooperative efforts to identify old-growth through the use of remote sensing and geographic information systems have been restricted to two large projects headed by The Wilderness Society (Morrison, 1990; Morrison et al., 1991) and Pacific Meridian Resources working in cooperation with the Forest Service Region 6 (Green and Congalton, 1990; Teply and Green, 1991).

Various image processing techniques were applied to Thematic Mapper (TM) imagery of the Marvine Lakes Valley in the White River National Forest in north-western Colorado. Prior on-site research by Veblen (1990, unpublished data) yielded a vegetation map which differentiates among landcover units (figure 1). The old-growth stands of interest in this study are referred to as OG1, OG2 and OG3. These stands were contrasted with the young post-fire stands referred to as YG1, YG2 and YG3. YG3 was the largest and least fragmented young-growth stand. The stands were ca. 300 to 400 meters in length and consisted solely of spruce (Picea engelmannii) and fir (Abies lasiocarpa). A spruce beetle epidemic in the 1940's killed many of the spruce trees in the old-growth stands.

The purpose of this study was to determine which image processing techniques best discriminate between old-growth and younger stands. The goal was not to obtain accurate estimates of old-growth



- Old-growth Engelmann spruce (*Picea*)/subalpine fir (*Abies*)

 Post-fire Engelmann spruce (*Picea*)/subalpine fir (*Abies*)
- 3 Post-fire Engelmann spruce/subalpine fir/aspen (Populus)
- 4 Douglas fir (Pseudotsuga)
- 5 Aspen (Populus)
- 6 Meadow
- 7 Avalanche/rockfall paths
- 8 Scree-talus
- 9 Blockfield
- 10 Bedrock

Figure 1. Vegetation units in the Marvine Lakes Valley, Colorado.

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forests but rather to guide ecologists to areas likely to consist of old-growth. The study focused on two structural differences between the forest types: 1) multi-storied (old-growth) vs. single-storied (young growth) canopies and 2) higher frequency of standing dead trees in old-growth. While the young post-fire

stands consisted predominantly of vigorously growing young trees, the old-growth stands consisted of both old trees as well as young trees regenerating within the numerous canopy gaps. It was hypothesized that the variance in old-growth spectral reflectance will be higher than that in young growth reflectance.

METHODS

Fieldwork

Ground measurements were made in order to facilitate explanation and verification of observations in the remotely sensed data. A LICOR line quantum sensor was used to measure intercepted photosynthetically active radiation (PAR) in the six coniferous forest stands (OG1, OG2, and OG3; YG1, YG2 and YG3) during July 1991. Canopy transmittance (or gap fraction) was obtained by dividing the belowcanopy PAR by the total incident above-canopy PAR.

Remote Sensing

It was hypothesized that differences in canopy structure of old-growth and young post-fire stands will give rise to differences in spectral reflectance. A Thematic Mapper image was radiometrically and atmospherically corrected and subsequently processed to enhance such differences in spectral reflectance. In order to examine the variance in spectral reflectances, individual digital number (DN) values along the lengths of the transects were extracted from TM bands 5 and 4 and subsequently plotted. Natural color and color-infrared images were displayed in order to evaluate the degree to which oldgrowth and young post-fire stands could be differentiated with minimal manipulation of digital data.

Other remote sensing techniques included texture analysis, color-ratio images and generation of vegetation indices. The texture channel was used to evaluate the spatial variability of the image and was created from TM band 5 by calculating the variance of the DN values within a three-by-three pixel moving window and replacing the central value in the window by the variance. Low values are usually characteristic of uniform areas and high values are indicative of edges and boundaries (Strahler, 1981).

Ratio images were prepared by dividing the DN value in one band by the corresponding DN value in another band for each pixel and then stretching the resulting values. Display of three bands in the order of red, green, and blue resulted in color-ratio images.

The remotely sensed vegetation indices (NDVI, NIR/R) were indicative of the amount of green vegetation present. The normalized difference vegetation index can be expressed as

$$NDVI = (NIR - R)/(NIR + R)$$
 (1)

where NIR refers to the near-infrared radiation measured in TM band 4 and R refers to the red wavelength radiation measured in TM band 3. Old-

growth stands were expected to have a lower mean DN value for the ratio bands NDVI and NIR/R (and therefore a darker coloration) than younger stands.

RESULTS AND DISCUSSION

Field Measurement of Gap Fraction

Due to the large number of fallen trees and canopy gaps in old growth, the variance in canopy transmittance data along the transects in the old-growth was higher than the variance in the relatively uniform, dense post-fire stands (figure 2). A one-way analysis of variance was performed on the old-growth and young growth data and the forest types were found to be significantly different (p=0.001).

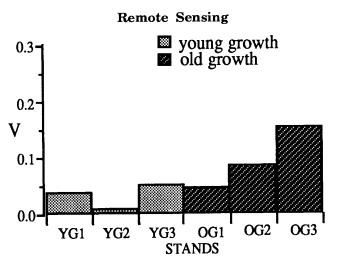


Figure 2. Average variance in gap fraction data for old-growth and young growth stands.

Figure 3 compares the average variance in DN values for the old-growth and young transects in both bands 4 and 5. In each case, the variance in oldgrowth stands was much higher than the variance in the younger stands and the two forest populations were found to be significantly different (p = 0.002, p = 0.000, respectively). These differences in variance were enhanced through image processing. Simple display of stretched radiometrically and atmospherically corrected image bands to yield natural color and color-infrared images did not allow for discrimination between the old-growth stands and young post-fire stands. However, in the texture channel, NDVI, NIR/ R and color-ratio images, the high old-growth variance resulted in a mixture of pixels with various color tones whereas the young post-fire stands were indicated by pixels of a uniform tone. In the texture channel, large continuous post-fire stands had a relatively uniform dark tone while old-growth appeared more mottled (figure 4).

In the NDVI and NIR/R images, young growth pixels had higher DN values than old-growth pixels

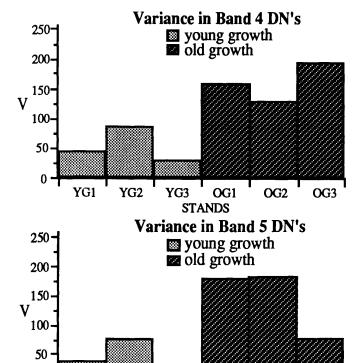


Figure 3. The average variance in DN values along the transects in old-growth and young post-fire stands in TM bands 4 and 5.

STANDS

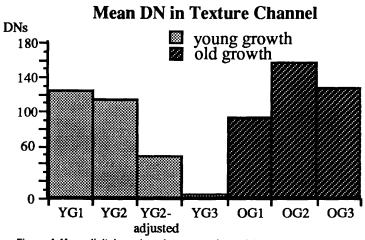


Figure 4. Mean digital numbers in texture channel. YG1 and YG2 have abnormally high values since a large majority of the pixels were detected as edge due to the narrow widths of the stands.

Table 1. Results of ANOVAs performed on gray-scale image populations.

Comparison of Old-Growth and Young-Growth Populations: Results of Analysis of Variance

F-ratio	Probability
12.534	0.001
5.496	0.023
15.319	0.000
15.257	0.000
	5.496 15.319

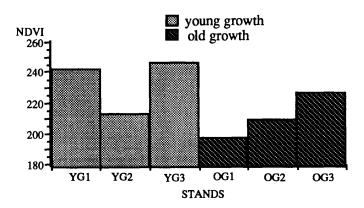


Figure 5. Average NDVI values per stand. Post-fire stands have bright tones and old-growth stands have dark tones.

and were therefore indicated by bright color tones (figure 5). Old-growth consisted of a mixture of dark and bright pixels.

For statistical verification, an analysis of variance was performed on each of the gray-scale image comparisons discussed thus far (table 1).

The display of color-ratio bands 5/4, 4/3, and 7 in the order of red, green and blue resulted in the best differentiation and color contrast within the forested stands. Young post-fire stands appeared bright green. While the majority of old-growth consisted of dark green pixels interspersed by bright green pixels, the spectral variance resulted in additional pixels of a wide variety of colors.

GIS Evaluation

Because of the extensive overlap in the DN ranges of old-growth and young growth stands, it was not possible to quantitatively evaluate the success of the remote sensing techniques in terms of the absolute percentage of pixels correctly identified as oldgrowth. Within each individual image, the success of old-growth differentiation was determined not by the range of the DNs but by the frequency distribution of pixels within the overlapping DN ranges. In the color-ratio, NDVI and NIR/R images, the majority of pixels in the old-growth subscenes had low to moderate DN values while histograms of the DN values of post-fire pixels revealed strong peaks at high DN values. A histogram of the texture channel revealed a peak at DN=1 for the young growth pixels and a slightly higher frequency of old-growth pixels in the moderate DN ranges.

The spatial distribution of the pixels on the ground should also be considered in determining the nature of the forest stand. In the color-ratio, NDVI and NIR/R images, bright pixels characteristic of vigorous young growth were clumped together in the young post-fire stands but were scattered throughout the old-growth stands. In the texture channel, dark pixels characteristics of uniform areas occurred in clumps in the post-fire stands and were more dispersed in old-growth stands.

CONCLUSIONS

Digital image processing techniques were successful in differentiating old-growth spruce-fir stands from young post-fire stands in the Rocky Mountains. The remote sensing techniques described in this paper will be valuable during the initial phases of large-scale old-growth inventories as well as in the monitoring of future stand conditions. This paper described a rapid, efficient and relatively inexpensive method of surveying large areas of continuous forest in order to locate sites likely to consist of old-growth. The remote sensing techniques should be used only as a screening mechanism by which unnecessary ground inventories on sites with little old-growth potential are avoided. On-site evaluations in the field are vital in determining the final status of the stands.

It should be noted that the spectral signal varies with old-growth stand types and with site conditions. The spectral signature of an old-growth spruce-fir stand differs from that of an old-growth ponderosa pine stand. Similarly, old-growth stands on mesic sites have slightly different signatures than stands on dry sites. Digital elevation models (DEMs) can be incorporated into the data base to differentiate north-facing slopes from south-facing slopes. Familiarity with the cover type and site conditions allows the operator to distinguish between variations in spectral signature.

ACKNOWLEDGMENTS

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* This paper is an excerpt from a masters thesis titled The Use of Remote Sensing in the Detection of Old-growth Spruce-fir Forests in the Rocky Mountains (Elizabeth M. Nel, graduation date: May, 1992).

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Structure and Dynamics of Old-Growth Engelmann Spruce-Subalpine Fir in Colorado¹

Alan J. Rebertus,² Thomas T. Veblen,³ Lynn M. Roovers,³ and Joy Nystrom Mast³

The development of old-growth spruce-fir forests in Colorado is highly variable and depends on disturbance history and site conditions. On relatively favorable post-fire sites, spruce sometimes develops a bimodal or discontinuous age structure that persists for >500 years. Some sites that were identified as high-quality old growth, physiognomically, were actually post-fire stands in a transition old-growth stage. On less favorable sites it appears that post-fire recruitment of spruce and fir is more gradual, and allaged populations develop. Fire, spruce beetle outbreaks, and windthrow all play an important role in shaping the development of old-growth spruce-fir forests, and ultimately in their demise. We need more long-term mortality studies to better understand the role of disturbance in old growth and implications for designating old-growth reserves.

INTRODUCTION

Old-growth Engelmann spruce (Picea engelmannii [Parry] Engelm.)-subalpine fir (Abies lasiocarpa [Hook] Nutt.) forests in Colorado have recently been the subject of considerable interest and controversy. The issue came to the forefront in 1989 when Louisiana Pacific Corporation was granted logging rights in a 1000-ha stand of prime old-growth spruce-fir in Bowen Gulch, west of Rocky Mountain National Park (Fig. 1). Protest led to reevaluation, and eventually a cooperative effort by environmentalists, the Forest Service, Louisiana Pacific, and Congress culminated in pending federal designation of 2590 ha of Bowen Gulch as an addition to the Never Summer Wilderness Area. What characteristics make Bowen Gulch and similar stands high-quality old growth? How do old-growth spruce-fir forests develop and what are the stand dynamics associated with this development? These are basic questions that need to be considered for designating and managing old-growth forests.

Definitions of "old growth" are rather elusive and depend on the particular forest type and the classifier's purpose or goals. Most management and recreational objectives emphasize a physiognomic definition of old growth. For example, in old-growth Douglas fir (Pseudotsuga menziesii)-western hemlock (Tsuga heterophylla). the characteristics most often associated with old growth are: an abundance of large, old trees, snags, logs, and a multi-layered canopy (Franklin et al. 1981, Old-Growth Definition Task Group 1986). These same characteristics, among other things, have been identified as key old-growth elements in many other forest types, including oldgrowth spruce-fir in the Rockies. In Colorado, the Forest Service and Colorado Environmental Coalition have been using various adaptations of an old-growth scorecard that was developed in the mid 1980s for use in subalpine forests of the Medicine Bow Mountains, Wyoming (U.S. Forest Service [1984?]; Smith 1990; Lowry, this volume) Basically, these survey procedures rate the quality of old growth based on structural characteristics similar to those identified above.

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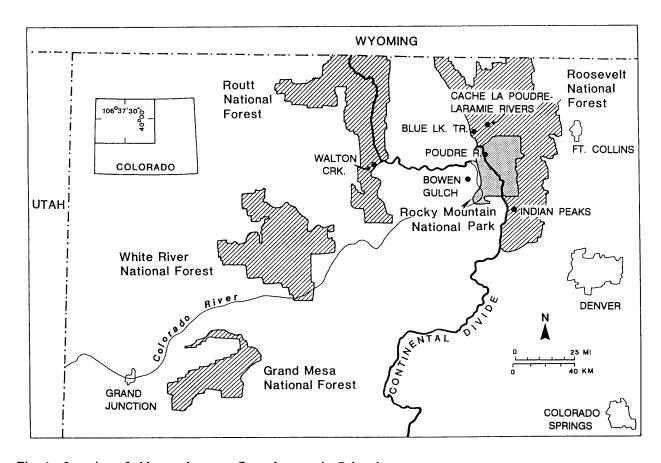


Fig. 1. Location of old-growth spruce-fir study areas in Colorado.

Another way to define "old growth" is based on the process of stand development. For example, Oliver and Larson (1990) defined "true old growth" as "stands composed entirely of trees which have developed in the absence of allogenic processes [stand-initiating disturbances]." Stands approaching this stage but still composed of old, post-fire relic trees, are considered "transition old-growth stands." A similar process-oriented definition was proposed by Hayward (1991), and is based on population dynamics and rates of regeneration and mortality rather than static processes. Hayward defined old growth as a "forest in which the rate of tree regeneration and the age structure are influenced by processes in the stand rather than being correlated to the timing of a major disturbance that influenced the majority of the stand." Ironically, the processoriented definitions of old growth do not necessarily complement the physiognomic definitions. For example, classic old-growth Douglas fir-western hemlock forests (sensu Old-Growth Definition Task Group 1986) are not in a true old-growth stage (sensu Oliver and Larson 1990), because in most areas Douglas fir is seral to

western hemlock (Sprugel 1990). In the following review of old-growth spruce-fir forests in Colorado, we will demonstrate the need to understand and integrate the physiognomic definitions of old growth and the processes that generate them. We emphasize that old-growth definitions should be multifaceted: physiognomic quality should be assessed based on particular goals, whereas an understanding of stand dynamics can reveal how the forest developed into old growth and possibly how it will change in the future. If large areas of spruce-fir are designated as old-growth preserves, such knowledge is important for planning and understanding the natural role of disturbance in the subalpine zone.

SUBALPINE FORESTS IN COLORADO

Over one million hectares of the subalpine zone in Colorado are characterized by Engelmann spruce and subalpine fir, with lesser amounts of aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), limber pine (*P. flexilis*), and/or

bristlecone pine (Pinus aristata) (Alexander et al. 1984, Alexander 1987, Whipple and Dix 1979, Peet 1988). Spruce-fir dominated stands occur on all but the most xeric sites above 3100 m, and in cool, sheltered valleys at elevations as low as 2500 m. The relative dominance of the two canopy tree species and the understory composition vary substantially over a gradient from excessively moist to xeric sites (Peet 1981). Open bog forests occur on the limited areas of level, poorly drained terrain above 2800 m. The mesic spruce-fir type occurs on cool, sheltered, but well-drained sites above 2700 m and is one of the most widespread forest types in the subalpi zone. Open slopes above 3100 m are typically characterized by Peet's (1981) xeric spruce-fir type, with varying amounts of lodgepole and limber pine. Towards lower elevations, the spruce-fir types give way, often along abrupt fire-induced boundaries, to lodgepole pine-dominated forests. A more complete review of the tremendous geographic and site variation in spruce-fir communities can be found in Peet (1981, 1988), Alexander (1985), and Allen and Peet (1990).

DEVELOPMENT OF OLD-GROWTH STANDS

Fires in the subalpine forests are typically standdevastating, resulting in the extensive exposure of mineral soil and initiating the development of new stands. Depending on site conditions, spruce and fir may share the post-fire site with shade-intolerant species such as lodgepole pine, limber pine, and quaking aspen. Lodgepole pine and limber pine seedlings are physiologically well adapted to grow under the dry conditions of the post-fire environment. Lodgepole pine rapidly colonizes from serotinous cones, limber pine from seed dispersal by nutcrackers, and aspen from suckers. Bare mineral soil exposed by fire is also more favorable to seedling establishment of the pines and spruce than to fir (Alexander 1987, Whipple and Dix 1979, Peet 1981, Knapp and Smith 1982). Depending on the availability of seed, spruce usually colonizes synchronously with, or soon after any shade-intolerant species present, but fir often does not establish abundantly until 50-150 years after stand initiation (Veblen 1986a, Rebertus et al. 1991). The timing and spatial distribution of spruce and fir colonization is strongly affected by the size of the burn and the location of seed sources with respect to prevailing winds (Peet 1981, Tomback et al. 1990). Usually the pines and aspen

are seral to spruce and fir, although the patterns vary markedly according to habitat variation and species availability (Whipple and Dix 1979; Peet 1981, 1988; Romme and Knight 1981; Veblen 1986a; Rebertus et al. 1991). On exceptionally harsh sites in the subalpine zone, the usually seral pines or aspen may form self-replacing stands (Moir 1960, Peet 1988, Rebertus et al. 1991). In contrast, on more mesic sites the replacement process may be accelerated (Romme and Knight 1981, Rebertus et al. 1991).

The development of spruce-fir stands has been examined by inference from static age and size structures of stands believed to represent different stages of stand development (Whipple and Dix 1979, Peet 1981, Veblen 1986a, Aplet et al. 1988). The use of static age and size structure for inferring patterns of stand development in spruce-fir forests is problematic for several reasons. First, age data is often imprecise (see Norton and Ogden 1990). With spruce and fir, in particular, there are problems with (1) lack of data on trees with rotten centers, (2) large variation in the difference between total age and age at coring height due to the extreme suppression of spruce and fir seedlings, and (3) difficulty in estimating rings-to-center, especially for trees that were initially suppressed. Second, size structure is not a suitable substitute for age structure because of the poor relationship between size and age in these forests (Veblen 1986a). The chronosequence approach, of course, is based on the assumption that any site differences among the stands selected are unimportant in explaining the differences in size and age structure. Given this untested assumption, and the lack of long-term studies of stand development based on remeasurement of permanent plots, models of stand development cannot be expected to be precise descriptions of the changes that have occurred at any specific site. Nevertheless, there are sufficient data available to generally describe the pattern of stand development expected following a standdevastating fire. The following description of general trends in the development of a spruce-fir post-fire stand is conceptually based on Oliver's (1981) general model of post-disturbance stand development and synthesizes the interpretations of numerous studies in the Colorado subalpine zone, mostly from the Front Range. There is a great need for complementary studies elsewhere in the state.

Aplet et al. (1988) applied Oliver's general

model of post-disturbance stand development to five stands of spruce-fir forest in the Medicine Bow Range. Their presumed chronosequence spans c. 400 years, from stem initiation to old-growth stages. All stands were assumed to have been initiated by wildfire, but they did not present any evidence of subsequent disturbance by fire or beetle outbreak. Their stands represented a substantial range of aspects, which in other studies (Whipple and Dix 1979, Peet 1981, Veblen 1986a) has been shown to have a major influence on the pattern of stand development. Hence, their stands may not represent an actual post-fire sequence. Nevertheless, their model is a useful approximation of some general trends in post-fire stand development of spruce-fir stands for sites lacking pines.

The early colonization of spruce on post-fire sites results in a peak in the age frequency distribution that is recognizable in some spruce-fir forests for >500 years (Figs. 2 and 3). According to Aplet et al. (1988), after 100-250 years of initial recruitment, spruce enters a stem exclusion phase that may last > 100 years. Fir seedlings, which establish more effectively on litter than do spruce seedlings (Knapp and Smith 1982), become increasingly more abundant during the first 100-200 years after fire. A wave of fir mortality typifies the third century of stand development as the oldest fir approach their maximum longevity (Aplet et al. 1988). Fir occasionally live >400 years, but most trees suffer from heart rot and die when they are much younger (Alexander 1987). As the older fir die, however, they are replaced by the abundant understory fir so that in stands > 250 years old, fir typically has an all-aged and all-sized structure (Whipple and Dix 1979, Peet 1981, Veblen 1986a, Aplet et al. 1988, Veblen et al. 1991a). According to Aplet et al. (1988), a second wave of spruce regeneration establishes 200-350 years after fire as the canopy opens up from treefalls of the original spruce and fir colonists (Fig. 3). This results in a bimodal age structure for spruce which persists for several centuries and is consistent with the age structures of some old-growth stands (Fig. 2A-B, H; Day 1972, Whipple and Dix 1976, Peet 1981, Stromberg and Patter 1991, Roovers 1992). Bimodal diameter and height structures are also evident in some old-growth stands within particular sites (controlling for aspect, moisture conditions, etc...); however, size parameters vary with site and degree of suppression, so distributions tend to be more continuous when data are pooled from several

different sites (Fig. 4, Roovers 1992).

In other old-growth stands, however, spruce age distributions are not clearly bimodal. They sometimes fit the negative exponential patterns associated with all-aged, self-replacing populations (Whipple and Dix 1979, Veblen 1986a, Veblen et al. 1991a). In many old-growth stands, spruce has a discontinuous or sporadic age frequency distribution in age classes greater than c. 250 years (Fig. 2C, 2F, 2G). In such cases it is not clear if two separate cohorts can be identified as Aplet et al. (1988) postulate as the general pattern.

There have been too few age structure studies of spruce-fir relative to the large amount of variation in developmental pattern expected from site variation to fully evaluate the applicability of the two cohort model of Aplet et al. (1988). It may be that on better quality sites with more rapid rates of stocking, the two cohort pattern holds true, but on less favorable sites the distinction between the postfire cohort and the stand reinitiation cohort may be blurred. On less favorable sites (either too dry or too wet to allow rapid stand development), an allaged population of spruce appears to develop without passing through a stage of two distinct cohorts (Whipple and Dix 1979, Peet 1981, Veblen 1986a). For example, in Poudre River Trail (Fig. 2C), the oldest trees in the stand have rapid initial growth and appear to be the initial colonists following a fire c. 450 years ago. Although the rate of establishment for spruce appears to have increased over the most recent 150 years, recruitment has been continuous throughout stand development. Likewise, in Bowen Gulch the age structure of spruce was bimodal on north and south aspects, but was relatively continuous on a boggy site (Roovers 1992).

If we consider the scorecard criteria used to evaluate old-growth spruce-fir stands in Colorado and Wyoming, the highest quality old growth is characterized by large-diameter trees (mainly spruce), abundant large snags and logs, and multistoried vegetation. On xeric or very wet sites, where presumably a more all-aged population develops, the quality of old growth probably develops asymptotically. On more favorable sites in the Front Range, however, we would expect the quality of some old-growth attributes, like density of large trees, to peak c. 500-700 post-fire (Fig. 5). As the original post-fire cohort of spruce reaches maximum longevity, in all likelihood there will

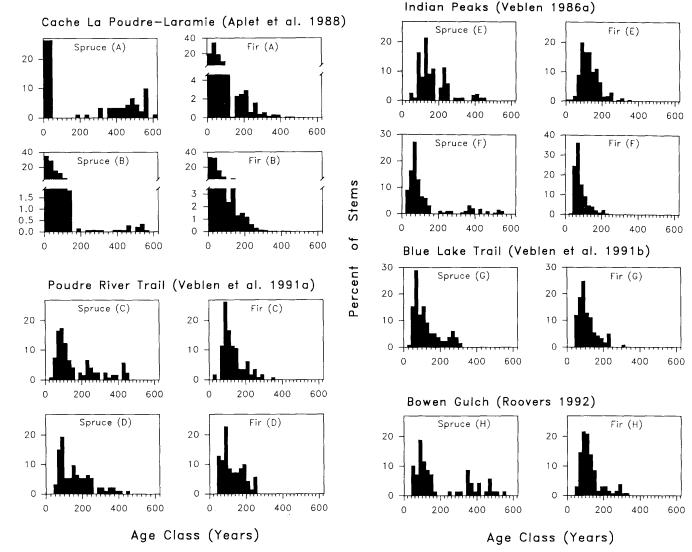


Fig. 2. Age structures for various old-growth stands in Colorado (A-H) reported in the literature (© Ecological Society of America, The Journal of Biogeography, The Torrey Botanical Club). For comparison, all have been expressed as percent of total stems. For (A) and (B), Aplet et al. (1988) used stratified random samples of trees, c. 150-210 trees per site; as well as random samples of stems <5 cm dbh, including seedlings. All other sites include only trees >4 cm dbh, and sample sizes range from 69-257. Ages are at coring height: <10 cm above ground for A and B, and at 40 cm for C-H.

never be as many big trees at one time in any subsequent stage. At Bowen Gulch, for example, most spruce in the oldest cohort display rapid initial growth, indicating they are of post-fire origin (Roovers 1992). Bowen Gulch has an exceptionally high density of large trees, but this appears to be a temporary condition characteristic of a transition old-growth stage, rather than true old-growth (sensu Oliver and Larson). As the post-fire cohort begins to die out, there may be few large spruce to replace them until the second cohort reaches maturity (Fig. 5). Likewise, if we consider large snags and logs, this parameter probably lags behind the density of large trees. As the original cohort dies out, large snags and then large logs will become increasingly abundant c. 500-800 years post-fire. The final old-growth attribute, maximum

Stems

ð

Percent

canopy stratification, is best described by a continuous and wide range of canopy heights, with moderate class diversity. In old-growth spruce-fir forests, maximum stratification is represented by a negative exponential distribution of heights from ground to 40 m (Fig. 4). Maximum stratification is probably attained gradually after c. 300 years of development as fir, and then the second cohort of spruce, become established in openings created by treefalls of the dominant canopy spruce (Fig. 5). As the original spruce colonists disappear, however, so will the upper stratum. The second cohort of spruce will probably rapidly fill these positions.

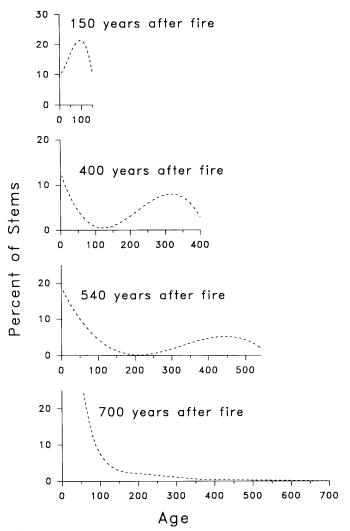
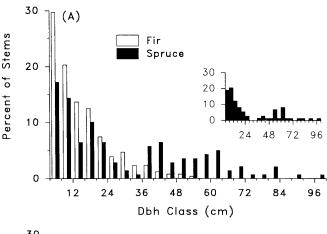


Fig. 3. Hypothetical post-fire development of age structure for Engelmann spruce (adapted from Day 1972 and Aplet et al. 1988).

THE FATE OF OLD GROWTH

Development of Mid and Late Old-Growth Stages

When the original post-fire cohort of spruce gradually disappears (c. 700 years post-fire), it is thought that the bimodal structure will gradually assume something approaching a reverse-j pattern (Fig. 3) (Day 1972, Peet 1981, Aplet et al. 1988). Although no one has demonstrated this development in a chronosequence, reverse-i or irregularly allaged populations are evident in many old-growth stands (Whipple and Dix 1979, Peet 1981, Shea 1985, Alexander 1987) (Fig. 2). Small peaks in the diameter or age distributions are thought to result from recruitment following disturbances and past variations in mortality (Miller 1970, Shea 1985, Alexander 1987). In old-growth spruce-fir forests periodically affected by spruce beetle outbreaks, wave-like oscillations in basal area are expected (Schmid and Hinds 1974).



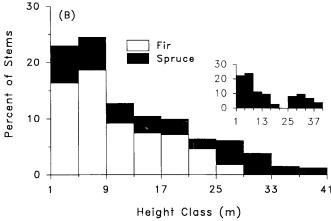
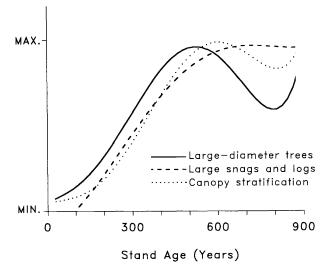


Fig. 4. Dbh (A) and height (B) structure for Engelmann spruce and subalpine fir in old-growth forest, Bowen Gulch, Colorado (after Roovers 1992). In (A) the percent of total stems for each species is given for comparison (n=139 for spruce and n=256 for fir). In (B) the percent of total stems for both species (n=391) is given to show the overall stratification of the canopy. The inset graphs are diameter and height for spruce alone in stands with southerly aspects (n=73 and 71, respectively).

Disturbance and the Landscape Mosaic

A popular notion with the public is that a primeval old-growth spruce-fir forest, stable and unchanged for centuries, covered most of Colorado's subalpine zone prior to European settlement. However, historical records and dendroecological evidence indicate that recurrent coarse-scale disturbances (fire, spruce beetle epidemics, and blowdowns) were an integral part of subalpine forest dynamics: "The coniferous forests of the Rocky Mountains can best be described as disturbance phenomena. Owing to the agencies of fire, wind and insect attack, these forests are periodically destroyed in a patchwork manner, resulting in a mosaic of stands of differing ages and



Relative Magnitude

Fig. 5. Hypothetical changes in the magnitude of key physiognomic attributes in old growth during the first 900 years of post-fire stand development, Colorado Front Range. Patterns will vary depending on site and disturbance history. See text for further discussion.

histories" (Peet 1981). Lowry (this volume) estimated that only 12.4% of the spruce-fir in the Arapaho and Roosevelt National Forests was old growth in 1992.

The fire regime of subalpine spruce-fir forests is not known with certainty, but the existing pattern of stand ages suggests that spruce-fir forests were subject to lightning-caused crown fires at intervals ranging from 200-400 years (Peet 1981). Many stands in the subalpine zone of the Colorado Front Range are of post-fire origin from c. mid 1700s (Veblen 1986a, Rebertus et al. 1991). In subalpine forests of Rocky Mountain National Park, Colorado, there was an estimated 1 fire >4 ha per 8100 km² per year, prior to 1870 (Clagg 1975, in Romme and Knight 1981). Stand-devastating crown fires were most common, but many fires were probably patchy, skipping across valleys, or burning as surface fires and crowning out wherever fuel and topography were favorable (Romme and Knight 1981, Baker and Veblen 1990). Light surface fires may have been common in open spruce-fir forests near timberline, where fuel loads were less (Baker and Veblen 1990). Standdevastating fires probably ranged from a few hectares to conflagrations covering tens of thousands of hectares, similar to the 1988 Yellowstone fires. Some areas undoubtedly remain unburned for many centuries or millennia, either by chance or because local physiography inhibits fire

(Romme and Knight 1981). There is some evidence of differences in fire frequency over moisture gradients in the Sangre de Cristo Range in southern Colorado compared to the Medicine Bow Range in southern Wyoming (Romme and Knight 1981, Allen and Peet 1990). The illumination of such patterns in the disturbance regime will help us understand where old-growth stands are likely to occur and how long they will persist.

Spruce beetle (Dendroctonus rufipennis) outbreaks may be as significant as fire in the development of spruce-fir forests (Baker and Veblen 1990). There have been five or six major outoreaks that have caused widespread mortality in the southern Rockies since the mid 1800s (reviewed by Baker and Veblen 1990). Spruce beetles may kill up to 99% of the spruce trees greater than c. 20 cm dbh, but do not attack subalpine fir or small spruce (Schmid and Frye 1977). Hence, the structure of old-growth forests may be severely altered (Schmid and Hinds 1974, Veblen et al. 1991b). The most serious outbreak of this century occurred in the 1940s and was probably triggered by debris from a severe windstorm in 1939 (Hinds et al. 1965). In White River National Forest 290,000 ha were devastated and variable amounts of damage occurred from Grand Mesa National Forest in the southwest to Arapaho National Forest in north-central Colorado (Hinds et al. 1965, Cahill 1977, Veblen et al. 1991b). Historical records, photographs, and dendroecological evidence also indicate that another major epidemic affected extensive areas of Colorado c. 1850-1880 (Baker and Veblen 1990, Veblen et al. 1991b). During this outbreak, 10-25% of the mature spruce died in the White River National Forest, and 25-40% of the mature spruce on the Grand Mesa were killed (Sudworth 1900a,b; in Schmid and Frye 1977). We know very little about long-term stand development following such outbreaks.

Wind disturbance in spruce-fir forests has been well documented (Alexander and Buell 1955). Blowdowns involving multiple treefalls may add to the mosaicism of spruce-fir stands, but this has not been well documented (Peet 1981). In 1973 a windstorm in Hidden Valley, Rocky Mountain National Park, severely damaged c. 15 ha of subalpine forest (Veblen et al. 1989). Old-growth stands studied by Veblen et al. (1991a) along the Poudre River were classified as 65-92% blowdown (i.e., gaps involving 3 or more canopy trees);

however, these were more fine-scaled windthrow events than the large block affected at Hidden Valley. The 1939 blowdown in White River National Forest and several of the windthrow events documented by Veblen et al. (1991a) appear to have been caused by regionally extensive windstorms.

Under a natural disturbance regime, subalpine forests were probably characterized by a mosaic of stands in various stages of recovery from disturbance, and old growth was just one part of the larger forest mosaic (Peet 1981, Romme and Knight 1981). This mosaic was constantly changing and highly variable from place to place, so the extent of presettlement old-growth forest is uncertain. Green and Van Hooser (1983) classified 75% of spruce-fir forests in Colorado as "sawtimber" in 1977, the majority of which was considered overmature (Alexander 1987). The current subalpine landscape is perhaps more homogeneous (in terms of stand age) than in the presettlement era, mainly due to the synchronizing effect of very extensive, regional disturbances (e.g., fires in the mid 1700s, beetle outbreaks in the mid to late 1800s).

Coexistence of Spruce and Fir

In the central and southern Rockies, spruce and fir coexist as dominants in old-growth stands. In these forests, subalpine fir seedlings and trees less than c. 8 cm dbh are generally severalfold more abundant than those of spruce. In contrast, Engelmann spruce dominates the older age classes (>250 years), but is often poorly represented in the younger age classes (Whipple and Dix 1979, Peet 1981, Veblen 1986b, Alexander 1987, Roovers 1992). The greater abundance of young subalpine fir in old-growth stands would imply a shift in dominance from Engelmann spruce to subalpine fir if the two species have similar mortality rates. Peet (1981) suggested that coexistence of spruce and fir is maintained by disturbance because, in the hypothesized absence of disturbance, the greater regeneration of fir in the understory would lead to the gradual elimination of spruce within c. 1000 years. The hypothetical result of this shift, extensive subalpine firdominated stands, however, is not found in the subalpine zone of Colorado (Peet 1981, Veblen 1986b).

The mechanisms permitting the coexistence of

spruce and fir are still not clear, although they have been the subject of much interest and debate (Fox 1977, Shea 1985, Veblen 1986b, Aplet et al. 1988). Three non-mutually exclusive explanations for the coexistence of spruce and fir were outlined by Veblen (1986b): (1) regeneration niche differences, (2) nonequilibrium coexistence, and (3) different life histories.

Differences in the regeneration niches of spruce and fir are evident in the establishment requirements for seedlings. Spruce seedlings establish best on bare mineral soil exposed by disturbances, whereas fir regeneration is better in heavy litter (Alexander et al. 1984, Alexander and Shepperd 1984, Knapp and Smith 1982). Where soils are very waterlogged, spruce also establishes well on logs. Although fir tends to be more abundant in the understory, both species are equally shade tolerant (Knapp and Smith 1982). Fir tends to have higher rates of photosynthesis under low light levels, however. In the Medicine Bow Range of Wyoming, Fox (1977) found that saplings of spruce and fir were more abundant in treefall gaps created by the alternate species, suggesting that niche differentiation in the regeneration phase would lead to reciprocal replacement, or alternation of species. Under this model, compositional equilibrium would be maintained by fine-scale treefalls. Shea (1985) found that spruce seedlings were more common under canopy fir. Fir seedlings were also more common under canopy fir in wet sites, but equally common under canopy fir and spruce in more xeric sites. Likewise, Veblen (unpublished data) found weak and inconsistent support for reciprocal replacement between spruce and fir in old-growth stands in the Front Range.

According to the nonequilibrium hypothesis, relatively frequent, coarse-scale disturbances (fire, blowdown, or spruce beetle epidemics) prevent the competitive exclusion of Engelmann spruce by subalpine fir (Day 1972, Peet 1981, Veblen 1986b. Aplet et al. 1988). Spruce tends to establish more abundantly on bare mineral soil exposed by fire compared to fir. Evidence that spruce regeneration is favored by blowdowns and spruce beetle epidemics is less convincing: some new seedlings may become established, but the primary response is the accelerated growth of already established spruce and fir in the understory (Veblen et al. 1989, Veblen et al. 1991b). After a severe canopy disturbance, dominance initially shifts toward fir. If enough spruce survive or re-establish, however,

spruce may eventually recapture its lost dominance (Peet 1981, Veblen et al. 1991b).

Finally, according to the hypothesis of different life histories, the greater abundance of young subalpine fir in the understory of old growth is balanced by a substantially lower death rate among adults of Engelmann spruce (Oosting and Reed 1952, Day 1972, Shea 1985, Veblen 1986b). In an old-growth stand studied by Veblen (1986b), fir accounted for only 37% of canopy trees but 76% of fallen trees. The consistently lower frequency of Engelmann spruce as treefalls and its greater longevity imply a lower mortality rate for canopy trees. In Colorado, spruce can live >600 years; whereas fir rarely surpass 350 years.

Aplet et al. (1988) suggested that the second cohort of spruce that establishes late in stand development ensures the continued presence of both species in the canopy for at least another 500 years. Although the fate of the second cohort is less certain, they believed that continued fir mortality would allow relatively continuous spruce recruitment, but also conceded that the second cohort could remain relatively even-aged until the next period of spruce mortality. The continued autogenic development of extensive stands of old growth for several generations is largely a moot point, however, given the susceptibility of oldgrowth stands to extensive windthrow, beetle attack, and fire (Peet 1981, Baker and Veblen 1990, Veblen et al. 1991a,b).

It is likely that all three factors--differences in regeneration niches, coarse-scale disturbance, and different life histories--all contribute to the continued coexistence of spruce and fir (Veblen 1986b). The relative importance of these mechanisms undoubtedly varies both spatially and temporally.

Mortality Patterns Over Time

Frequently the timber industry and many silviculturalists contend that old-growth spruce-fir forests will only become more decadent with time, i.e., they are a perishable resource (LeBarron and Jemison 1953). The degree to which old-growth forests persist is a critical issue in the preservation of extensive stands, such as Bowen Gulch, and can only be understood by long-term mortality records. Mortality patterns in old-growth spruce-fir in Colorado have been explored using four methods:

(1) inference from stands of different ages (chronosequence), (2) re-measurement of permanent plots, (3) estimating dates of tree death by cross-dating snags and logs, and (4) release frequencies.

The chronosequence approach is probably the least reliable method for documenting mortality patterns. Age and size structures from stands of different ages often provide clues of mortality patterns with development, but slight differences in site (e.g., topographic position) may result in very different trends (e.g., Whipple and Dix 1979, Veblen 1986a). Aplet et al. (1988) used the basal area of live and dead-standing trees and logs from stands of various ages to infer mortality patterns through 600 years of stand development. The dead basal area for fir was maximum in a stand c. 275 years of age, and for spruce at 375 years of age. These hypothetical waves of mortality were often supported by their age structure data, but changes in live basal area along the chronosequence may merely reflect site differences. Changes in dead basal area may reflect slightly different disturbance histories, rather than a trend through stand development.

The repeated censusing of permanent plots is the most accurate and reliable method for documenting mortality and recruitment patterns in old growth, but few long-term studies exist. In 1981, permanent plots were established by T. Veblen in old-growth spruce-fir stands near the Rocky Mountain Biological Station and Brainard Lake. Monitoring of tree death in 6 permanent plots of old growth containing > 2000 trees (>4 cm dbh) over 9 years indicated annual average death rates of 0.1 to 0.4% for spruce and fir; however, the number of tree deaths was too small for interspecific comparisons. Cross-dating of snags in the plots suggested that mortality for spruce has been highly episodic in the past. In the Fraser Experimental Forest, a 3.2-ha permanent plot in old-growth spruce-fir has been monitored since 1944, but the small size of the plot in relation to surrounding silvicultural treatments complicates the interpretation of mortality data (Alexander and Watkins 1977).

Mortality patterns can also be documented directly by cross-dating intact snags and logs with a chronology developed from live trees. Trees with bark and >60 intact outer rings, usually can be cross-dated, and an estimate of the date of death can be determined. Even if the tree lacks bark,

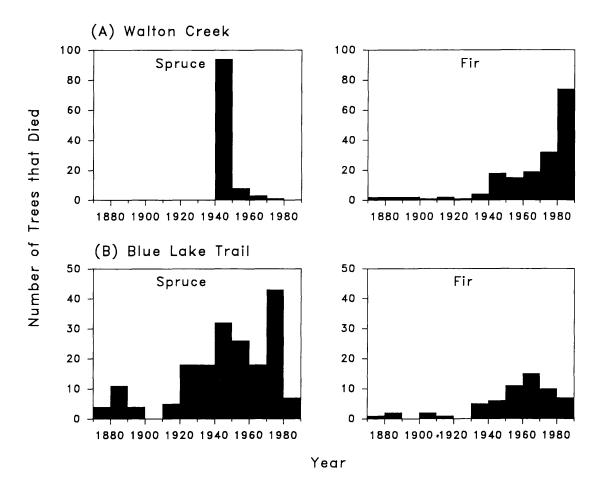


Fig. 6. Mortality patterns for dead-standing spruce and fir from old-growth forests: (A) Walton Creek and (B) Blue Lake Trail (after Mast 1991). The number of trees that died from 1870-1990 by decade is shown. The percentage of dead-standing trees successfully cross-dated ranged from 54-79. Total dead-standing trees/ha were as follows: Walton Creek spruce, 71; fir, 171; Blue Lake Trail spruce, 85; fir, 129.

weathering of the bleached wood is very slow and usually few, if any, outer rings are lost (Mast 1991). Occasionally, spruce remain dead-standing with bark attached for > 100 years. A relatively continuous pattern of mortality is illustrated by fir at Walton Creek (Fig. 6A), with the number of trees that died in any particular decade increasing exponentially from 1870-1990 (Mast 1991). Spruce at Blue Lake Trail also displayed continuous mortality since 1870, but the rates were far more episodic, with below average mortality in the 1980s and above average mortality in the 1890s, 1940s, and 1970s (Fig. 6B). This pattern of mortality is also consistent with the release frequencies recorded from live trees throughout the stand (Fig. 7B). In contrast, the mortality patterns for spruce at Walton Creek indicate that this stand was

affected by the 1940s beetle outbreak (Fig. 6A, Veblen 1991b, Mast 1991). Further studies on decay rates of spruce and fir will improve our understanding of rates of mortality based on dead-standing trees.

When a canopy spruce or fir dies, the increase in light and other resources results in abrupt and often sustained increases in growth (diameter and height) of subcanopy spruce and fir. Such releases can be dated from tree cores, and if enough cores are sampled throughout the stand, they can indicate the general pattern of past mortality (Lorimer 1985). A 200-year record of releases from three oldgrowth forests in the Colorado Front Range illustrates some striking patterns (Fig. 7). All three sites (Blue Lake Trail, Poudre River Trail, and

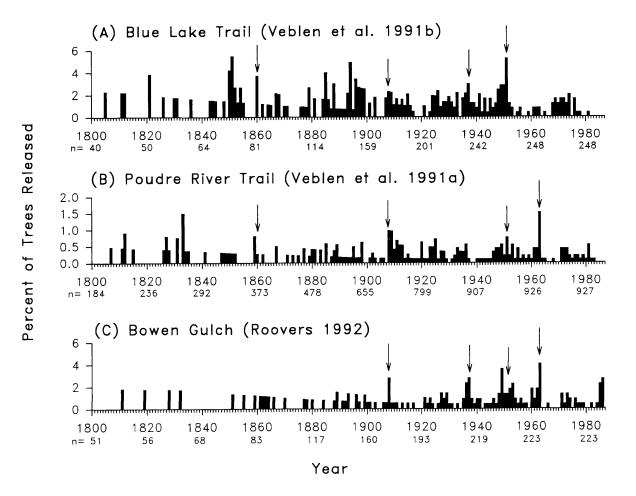


Fig. 7. Percentage of live trees (current cohort) that were released from 1800-1986 for all species in old-growth forests: (A) Blue Lake Trail (after Veblen et al. 1991b; [®] Ecological Society of America), (B) Poudre River Trail (after Veblen et al. 1991a; [®] Journal of Biogeography), and (C) Bowen Gulch (after Roovers 1992). A release is defined as a 150% increase in ring width when consecutive groups of five years are compared. Sample sizes (n) are given only every 20 years and appear beneath the year-axis labels. Coincident release dates are indicated by arrows.

Bowen Gulch) exhibit coincident release dates suggesting years of regionally extensive windthrow (e.g., 1860, 1908-09, 1924-25, 1947-51, and 1961-63). At the Poudre River Trail site, many gaps originated during these years (Veblen et al. 1991a). Periods of above average release frequencies, c. 1850-1860 and again in the mid to late 1940s, coincide with major spruce beetle outbreaks in Colorado, but the percentage of trees released was very low compared to severely affected stands in the White River and Grand Mesa National Forests (Veblen et al. 1991b). For example, in old-growth stands at Big Creek Reservoir, Grand Mesa National Forest, 18% of the sampled spruce showed release in a single year, 1946. Hinds et al. (1965) estimated that beetle-killed spruce fall at the

rate of c. 1.5% per year, so releases of surviving trees may be associated with tree mortality and/or subsequent windthrow.

The prevalence of wind-snapped treefalls along the Poudre River Trail suggested that trees were often dead or diseased before they fell (Veblen et al. 1991a). We lack etiological studies, however, that demonstrate causes of windthrow. Undoubtedly, many interacting factors are involved, such as wood-rotting fungi (reviewed by Alexander 1987) and low-level attack by endemic spruce beetle populations (Schmid and Frye 1977).

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There is some indication that the frequency of windthrow has increased at Bowen Gulch since

1900 (Fig. 7C); however, it is unclear whether this is a long-term trend. This forest is nearing the end of its fifth century of development, and the original spruce colonists are reaching their maximum longevity (Fig. 2H). Thus, increased mortality and windthrow should be expected for the next c. 100 years. Thereafter, windthrow may decline until the second spruce cohort reaches 500-600 years of age. Unfortunately, we lack information on old-growth stands that have developed in the absence of coarsescale disturbance for >600 years. Veblen et al. (1991a) also provide some evidence that the scale and frequency of disturbance by windthrow steadily increase after c. 300 years of stand development. This increase in windthrow increases the likelihood of another stand-initiating fire or extensive beetle outbreak (Schmid and Frye 1977, Veblen et al. 1991a).

CONCLUSIONS

Despite numerous publications, we really have very few detailed age structure analyses in oldgrowth spruce-fir forests. In the harsh subalpine environment, slight differences in site may result in major differences in stand development patterns, and ultimately in the characteristics of old growth. It is clear that some very high-quality old-growth stands, like Bowen Gulch, are in a transition oldgrowth stage, and some of the structural attributes of the forest may change significantly in the next few hundred years. Additional studies also are needed to monitor (or extract dendrochronologically) the patterns of mortality in old growth over longer periods. We have a general idea of how stands develop into old growth, but only a vague notion of what happens thereafter. The susceptibility of old-growth stands to fire, beetle outbreak, and blowdowns still brings into question whether any spruce-fir stands can persist for a thousand years. Ironically, lack of disturbance threatens the persistence of oak (Quercus spp.)-dominated old growth in the Midwest, and poses serious management questions of preservability (Boerner and Kooser 1991). In Colorado, the issue is not whether or how long we can preserve an old-growth spruce-fir forest; rather, we need to understand the dynamics of oldgrowth spruce-fir to plan for continued existence and renewal of places like Bowen Gulch, which add immeasurably to the richness of the landscape.

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Old-Growth Forests of the San Juan National Forest in Southwestern Colorado¹

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Abstract.—Very little information exists regarding old-growth forests on the San Juan National Forest. Several species appear to be largely restricted to old-growth habitats, including mosses (e.g., Buxbaumia piperi, Tetraphis pellucida, and Hylocomium splendens), fungi (e.g., Echinodontium tinctorium, Fomitopsis officinalis, and Sparassis crispa), and vertebrates (e.g., Martes americana, Phenacomys intermedius, Strix occidentalis lucida). The areas of research that are most urgently needed to improve our understanding of these ecosystems are (1) determining disturbance history and natural stand dynamics, and (2) testing the hypothesized restriction of these species to old-growth forest habitats.

The long-range objective of this study is to describe the structure, composition, and function of old-growth forests on the San Juan National Forest (SJNF), and to compare and contrast these forests with old-growth forests that have been studied elsewhere, e.g., the Pacific Northwest. However, we presently lack the data necessary to accomplish this ultimate objective. Therefore, the immediate objective of this paper is to compile the limited information that does exist, and from it to generate hypotheses and questions which can lay the groundwork for more detailed studies in the future. We restrict ourselves to ecological/scientific issues and do not deal with management questions in this paper.

Overview of Forest Diversity on the SJNF

Forest composition, structure, and function vary not only with stages of stand development (e.g., young vs. mature stands), but also in relation to environmental gradients of climate and substrate. The SJNF contains a variety of vegetational communities including forests, woodlands, shrublands and grasslands. The major forest types make up about 71% of the Forest's total acres. The lower elevations. where climates are driest and warmest, support pinyon/juniper woodlands, which are of limited extent in the SJNF. These grade into ponderosa pine forests as elevations increase, followed by mixed conifer forests, and finally spruce/fir forests at the highest elevations where precipitation is highest and temperatures are lowest. Aspen communities, which generally are successional to mixed conifer and spruce/fir types, are found at elevational ranges where these coniferous types occur.

Spruce/Fir Forest Type: The Spruce/Fir forest type occupies about 28% of the total acres on the SJNF, and is found at the highest elevations (2730-3580 m) extending up to timberline. Mean annual precipitation is about 75-100 cm, and frost free period is about 45 to 75 days per year.

These forests are dominated by Picea engelmannii (Engelmann spruce) and Abies lasiocarpa var arizonica (corkbark fir). The regeneration success of these two species is characteristic of this forest type. At the highest elevations *Picea* usually dominates the overstory, while at slightly lower elevations *Picea* and Abies codominate. Abies typically outnumbers the less shade tolerant *Picea* in the understory of these forests. Pseudotsuga menziesii (Douglas-fir) and Abies concolor (white fir) are also common species within the lower elevational portions of this forest type, and typically occur as seral or minor climax components, although Douglas-fir may be a major climax species. Populus tremuloides (aspen) is a major seral species and often colonizes large areas following major disturbance events, such as fire. Pinus flexilis (limber pine) and Pinus strobiformis (southwestern white pine) occur to a minor extent and tend to be found on steep slopes with southerly aspects. Most of the 5-needle pines in this area appear to be P. strobiformis (O'Hara 1986). This species and the corkbark fir both demonstrate the general floristic similarity of the San Juan Mountains to the mountains farther south in Arizona and New Mexico. Pinus aristata (bristlecone pine) occurs to a very minor extent, and is found in isolated places at the highest elevations of this forest type. Picea pungens (blue spruce) is also a minor component in spruce/fir forests, and tends to occur in cool moist environments often on the lower slopes of steep canyons. Series level vegetational classifications within this forest type include Abies lasiocarpa and Picea engelmannii, and to a minor extent Pinus

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flexilis, Picea pungens and Pinus aristata (DeVelice et al. 1986).

Understory vegetation within spruce/fir forests is highly variable. Vaccinium species are the most characteristic plants and occur throughout the elevational range of this forest type. Other common species include Juniperus communis, Lonicera involucrata, Pachistima myrsinites, Ribes montigenum, Rubus parviflorus, Ramishia secunda, Erigeron eximius, Oreochrysum parryi, Arnica cordifolia, Pedicularis racemosa, Artemisia franserioides, Fragaria ovalis, Vicia canadensis, Geranium richardsonii, Lathyrus arizonicus/leucanthus and Bromopsis ciliata.

Mixed Conifer Forest Type: The Mixed Conifer forest type occurs at mid elevations from about 2420-2880 m, and occupies about 12% of the total acres on the SJNF. Mean annual precipitation is about 62-75 cm, and frost free period is about 75 to 90 days per year.

These forests are dominated by Pseudotsuga menziesii, Abies concolor and Pinus ponderosa (ponderosa pine). The abundance and distribution of these species is highly variable, dependent primarily on elevation and aspect. Successful regeneration of white fir and Douglas-fir is characteristic of these forests. These two species often occur together as codominants at higher elevations, and on slopes with northerly aspects throughout the elevational range of this forest type. Ponderosa pine is often codominant with white fir and Douglas-fir at the lower elevations and on steep slopes with southerly aspects at higher elevations, and can regenerate successfully in these places particularly when sites are opened by disturbance. At the lowest elevations of this forest type and on the western portion of the SJNF where white fir is uncommon, ponderosa pine is often codominant with Douglas-fir.

Aspen is a major seral species in mixed conifer forests and often colonizes large areas following major disturbances. Limber pine, southwestern white pine and blue spruce are minor components at the higher elevations of these forests, and tend to occur in specialized environments similar to those described above for the spruce/fir type. Series level vegetational classifications within this forest type include Abies concolor, Pseudotsuga menziesii, Pinus flexilis and Picea pungens (DeVelice et al. 1986).

Understory vegetation within the mixed conifer type is highly variable. Most of the species mentioned above for the spruce/fir type will also be present in the cooler, moister sites at the higher elevations of this type, particularly the herbaceous plants. Additional species common to these forests include Quercus gambelii, Symphoricarpos rotundifolius, Acer glabrum, and Carex species. Quercus gambelii is commonly abundant on warm, dry sites, and can be a major seral species following disturbance particularly on steep slopes with southerly aspects.

Ponderosa Pine Forest Type: The ponderosa pine forest type is found at the lower elevations, ranging from about 2120-2580 m, and occupies about

16% of the total acres on the SJNF. Mean annual precipitation is about 50-62 cm, and frost free period is about 90 to 110 days per year.

These forests are dominated by a single species in the overstory, Pinus ponderosa, and are characterized by sites where this shade intolerant tree dominates regeneration. Douglas-fir, white fir, blue spruce and aspen may be minor components at the higher elevations and cooler, moister sites within this forest type, but succession to a mixed conifer type is not anticipated. Juniperus scopulorum (Rocky Mountain juniper) and Juniperus osteosperma (Utah juniper) are minor components within this forest type, the latter at lower elevations and the former throughout. *Pinus edulis* (pinyon pine) is often codominant with ponderosa pine at the lowest elevations where ponderosa pine forests grade into pinyon/juniper woodlands. Juniperus utahensis (Utah juniper) is a minor component in these ecotonal areas. The series level vegetational classification associated with this forest type is Pinus ponderosa (DeVelice et al. 1986).

As in the other forest types, understory vegetation in ponderosa pine forests is highly variable. Quercus gambelii and Festuca arizonica are important indicator species, and are often locally abundant. Other common species include Mahonia repens, Ceanothus fendleri, Purshia tridentata, Cercocarpus montanus, Erigeron formosissimus, Potentilla hippiana, Antennaria rosea, Achillea lanulosa, Danthonia parryi, Muhlenbergia montana, Koeleria macrantha, Poa fendleriana, Sitanion hystrix, Bouteloua gracilis and Carex species (mostly Carex geyeri). Quercus gambelii is a major seral species in this forest type, and is quick to colonize openings created by disturbance.

Aspen Forests: The aspen forest type is widely distributed and very abundant on the SJNF. It is normally found in association with spruce/fir and mixed conifer forest types at an elevational range of roughly 2420-3330 m. It occupies about 15% of the total acres on the Forest at the present time. Mean annual precipitation is about 62-88 cm, and frost free period is about 55 to 90 days per year.

These forests are dominated by *Populus* tremuloides (aspen) and normally occur as a result of major disturbance events, such as fire. *Populus* is quick to colonize openings created by such events. Since this forest type is predominantly successional to spruce/fir and mixed conifer types, a variety of coniferous trees may be present, mostly displayed as understory or minor overstory components. These species include *Picea engelmannii* and *Abies lasiocarpa* at higher elevations and *Abies concolor*, *Pseudotsuga menziesii* and *Picea pungens* at lower elevations.

Understory vegetation within the aspen forest type is commonly quite lush, consisting of a wide variety of herbaceous and shrubby species. Some common species include Symphoricarpos oreophilus, Pteridium aquilinum, Rubus parviflorus, Mahonia repens, Thalictrum fendleri, Arnica cordifolia, Geranium richardsonii, Lathyrus arizonica/

leucanthus, Ligusticum porteri, Pseudocymopterus montanus, Galium borealis, Fragaria ovalis, Bromopsis ciliata, Elymus glaucus and Carex species. Any of the species mentioned above for the spruce/fir and mixed conifer forest types may also be present.

Problems of Defining "Old-Growth" Forests

Defining or identifying old-growth forests in the San Juan Mountains (or anywhere) is somewhat problematic. Old-growth cannot be delineated simply by some arbitrary age of the dominant trees, since each species has a characteristic maximum life span; what is old for an aspen stand (100-200 years) would be young for Douglas-fir (life span 400+ years in this area). With the extremely limited data presently available on stand ages and tree age distributions in this area, we do not know for certain that there even are any truly ancient forests in the San Juans. The documented frequency of fire in the relatively dry forests at lower elevations (Dieterich 1980, Tanner 1985), and the widespread occurrence of aspen even in the more mesic high elevation forests, require us to at least consider the hypothesis that nearly all forest stands in this area have developed following major disturbances within the past 500 years.

Several definitions of old-growth have been proposed for other areas (e.g., Old-Growth Definition Task Group 1986, Norse 1990). Perhaps the most widely applicable definition is that of Franklin et al. (1981), who characterized old-growth Douglas-fir forests of the Pacific Northwest in terms of composition (high floristic and faunistic diversity), structure (large living and dead stems, large fallen boles, multiple foliage layers), and function (distinctive processes of energy flow, and nutrient cycling). We found even this definition difficult to apply in the San Juan Mountains, however, because of a virtual absence of data on forest history and changes in composition, structure, and function during the development of forest stands in this region.

In the absence of clear criteria for distinguishing old-growth forests in this area, we adopted a rather liberal – and tentative – definition of old-growth based on generalized trends during succession following major disturbances. We define old-growth forest stands as those that have passed through the stem initiation and stem exclusion stages of development (Oliver 1981, Aplet et al. 1988). We thus include stands that have just recently entered the second stem initiation stage, when trees that established after the last major disturbance are still present in the canopy – as well as older stands in which all of the initial post-disturbance individuals may have died and been replaced by a second generation of canopy dominants.

We have little experience in distinguishing between these two stages of old-growth, but the distinction may be important (Romme and Knight 1981). In fact, the structural, compositional, and functional characteristics commonly associated with old-growth (e.g., as described by Franklin et al. 1981), actually

could be expressed more strongly in the former type of stand than in the latter (and older) type.

Our working definition of old-growth forests does not exclude stands subjected to small-scale disturbances, such as individual tree-falls, localized fires, or death of trees due to insects or disease. These kinds of disturbances in fact promote the second stem initiation stage, and they contribute a substantial portion of the structural and compositional diversity that we associate with old-growth. We also recognize that there are many sites where forests may not go through the general course of succession following disturbance. Dry, rocky sites, for example, or sites near treeline, may never develop a closed canopy or a stem-exclusion stage of succession. Therefore, we restricted ourselves in this study to forest stands that exhibit the kind of successional development described by Oliver (1981) and Aplet et al. (1988).

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TAXONOMIC COMPOSITION OF OLD-GROWTH FORESTS

The first question we address is whether there are any species that are entirely or even largely restricted to old-growth habitats, or that require an old-growth forest environment for a critical stage in their life histories. Obligate old-growth species of this kind have been identified elsewhere, e.g., bryophytes in the northern Rockies (Lesica et al. 1991), mammals and amphibians in the Pacific Northwest (Carey 1989, Welsh 1990).

Apparently nobody has addressed this question for the SJNF. We examined a variety of sources to identify possible obligate old-growth species of bryophytes, fungi, invertebrates, and vertebrates in this area. Generally our data sources were not originally designed with this question in mind, so none of our findings can be considered conclusive. Nevertheless, we did uncover a number of species that we can hypothesize to be restricted to the old-growth environment; further research is required to test these hypotheses.

Bryophytes

We systematically reviewed the detailed field notes of D. W. Jamieson's extensive bryophyte collections in the SJNF over the last 12 years. For each species collected in a forested environment, we used the habitat description to subjectively place the specimen into one of three habitat categories: probably an oldgrowth forest; possibly an old-growth forest; probably not an old-growth forest. Descriptions of such things as deep shade, large rotting logs, and large trees led us to place the site in the probably old-growth category. We then tallied the number of occurrences of each moss species in each habitat category.

Of 63 moss species collected in forests, 13 were associated exclusively with the probably and possibly old-growth categories, 31 were entirely in the possibly old-growth category, and 19 were in the probably

not category (Table 1). This analysis suggests that there may be several moss species in the SJNF that are restricted to old-growth forests. Lesica et al. (1991) found several species of lichens and liverworts that were more abundant in unmanaged old-growth than in managed second-growth grand fir forests in northwestern Montana. Because bryophytes are small, sessile, and non-vascular, they may be particularly sensitive to subtle differences in habitat conditions.

Examples of possible old-growth bryophytes in the SJNF include Buxbaumia piperi, Buxbaumia viridis, Tetraphis pellucida, and Hylocomium splendens, which we have observed growing only on well rotted logs and stumps or on deep organic duff in humid forests. Others are Kiaeria starkei and Plagiobryum zeirii, which we only have found on streamside rocks or cliffs surrounded by old-growth spruce forests. These last two species are very rare in Colorado, and have been reported from only a few locations including the SJNF. None of the bryophytes listed here have been observed in managed second-growth forests in the SJNF, though exhaustive surveys have not been conducted.

Fungi

Several wood-rotting fungi are found in unmanaged older forests that are rare in younger stands. The species found are usually dependent upon the host trees available, as many wood-rotting fungi are genus or family specific. Our analysis of the fungi was based on a literature review and on J. P. Lindsey's extensive observations of wood-rotting fungi in the SJNF over the last 12 years. As described below and in Table 2, we turned up several species that appear restricted to older, unmanaged forests. Ironically, most of these have traditionally been viewed as pests – but now may be regarded as important elements of biological diversity in our National Forests.

In aspen stands in the western United States, Ganoderma applanatum (Pers. ex Wallr.) Pat. causes a white root and butt rot in older trees. In a study done in the SJNF (Landis and Evans 1974) in the aftermath of a violent windstorm which occurred in the fall of 1971, 2.3% of the bole biomass was lost in the aspen stand surveyed. A previous study done in the central Rocky Mountains (Baker 1925) indicated that decay from this fungus is not significant until trees are 80-90 years old. In the Landis and Evans study, most of the overstory aspen were in the 110 year age class. All standing aspen larger than 14 inches dbh had no basidiocarps. This fungus performs a natural thinning function in aspen stands.

Echinodontium tinctorium Ell. and Ev., the Indian Paint Fungus, is considered the most serious decay species of Abies and Tsuga in the western U.S. Virtually every old stand of Abies concolor and Abies lasiocarpa in Colorado shows evidence of this heart

Table 1. Habitats of forest bryophytes collected by D. W. Jamieson in the SJNF from 1979-1991. Numbers in the columns refer to the number of collections of a species from a particular type of habitat. "Probably" means probably an old-growth forest, based on habitat description in the field notes; "possibly" means possibly an old-growth forest; "not" means probably not an old-growth forest (see text).

growth lorest (see text).			
Species	Probably	Possibly	Not
Barbilophozia lycopodioides	1	0	0
Brachythecium collinum	1	4	0
Brachythecium rutabulum	$\overline{2}$	ō	Ŏ
	1	5	
Dicranum muhlenbecki			0
Dicranum rhabdocarpum	8	16	0
Dicranum scoparium	1	8	0
Hylocomium splendens	1	0	0
Lophozia ventricosa	3	0	0
Mnium arizonica	2	7	0
	$\frac{2}{2}$	Ö	ŏ
Pylaisiella polyantha			
Polytrichadelphus lyallii	1	4	0
Tetraphis pellucide	1	0	0
Timmia megapolitanica	2	2	0
Andreaea rupestris	0	7	0
Atrichum selwynii	0	1	0
	ŏ	î	ŏ
Aulacomnium palustre	-		
Blindia acuta	0	1	0
Buxbaumia piperi	0	3	0
Buxbaumia viridis	0	4	0
Cratoneuron filicinum	0	1	0
Dichodontium pellucidum	0	$\bar{1}$	0
	ŏ	2	ŏ
Dicranum fuscescens	-		
Encalypta procera	0	4	0
Eurhynchium pulchellum	0	1	0
Grimmia elatior	0	1	0
Hypnum cuppressiforme	0	1	0
Isopterysium pulchellum	0	2	0
Kiaeria starkei	ŏ	$\tilde{2}$	Ŏ
	- I		0
Lescuraea incurvata	0	1	-
Lescuraea radicosa	0	1	0
Marsupella emarginata	0	1	0
Oncophorus wahlenbergii	0	2	0
Orthotrichum hallii	0	3	0
Orthotrichum laevigatum	Ö	1	Ō
		2	Ŏ
Orthotrichum obtusifolium	0		
Paraleucobryum enerve	0	4	0
Plagiobryum zeirii	0	1	0
Plagiopus oderiana	0	1	0
Plagiothecium laetum	0	2	0
Platydicta jungermannioides	0	5	0
Dolugon otum alainum	ŏ	4	ŏ
Polyganatum alpinum	-		
Tayloria acuminata	0	1	0
Thuidium abietinum	0	1	0
Tortula norvegia	0	1	0
Cratoneuron commutatum	0	2	2
Fissidens bryoides	0	6	3
Onocophorus virens	Ö	1	5
Deleteriele delebera le allii	0	5	4
Polytrichadelphus lyallii	•	-	
Pogonatum alpinum	0	2	1
Pseudoskeella tectorum	0	1	1
Rhacomitrium canescens	0	6	2
Campylium halleri	0	0	7
Cratoneuron decipiens	Õ	0	3
Distiliance and the same	Ŏ	ŏ	2
Distichium capillaceum			
Encalypta ciliata	0	0	6
Encalypta rhaptocarpa	0	0	1
Encalypta vulgaris	0	0	4
Grimmia apocarpa	0	0	ī
Hymohymnum luridum	Ŏ	ŏ	4
Hygrohypnum luridum	-		
Leskeella nervosa	0	0	7
Plagiothecium denticulatum	0	0	4
Polytrichum juniperinum	0	0	2
Polytrichum piliferum	0	0	3
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Table 2. Wood-rotting fungi commonly found in old-growth forests of the southwestern USA, compiled from the literature and from collections by J. P. Lindsey in the SJNF between 1979-1991 (see text).

Fomitopsis cajanderi (Karst.) Kotl. et Pouz. - Brown slash rot of standing and down Douglas-fir; subtropical to subarctic

Fomitopsis rosea (Alb. et Schw: Fr.) Karst. - Brown rot of dead standing trees or 7large slash at higher elevations; causes a top rot of live aspen, Douglas-fir and spruce

Fomitopsis pinicola (Swartz: Fr.) Karst. - Brown rot of dead trees and large slash; conifers, aspen Phellinus tremulae (Bond.) Bond. et Boriss. - White trunk rot of living aspen; enters through branch stubs

Phellinus pini (Thore.: Fr.) A. Ames - White pocket rot of conifer heartwood; enters through branch stubs and is the major cause of volume loss in conifers

*Phaeolus schweinitzii (Fr.) Pat. - Brown cubical butt and root rot of living conifers; especially common on trees with fire scars

Cryptoporus volvatus (Pk.) Shear - White saprot of recently-killed conifers (beetle, fire, etc.), especially **Pinus**

*Heterobasidion annosum (Fr.) Bref. - White butt rot of live and dead conifers; common on old-growth **Abies** in western U.S.

Echinodontium tinctorium (Ell. and Ev.) Ell. and Ev. - White stringy heartrot of living **Abies** in Southwest; main cause of heartrot and volume loss in true firs

Ganoderma applanatum (Pers.) Pat. - White root and butt rot of living hardwoods, especially aspen; commonly causes windthrow of mature aspen

Amylocystis lapponicus (Rom.) Sing. - Brown slash rot of high elevation conifers

Bjerkandera adusta (Willd.: Fr.) Karst. - White slash rot of dead aspen

Inonotus andersoni (Ell. and Ev.) Cerny - oaks, including **Quercus gambelii**; a true parasite, it encroaches on sapwood of living trees and eventually kills them by causing breakage or girdling; creates habitat for cavity-nesting birds

Dichomitus squalens (Karst.) Reid - heartrot of **Pinus ponderosa** roots and butt as well as other conifers in the Southwest

*Inonotus tomentosus (Fr.) Teng. - White butt and root rot of heartwood of living spruce, as well as other Pinaceae

*become pathogens in young forests ... all others likely to disappear after cutting because they require the old trees and other substrates

rot fungus. Maloy (1967) reviewed the biology of this fungus in *Abies grandis*. He mentions Weir and Hubert's 1918 study of hemlock in which they found basidiocarps on 64 of 112 trees in the 41-100 age class. Maloy and Gross (1963) found no basidiocarps

on grand fir trees less than 90 years old. Decay is usually advanced by the time conks appear. Fire scars were shown to be the main infection court for this fungus in Abies concolor (Meinecke 1914); he determined the earliest age of infection to be 60 years, but suggested 130 years to be the age when trees begin to show decay due to suppression and injury. Most grand fir infection is at 40-60 years. with western hemlock infection at 78-165 years (Maloy 1967). Trees harvested after infection but before basidiocarp formation would create a serious depression in reproductive rate for this fungus, since basidiospores are undoubtedly the main infection propagule. Foster (1954), working with Abies lasiocarpa var. lasiocarpa, did not consider decay a problem until trees were 100 years old in even-aged stands.

Fomitopsis officinalis (Vill.: Fr.) Bond. et Sing. causes a brown cubical heartrot of living conifers and is particularly common on old-growth western larch and Douglas-fir (Gilbertson and Ryvarden 1986). It is entirely restricted to old growth habitat.

Sparassis crispa Wulf. ex Fr. (formerly known as Sparassis radicata Weir) is found on old-growth Pinaceae in the western U.S. The main host is Douglas-fir, although collections are known from ponderosa pine, southwestern white pine, and white fir. Only one collection (from ponderosa pine) has been reported from Colorado, from the Williams Creek area near Sand Bench in the SJNF (J.P. Lindsey, personal observations). The fungus is abundant in Arizona old-growth, although basidiocarp production is sporadic and only lasts for two to three weeks in August; hence many infections from this fungus are often attributed to other causes. The fungus produces a brown carbonizing butt and root rot (Martin 1978).

Invertebrates

We know virtually nothing about invertebrates in the SJNF. A bibliogaphic search turned up nothing for this area on this topic. However, in reviewing the literature on insects in other forested areas (also rather scanty except for pest species) we found that plant community successional patterns in managed and old-growth forests are associated with changes in the invertebrate fauna.

Canopy arthropod communities in old-growth coniferous forests in western Oregon exhibited greater species and functional diversity than did younger stands. In contrast, aphid biomass was greater in the younger trees and suggests a shift in trophic level ratios of defoliator/sap-feeding mechanisms (Schowalter 1989). A similar trend was observed in eastern forests (North Carolina) which indicates a general mechanism in the shift of insect herbivore community structure, especially at the trophic level. Older and younger plants differ in numerous chemical and morphological properties that dictate concomitant changes in herbivore populations. Scale insects exhibited greater reproductive capacity, faster developmental time and reduced

mortality on younger leaves of several genera and species of conifers. The younger leaves also possessed greater available nitrogen than older leaves (McClure 1980). Secondary chemical composition of plants also changes with age. Some chemicals, such as nitrogenbased toxins, decrease with time and others, such as resins, tannins, and phenolics increase with age (Krischik and Denno 1983). These changes may influence variations in herbivore populations in second-growth and old-growth forest stands.

Insects colonizing early successional herbaceous plants exhibit opportunistic characteristics, including high mobility associated with movement within an exposed area, reduced generation time, small size, increased reproductive capacity, and a tendency for generalist feeding strategies (Brown 1984). This and the other theoretical considerations discussed above suggest that there may be important differences in invertebrate communities between old-growth and younger stands. However, this question has not been studied on the SJNF.

Vertebrates

As with the invertebrates, we have little specific information about the ecology of vertebrate species in the SJNF. It appears, however, that no vertebrate species in Colorado is strictly dependent on or limited to forest habitats. Virtually all of them will be seen occasionally in non-forested environments. Nevertheless, several species appear to spend the majority of their time in old forests and may require such habitats for completion of their life cycles. We attempted to estimate the proportion of time spent by each species in a variety of habitats, based on the literature and on personal observations by ourselves and other scientists.

This analysis is presently incomplete, but we tentatively identified five mammals that may be largely associated with old-growth forests. These are the snowshoe hare (Lepus americanus), pine marten (Martes americana), chickaree (Tamiasciurus hudsonicus), red-backed vole (Clethrionomys gapperi), and heather vole (*Phenacomys* intermedius). Snowshoe hares feed mainly in small forest openings, but rarely venture far from a forest canopy. Pine martens are expert aborealists, and the chickaree is one of their principal prey species (Strickland et al. 1982); martens also seem to prefer spruce/fir forests with large amounts of coarse woody debris for travel and resting sites in the winter (Snyder and Bisson 1987, Buskirk et al. 1989). Chickarees depend not only on mature cone-producing trees for food, but also on fruits, fungi and perhaps insects on the forest floor (see Flyger and Gates 1982). The two vole species are most often captured in forest environments, although they may be found in a variety of habitats.

A few bird species, e.g., the goshawk (Accipiter gentilis), Mexican spotted owl (Strix occidentalis lucida), and flammulated owl (Otus flammeolus), are thought to prefer old-growth forests in the southwest

(Northern Goshawk Scientific Committee 1991, McDonald et al. 1991, and Reynolds, this volume, respectively). In addition, there are numerous cavity nesters that thrive in old-growth habitats, although they can persist as well in other forested environments so long as large dead trees are available. Examples of cavity nesters in the SJNF that appear to especially favor old forests with large trees include the northern pygmy owl (Glaucidium gnoma) and three-toed woodpecker (Picoides tridactylus). There is an important interaction between cavity nesting birds and wood-rotting fungi in that heart rots produce softer wood and thereby facilitate the excavation of holes by woodpeckers (Gilbertson 1979).

We know of no reptiles, amphibians, or fishes that might be restricted to old-growth forests in the SJNF. There are salamanders that are closely associated with old-growth forests in the Pacific Northwest (Carey 1989, Welsh 1990) and possibly in New Mexico, though the old-growth requirements of the latter are questionable (N.J. Scott, this volume).

OLD-GROWTH FOREST STRUCTURE

We sampled three stands in the Sand Bench area (Jamieson and Romme 1991) along an elevational gradient extending from spruce-fir forest at 2900 m through mixed conifer at 2800 m to ponderosa pine/ mixed conifer forest at 2700 m. We also sampled a fourth stand with ponderosa pine forest at 2600 m in the nearby Corral Mountain area (Bigsby 1991). Soils and topography were similar in all four stands, and consisted of sandy loams on flat or gently sloping sites. None of the stands had any evidence of human disturbance. The vegetation was found to change gradually as predicted by the continuum concept of vegetation (Whittaker 1975). Some aspen stands had fairly sharp borders with adjacent conifer-dominated stands, apparently reflecting the spatial pattern of past fires, but there were no sharp boundaries between stands dominated by various species of coniferous trees.

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The highest stand (2900 m) was dominated by Engelmann spruce (*Picea engelmanii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*), with some Douglas-fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) also present (Table 3). The spruce were generally larger than the fir, although the largest individual trees actually were aspen and Douglas-fir (Table 4).

Spruce dominated the canopy, but corkbark fir dominated the understory (Table 3). This pattern is common in spruce-fir forests elsewhere in Colorado, e.g., the Front Range (Veblen, 1986a,b), and in the Medicine Bow Mountains of southeastern Wyoming (Oosting and Reed 1952). The abundance of small fir suggests that this species may eventually replace the spruce as the canopy dominant, but research in the Front Range has shown that fir suffers higher mortality rates than spruce in all size classes, and so the

Table 3. Density (stems/ha) of canopy trees (c), understory saplings (u), and standing snags (s) in the upper, middle, and lower portions of the Sand Bench study area and in the Corral Mountain study area (see text). Snags were sampled only in the Corral Mountain area.

Species		Upper 2900 m	Middle	Lower 2700 m	Corral 2600 m
Abies lasiocarpa	c:	96	28	0	0
var arizonica	u:	424	48	Õ	Ŏ
	s:		••	·	ŏ
Picea engelmanii	c:	244	262	0	Ö
9	u:	258	51	0	Ö
	s:		••	· ·	Ŏ
Populus	٠.				U
tremuloides	c:	64	152	35	22
	u:	18	0	10	$\frac{22}{24}$
	s:		•		9
Pseudotsuga					
menziesii	c:	21	97	67	34
	u:	18	13	38	40
	s:		10	•	3
Abies concolor	c:	0	14	58	95
	u:	18	16	34	361
	s:			••	11
Pinus ponderosa	c:	0	0	53	157
F	u:	Õ	Õ	0	24
	s:	•	ŭ	v	9
Picea pungens	c:	0	0	0	28
1	u:	Ö	Ŏ	Ŏ	32
	s:	-	-	•	1
	υ.				T .

Table 4. Statistical distribution of diameters at breast height (cm) of canopy trees in upper, middle, and lower portions of the Sand Bench study area (see text). S = standard deviation; N = sample size; SE = standard error of the mean.

end of the mean.				
– UPPER	AREA (2900 m) –		
Species	Mean	Maximum	S	N
Abies lasiocarpa	20.5	39.4	11.9	9
Picea engelmanii	30.2	66.0	13.6	23
Populus tremuloides	48.0	53.3	4.0	6
Pseudotsuga menziesii	52.1	72.4	-	$\tilde{2}$
– MIDDLE		(9900)		-
Species	Mean	Maximum	S	N
			3	
Abies lasiocarpa	12.1	12.7	-	2
Picea engelmanii	30.9	54.6	13.9	19
Populus tremuloides	30.0	50.8	10.1	11
Pseudotsuga menziesii	54.6	74.9	12.3	7
Abies concolor	-	(12.7)	-	1
– LOWER	AREA (2700 m) –		
Species	Mean	Maximum	\mathbf{S}	N
Populus tremuloides	16.7	27.9	$\tilde{5}.0$	8
Pseudotsuga menziesii		61.0	13.4	15.
Anies concolor	777	45.7	u 7	1.7
Abies concolor Pinus ponderosa	$\frac{22.7}{49.5}$	45.7 66.0	9.7 13 3	13 19
Pinus ponderosa	49.5	66.0	13.3	13 12
Pinus ponderosa - CORRAL M	49.5 OUNTA	66.0 IN (2600 m) -	13.3	12
Pinus ponderosa - CORRAL Mo	49.5	66.0	13.3	
Pinus ponderosa - CORRAL Mo Species (Living trees)	49.5 OUNTA Mean	66.0 IN (2600 m) - Maximum	13.3 S	12 N
Pinus ponderosa - CORRAL Monday Species (Living trees) Populus tremuloides	49.5 OUNTA Mean 20.0	66.0 IN (2600 m) - Maximum 25.4	13.3 S 3.2	12 N 4
Pinus ponderosa - CORRAL Monderose Species (Living trees) Populus tremuloides Pseudotsuga menziesii	49.5 OUNTA Mean	66.0 IN (2600 m) - Maximum	13.3 S	12 N
Pinus ponderosa - CORRAL Monday Species (Living trees) Populus tremuloides	49.5 OUNTA Mean 20.0	66.0 IN (2600 m) - Maximum 25.4	13.3 S 3.2	12 N 4
Pinus ponderosa - CORRAL Monderose Species (Living trees) Populus tremuloides Pseudotsuga menziesii	49.5 OUNTA Mean 20.0 45.3	66.0 IN (2600 m) - Maximum 25.4 63.5	13.3 S 3.2 12.1	12 N 4 6
Pinus ponderosa - CORRAL Monderose (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor	49.5 OUNTA Mean 20.0 45.3 24.0	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2	13.3 S 3.2 12.1 18.4	12 N 4 6 17
Pinus ponderosa - CORRAL Months Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3	13.3 S 3.2 12.1 18.4 17.0 18.0	12 N 4 6 17 28 5
Pinus ponderosa - CORRAL Months Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species	49.5 OUNTA Mean 20.0 45.3 24.0 52.0	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4	13.3 S 3.2 12.1 18.4 17.0	12 N 4 6 17 28
Pinus ponderosa - CORRAL Months Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species (Standing snags)	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0 Mean	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3 Maximum	13.3 S 3.2 12.1 18.4 17.0 18.0 S	12 N 4 6 17 28 5 N
Pinus ponderosa - CORRAL Me Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species (Standing snags) Populus tremuloides	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0 Mean 23.1	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3 Maximum 39.6	13.3 S 3.2 12.1 18.4 17.0 18.0 S 8.5	12 N 4 6 17 28 5 N
Pinus ponderosa - CORRAL Months Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species (Standing snags) Populus tremuloides Pseudotsuga menziesii	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0 Mean 23.1 34.8	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3 Maximum 39.6 48.3	13.3 S 3.2 12.1 18.4 17.0 18.0 S 8.5 10.1	12 N 4 6 17 28 5 N 16 6
Pinus ponderosa - CORRAL Months Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species (Standing snags) Populus tremuloides Pseudotsuga menziesii Abies concolor	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0 Mean 23.1 34.8 38.2	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3 Maximum 39.6 48.3 73.7	13.3 S 3.2 12.1 18.4 17.0 18.0 S 8.5 10.1 20.4	12 N 4 6 17 28 5 N 16 6 19
Pinus ponderosa - CORRAL Me Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species (Standing snags) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0 Mean 23.1 34.8 38.2 41.2	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3 Maximum 39.6 48.3 73.7 80.0	13.3 S 3.2 12.1 18.4 17.0 18.0 S 8.5 10.1 20.4 18.3	12 N 4 6 17 28 5 N 16 6 19 17
Pinus ponderosa - CORRAL Months Species (Living trees) Populus tremuloides Pseudotsuga menziesii Abies concolor Pinus ponderosa Picea pungens Species (Standing snags) Populus tremuloides Pseudotsuga menziesii Abies concolor	49.5 OUNTA Mean 20.0 45.3 24.0 52.0 28.0 Mean 23.1 34.8 38.2	66.0 IN (2600 m) - Maximum 25.4 63.5 59.2 86.4 53.3 Maximum 39.6 48.3 73.7	13.3 S 3.2 12.1 18.4 17.0 18.0 S 8.5 10.1 20.4	12 N 4 6 17 28 5 N 16 6 19

composition of these stands probably is more or less stable in the absence of major disturbance such as fire or cutting (Veblen 1986a,b; Aplet et al. 1988).

The middle stand (2800 m) was dominated by Engelmann spruce, aspen, and Douglas-fir, with small amounts of corkbark fir and white fir (Abies concolor) also present (Table 3). Douglas-fir was by far the largest tree in this area, and individual Douglas-fir trees in this middle portion were among the largest trees that we encountered anywhere in the Sand Bench study area (Table 4). The transitional composition of this middle portion of Sand Bench can be seen by the declining numbers of corkbark fir, characteristic of higher elevations, and the first appearance of white fir, a species of lower elevations (Table 3). The corkbark and white firs here also were substantially smaller than the individuals at higher and lower elevations, respectively (Table 4). All of the canopy species were represented as well in the understory, with the conspicuous exception of aspen which had little or no regeneration (Table 3). This pattern suggests that the present aspen dominance in this area is the result of past fires or other kinds of disturbance. The paucity of aspen in the understory also suggests that aspen may decline in abundance in the future if no major disturbance occurs. We did not determine the ages of any of the canopy trees, but the aspen stems appeared to be 50-100 years old. The maximum life span of aspen stems in the Rocky Mountain region usually is a little over 100 years (DeByle and Winokur 1985). Even if the aspen stems decline in abundance in this area over the next several decades, however, the root systems will persist for decades or even centuries longer and probably will be able to resprout and regenerate the stands following any future disturbance that reduces the coniferous dominants (DeByle and Winokur

All four stands contained the large canopy trees and the diversity of understory heights and species (Tables 3, 4) that apparently characterize old-growth forests in general (Franklin et al. 1981). It was beyond the scope of this present study to quantitatively inventory the dead woody material on the forest floor at Sand Bench, but we observed subjectively that, especially in this middle area, there generally were not the great numbers of large fallen trees that one commonly associates with old-growth, especially that in the Pacific Northwest. The Sand Bench and Corral Mountain stands were well stocked with trees, but the forest floor was relatively open and easy to walk through. This may be simply the nature of old-growth forests at middle elevations in the San Juan Mountains. Alternatively, these stands may be at the penultimate stage of forest succession following past disturbances, in which the trees that first became established after the disturbance have reached full size and maturity but have not yet begun to succumb to extensive mortality (Oliver 1981, Aplet et al. 1988). The aspen-dominated stands and the forest structure described above both indicate that fire occurred historically in this area. However, we

observed few fire-scarred trees, and no evidence of recent fire, which suggests that fire may be relatively infrequent in this ecosystem.

The lowest stand on Sand Bench (2700 m) and the Corral Mountain stand (2600 m) were the only ones in which ponderosa pine was a major canopy species. Douglas-fir and white fir were co-dominants (Table 3). The largest trees were the ponderosa pine and Douglas-fir (Table 4). Aspen also was present in these areas, but the other tree species that characterized the upper and middle portions of Sand Bench were absent here (Table 3).

The Douglas-fir, white fir, and aspen were all represented in both the canopy and understory strata, indicating that they are regenerating under current stand conditions, but ponderosa pine was absent or rare in the understory (Table 3). This suggests that the present conditions do not permit pine reproduction. We did not determine the ages of any of the trees, but the ponderosa pine all appeared to be 70+ years old, and some individuals obviously were centuries old. The paucity of pine reproduction might indicate that this species will eventually disappear from the stand. However, ponderosa pine typically persists through episodic reproduction (Peet 1981, Heidmann et al. 1982, White 1985); thus, the present scarcity of young pine does not necessarily indicate declining importance of this species.

Fire histories have been reconstructed in ponderosa pine forests elsewhere in the southwest, and have shown that this forest type burned at intervals of roughly 2-45 years prior to European settlement and modern fire suppression (e.g., Ahlstrand 1980, Dieterich 1980, Laven et al. 1980, Madany and West 1983). No detailed fire history studies have been conducted in the San Juan Mountains, but anecdotal observations suggest that presettlement fire intervals in this area fell within a similar range, and perhaps were a little toward the long end. A single firescarred ponderosa pine tree at 2000 m near Durango - near the lower elevational limit of ponderosa pine revealed an average interval between successive fires of 14 years between 1729-1896 (Tanner 1985). A sample of 10 fire-scarred ponderosa pine trees from across the San Juan National Forest yielded intervals of 7-35 years between successive fires (Dieterich 1980).

The Sand Bench and Corral Mountain ponderosa pine stands, lying near the upper elevational limit of this species, probably are characterized by fire-free intervals that are relatively long for the ponderosa pine type as a whole, as a consequence of cooler temperatures and higher precipitation in this area. Even before the advent of twentieth century fire suppression, these stands probably escaped fire for periods of many years or decades. We observed fire scars on some of the old ponderosa pine, but fire scars were not abundant. Nevertheless, fire probably is an important natural process that helps to maintain the

structure, composition, and function of old-growth ponderosa pine forests in the SJNF (Moir and Dieterich 1988).

An important component of the structure of old-growth forests is standing dead trees or snags (Franklin et al. 1981). Snags provide nesting and perching sites for numerous birds and other vertebrates, feeding and breeding substrates for invertebrates and fungi, and eventually contribute to soil structure and microbial activity when they fall and decompose (e.g., Balda 1975, Gilbertson 1980, Franklin et al. 1981, Harvey et al. 1986, Harmon and Chen Hua 1991). We sampled density, species composition, and size distribution of standing snags only in the Corral Mountain study site (Tables 3,4). Additional comparative studies are needed to ascertain how representative these results are of old-growth forests in the SJNF in general.

Age Structure of an Old-Growth Spruce-Fir/Mixed Conifer Forest

The upper stand that we had sampled in the Sand Bench area in 1988 was logged in 1991. We revisited the site that year and counted the annual rings on the logs or stumps of 16 large trees that had been felled for road construction. We did not take a complete or random sample of tree ages in the stand; rather we sampled what appeared to have been representative canopy dominants. Our ring counts (Table 5) represent *minimum* estimates of tree age, since the trees had required some unknown number of years to grow to the height at which they were cut. This is the only data set that we know of for tree ages in old-growth forests of the SJNF.

Our results (Table 5) showed that the trees in this area ranged from at least 105-370 years in age. Moreover, the rings revealed a variety of growth patterns during the lives of the trees. Several trees had grown very slowly when they were young, suggesting that they were suppressed by larger, presumably older trees already present in the forest.

The wide range in tree ages, including some very old trees, plus the variation in growth rate, including evident suppression during the lives of several trees, strongly support the conclusion that the forests of Sand Bench have not been subjected to any major or catastrophic disturbance for at least 370 years (the oldest tree age that we sampled). The fact that this oldest tree showed periods of extremely slow growth suggests that it germinated under an existing forest canopy, which would mean that the forest actually may have been undisturbed for more than 400 years. By contrast, a forest that had originated following a major or catastrophic disturbance typically would be expected to show an even-aged structure in which all of the canopy dominants were about the same age. and all or most of the dominants would show rapid early growth in an open environment free of competing vegetation (Romme and Knight 1981).

Table 5. Approximate age class distribution of trees in the upper Sand Bench area, San Juan National Forest, Colorado (see text). Minimum age reported here is the number of rings counted at stump height; since the trees all required an unknown additional amount of time to grow to the height at which they were cut, the actual ages are all older than the minimum ages reported here. Diameters are of the wood only, as many trees had been stripped of bark. Douglas-fir is *Pseudotsuga menziesii*. Spruce is *Picea engelmannii*.

Tree		Diameter	Minimum	Ū
No.	Species	(inches)	Age	Growth Pattern
1	Douglas-fir	28	370	Alternating slow and fast
2	Douglas-fir	26	352	Fast initially, then slow
3	Douglas-fir	27	333	Fast initially, then slow
4	Spruce	23	330	Alternating slow and fast
5	Douglas-fir	17	310	Alternating slow and fast
6	Douglas-fir	28	278	Alternating slow and fast
7	Douglas-fir	30	260	Fast initially, then slow
8	Spruce	40	216	_
9	Spruce	22	200	Fast initially, then slow
10	Spruce	28	190	Relatively fast throughout
11	Douglas-fir	15	189	Slow throughout
12	Douglas-fir		181	Slow throughout
13	Spruce	23	161	Slow initially, then faster
14	Spruce	14	161	Relatively fast throughout
15	Douglas-fir	17	150	Fast initially, then slow
16	Spruce	15	105	Relatively fast throughout

Several of the trees in this stand were relatively young, i.e., 100-200 years old, and several of them grew rapidly when they were young. The stand also contained numerous aspen trees, which rarely live beyond 150 years and are considered indicators of past disturbances. The presence of these younger trees suggests that minor disturbances have occurred repeatedly during the history of the forest. These minor disturbances – individual large trees dying

from insect attack, disease, or other causes, and falling over; localized severe wind storms; spot fires; and the like – have created openings in the forest canopy where new trees can become established or suppressed understory saplings can be released and grow to maturity (see Veblen et al. 1989). Small, localized disturbances of this kind are characteristic of old-growth forests throughout the world; in fact, they contribute to the structural complexity that is associated with old-growth.

Downed Woody Material

Downed woody material was sampled in the Corral Mountain area (Cowen and Kreykes 1991), which was at 2600 m elevation and dominated by ponderosa pine (Tables 3,4). To our knowledge, these are the only existing data on dead and down woody materials in old-growth forests of the SJNF.

Samples were taken at 23 points using the planar intersect method (Brown 1974). The mean total mass of woody material (excluding duff) was 26.6 t/ha (Table 6) Quantities increased progressively as the class size of the material increased (Table 6). The largest single contributor to the amount of woody material was the rotten logs greater than 3 inches in diameter, which comprised 11.6 t/ha. The sound logs of 3 inches or greater diameter accounted for the next largest amount at 8.0 t/ha.

We compared these results from the Corral Mountain study area to other old-growth forests described in the literature, and found some similar patterns among diverse forest types. An old, uncut northern hardwoods forest in northern New Hampshire (Gore and Patterson 1985) had similar total quantities of dead woody material, and a similar steady increase in quantities as size class increased. By contrast, a Douglas-fir/western hemlock forest on Washington's Olympic Peninsula (Agee et al. 1987) showed not only a greater total mass of dead woody material - as would be expected - but also a different distribution among size classes. There was more in the smallest size class than in the next smallest class, and an even greater preponderance of material in the largest size class. Additional comparisons of this kind could provide insights into patterns and reasons for similarities and differences among old-growth forests of all forest types. For example, the unusually large mass of large materials on the Olympic Peninsula can

Table 6. Dead woody material (tons/ha) on the forest floor of a ponderosa pine forest at 2600 m in the Corral Mountain area on the SJNF. See text and Cowen and Kreykes (1991) for details.

	<1/4 inch	1/4 - 1 inch	1 - 3 inch	>3 inch sound	>3 inch rotten	>3 inch combined
Mean	.27	3.27	3.51	7.98	11.58	19.56
St. Dev. (S)	.22	2.21	3.57	13.97	18.71	21.34
95% Conf. Int.	(.176,.370)	(2.31,4.22)	(1.97,5.05)	(1.95,14.03)	(3.49,19.68)	(10.3,28)
St. Error	.05	.46	.74	2.91	3.90	4.45
Min.	.04	.75	0	0	0	0
Max.	.86	11.27	11.96	46.46	69	69

be explained by greater tree volume and diameters to begin with. The higher humidity and temperatures in that region, relative to Colorado, also may result in more rapid decomposition of small materials. By contrast, trees in Colorado are smaller, net primary productivity is lower, and decomposition probably is slower in all size classes (see Arthur and Fahey 1990).

RESEARCH NEEDS

The data compiled here suggest that old-growth forests on the SJNF have some interesting and distinctive characteristics of composition, structure, and dynamics, but none of our findings can yet be considered conclusive. Additional research is needed in all of the areas that we have touched upon here. Because of the large area, remote and rugged conditions, and distance from major research centers, the flora and fauna of the San Juan Mountains are still far from completely known. We suggest, however, that there are two areas of research that are needed most urgently to improve our understanding and to help guide upcoming management decisions on the SJNF:

- 1. We know almost nothing of the disturbance history and stand dynamics of ponderosa pine, mixed conifer, and spruce/fir forests on the SJNF. We can extrapolate findings from other areas (e.g., central Arizona and the Colorado Front Range), but given the unique climatic and biogeographic location of the San Juan Mountains, these extrapolations are questionable.
- 2. We have identified a substantial number of taxa that appear to be restricted to or dependent upon the old-growth stage of forest development on the SJNF. More systematic and focused studies now are needed to rigorously test these hypothesized affinities. High priority here should be given to the bryophytes, fungi, and invertebrates. These groups are poorly known and little studied in general, yet they exhibit high diversity and perform essential ecosystem functions. It is particularly important to identify the special microhabitats that may harbor rare or unusual fauna and flora, and to determine whether these unusual habitats are created by oldgrowth conditions or have other origins. Although the vertebrate and vascular plant species are somewhat better known on the SJNF and some have been studied elsewhere, specific research on the distribution and ecology of these species on the SJNF also is needed.

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Flammulated Owls in Ponderosa Pine: Evidence of Preference for Old Growth¹

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Abstract.—In Colorado, nesting flammulated owls (*Otus flammeolus*) showed a preference for old trees and stands of ponderosa pine and Douglas-fir. Owls more often settled in areas dominated by older forests then young forests when they returned in the spring to nest. Flammulated owls used old trees and forest stands more often for foraging and for defending territories. Individual owls returned more often to territories that were in old stands of ponderosa pine mixed with Douglas-fir compared to territories composed of mosaics of stands of other tree species and ages.

INTRODUCTION

The flammulated owl is a little known migratory owl that occurs in dry, montane coniferous forests in Central and western North America (Bent 1938, Sutton and Burleigh 1940, Johnsgard 1988). The owl is an obligate cavity-nester (Earhart and Johnson 1970), and breeds from the Rocky Mountains to the Pacific Coast Mountains and from southern British Columbia south to Vera Cruz, Mexico (Sutton and Burleigh 1940, Winter 1974, Cannings et al. 1978, Reynolds and Linkhart 1984 1987b, and others). The winter range is thought to be from Guatemala and El Salvador north to Jalisco, Mexico (Phillips 1942). It is possible that some individuals winter in the extreme southern portion of the United States (Phillips et al. 1964, Winter 1979).

Throughout their range flammulated owls are found in the yellow pine belt - from lower elevations where the pine is mixed with oak (Quercus spp.) or pinyon pine (Pinus monophylla) to the higher elevations where the pine is mixed with firs (Abies spp.), Douglas-fir (Pseudotsuga menziesii), incense-ceder (Calocedrus decurrens), or quaking aspen (Populus tremuloides) (Huey 1932, Marshall 1939, Marshall 1957, Johnson and Russell 1962, Phillips et al. 1964, Bull and Anderson 1978, Marcot and Hill 1980, Webb 1982, Reynolds and Linkhart 1984 1987b, McCallum and Ghelback 1988). With the exception of one nest in a pinyon pine stand in the Argus Mountains in California (Huey 1932), all reported nests of the flammulated owl were in forest stands containing at least some yellow pines (subsec. Ponderosae: Critchfield and Little 1966) mixed with one or more of the above tree species. In reports where forests surrounding nests were described or photographed, all nests were in, or adjacent to, mature or old-

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growth stands (Hanna 1941, Bull and Anderson 1978, Canning et al. 1978, Hasenyager et al. 1979, Cannings 1982, Bloom 1983, Reynolds and Linkhart 1984 1987b, Fix 1986, Goggans 1985, Hayward 1986, Howie and Ritcey 1987, McCallum and Ghelback 1988). However, Hasenyager et al. (1979) and Bloom (1983) reported nests in forests that had been partially cut but contained large, residual trees, and Winter (1974) found the owl in second-growth forests, although he did not report nesting in this age-class.

Flammulated owls are entirely insectivorous (Ross 1969, Goggans 1985, Hayward 1986, Reynolds and Linkhart 1987b). During cold spring and early summer nights, the owls feed almost entirely on the only insects available – nocturnal adult lepidoptera (Reynolds and Linkhart 1987b). As summer progresses and other arthropods become available, lepidopteran larvae, grasshoppers, spiders, crickets, and beetles are added to the diet (Goggans 1985, Reynolds and Linkhart 1987b).

Habitat selection by birds occurs in an hierarchically ordered series of choices: first, a geographic location must be chosen, then a habitat in which to settle, and finally, specific microhabitats for nesting, foraging, and other activities must be selected (Hilden 1965, Johnson 1980, Hutto 1985). Because movements of a nesting bird are energetically limited to a finite area around its nest, the kinds of microhabitats available are constrained by the first two choices. To determine more clearly the habitat associations of flammulated owls, we began a longterm study (1980-present) of (1) the types of forests into which flammulated owls settled in the spring, (2) the species and age of trees used for territorial defense, foraging, and nesting, (3) the species composition and age of forests in which they forage, (4) their diets and foraging behavior (5) and differences in fidelity to territories in forests of different tree species and ages. The following is a compilation of evidence of preference for older forests in flammulated owls presented originally in Linkhart (1984) and Reynolds and Linkhart (1987a, 1987b, 1990) and in our yet unpublished work.

STUDY AREA AND METHODS

The study was conducted on 452 ha of the Manitou Experimental Forest in central Colorado. Terrain was moderately steep (20-80% slopes) and elevations ranged from 2,500 to 2,800 m. Forests on the area formed a mosaic of types and ages, the most abundant (75% of area) of which was old-growth (> 200 yrs) ponderosa pine (Pinus ponderosa) and Douglasfir. These mixed ponderosa pine and Douglas-fir stands, which contained scattered limber pine (P. flexilis), were mainly on ridge tops and east-, south-, and west-facing slopes. Small (< 3 ha) stands of young (< 100 yr-old) Douglas-fir mixed with blue spruce (Picea pungens) (8% of area) as well as mixed stands of mature (100-200 yr-old) quaking aspen and blue spruce (9% of area) were scattered throughout on north- and east-facing slopes. Mature stands of pure quaking aspen (7% of area) were scattered within these three types of forests, but occurred primarily in moist creek bottoms (Linkhart 1984, Reynolds and Linkhart 1987b). Forests surrounding the study area formed a similar mosaic of stand compositions and ages. The study area was located and established as follows: after confirming the presence of some territorial owls, boundaries were drawn to include sufficient area for 10-20 territories based on Marshall's (1939) estimate of territory size (274 m diameter), and nest searches and census for owls were then expanded to the boundaries.

Intensive broadcast censuses and nest searches were conducted in and around the study area each year (May through July) to determine densities and locations of flammulated owls. Territorial fidelity was determined by capturing (and recapturing) all owls and banding them with Fish and Wildlife Service aluminum leg bands (Reynolds and Linkhart 1984). The foraging behavior and habitat use of 7 nesting males (7 of the 9 males that nested on the study area; 1 nest failed, 1 male could not be captured) were intensively studied with radio-telemetry (Reynolds and Linkhart 1984, Linkhart 1984, Reynolds and Linkhart 1987, Linkhart et al. MS.). Each of the 4 forest types within 1) the study area and 2) each of the 7 males' territories was mapped and the amount and proportion of each type in these areas was measured with a planimeter (Linkhart 1984). Locations of foraging and territorial song trees were mapped and the associated forest type, tree species and age (determined with increment borers) were recorded. Species and age of trees used by the owls were compared to 615 trees at random points within the study area. Size of territories and foraging areas were estimated using the minimum convex polygon method (Mohr 1947).

The choice of habitat by owls settling in the spring was examined by comparing the proportion of forest types within territories to the proportion of types available within the study area. The owl's preference of forest type for foraging was determined by comparing the proportional use of forest type by owls to the availability of types within territories.

RESULTS AND DISCUSSION

Study Area vs Territories. A comparison of the proportions of forest types and ages within the study area and within territories showed that the owls settled into areas having greater proportions of oldgrowth ponderosa pine/Douglas-fir, lesser proportions of young Douglas-fir/blue spruce, and about the same proportions of mature blue spruce/quaking aspen and mature quaking aspen (Table 1) (Linkhart et al. MS).

Table 1. Percent of area of 4 forest types and ages in the study area (452 ha) and in 7 flammulated owl territories (x=14.7 ha) in central Colorado.

	Study	
Forest Type ¹	$Area(\%)^2$	Territories(%)
old-growth PIPO/PSME	58	78
young PSME/PIPU	27	7
mature PIPU/POTR	11	8
mature POTR	3	6

¹ PIPO/PSME = ponderosa pine/Douglas-fir, PSME/ PIPU = Douglas-fir/blue spruce, PIPU/POTR = blue spruce/aspen, POTR = aspen.

Habitats Used Within Territories. As in most other raptors, male flammulated owls are the principal food providers for the family. Males mainly gleaned arthropods from needle bunches and the bark of limbs and trunks of large conifers. Occasionally the owls hawked flying insects between tree crowns, or dropped from the lower crown branches to arthropods on the ground (Reynolds and Linkhart 1987b). Mean territories of the 7 males was 14.7 ha (range, 8.5 - 24.0 ha) (Linkhart et al. MS.).

A Bonferroni simultaneous comparison of the frequency of 221 total observations of foraging males in each of the forest types to the availability of the types within territories showed a significant selection for old-growth ponderosa pine/Douglas-fir (190 foraging bouts observed vs. 169 expected), and a significant avoidance of young Douglas-fir/blue spruce (1 observed, 17 expected) and mature quaking aspen (7 observed, 15 expected). Mature blue spruce/quaking aspen was used in about the same proportion as its availability (23 observed, 20 expected) (Linkhart et al. MS.).

Foraging Trees. Of 167 trees in which an arthropod was known to have been captured (excluding cases of hawking and ground foraging), 80 percent were ponderosa pine and Douglas-fir (Table 2). A random sample of 77 of the 167 foraging trees had a mean age of 199 years (range, 72 - 395 yrs), considerably older than the mean of 111 years for 615 trees randomly chosen in the study area.

Song Trees. During territorial-song bouts (periods when males defended territories by singing) males sang from 1 to 10 trees. Males sang from hidden positions next to tree trunks or in dense clumps of foliage. Ponderosa pine and Douglas-fir were the only species used as song trees, and the mean age of 22 of

Table 2. Percent by tree species in which foraging and territorial singing were observed and the percent by species of 615 randomly chosen trees on the study area.

Tree species	Foraging	Song	Available
Douglas-fir	61	50	39
ponderosa pine	19	50	29
quaking aspen	9	-	17
limber pine	6	_	10
blue spruce	5	-	5
total trees (n)	167	22	615

these trees (exact tree unknown in 76 cases) was 289 years (range, 94 - 419 yrs) (Linkhart et al. MS.) (Table 2).

Intensive Foraging Areas. Radio-telemetry data showed that male flammulated owls had favored areas within their territories where they foraged repeatedly (Linkhart et al. MS). Eighty-one percent of 221 total observed foraging attempts occurred in 15 intensive foraging areas (IFAs). IFAs were distributed among the 7 territories as follows: 3 territories contained 2 IFAs, 2 contained 1 IFA, 1 contained 3 IFAs, and 1 contained 4 IFAs. Mean size of the 15 IFAs was 0.5 ha (SD = 0.4, range = 0.1-1.4 ha) and mean total area contained in IFAs in the 7 territories was 1.0 ha (SD = 0.3, range = 0.7-1.5 ha).

The composition of forests within IFAs suggests the importance of old ponderosa pine/Douglas-fir in the foraging of the owl. Thirteen of the 15 IFAs were composed of old-growth ponderosa pine/Douglas-fir (1 of these contained some quaking aspen trees), and 2 IFAs were composed of mature quaking aspen/blue spruce.

Territorial Fidelity. Strong annual fidelity to territory is more common in longer-lived birds that occupy stable habitats (Harvey et al. 1979). Flammulated owls show strong fidelity to their territories. Once they establish a nesting territory, males return every year for what appears to be the remainder of their lives, only rarely moving to an adjacent, unoccupied territory. Females also return to their territories and to their previous year's mate. However, when a female's mate did not return in the spring, it moved to an adjacent territory and paired with an experienced male whose prior mate did not return (Reynolds and Linkhart 1987a, Reynolds and Linkhart 1990). In our 12-year study, all territories that contained contiguous old-growth ponderosa pine/ Douglas-fir forest were occupied every year of the study. If an established male did not return in the spring, a new male quickly claimed the territory. In contrast, territories that contained less than 75 percent old-growth ponderosa pine/Douglas-fir, were occupied only as long as the original male returned to nest (1 to 3 years) (Linkhart et al. MS.).

Why Old-growth Ponderosa Pine Forests? The association of flammulated owls and old ponderosa pine/Douglas-fir forests likely involves both habitat composition and structure, and food. The owl is an

obligate secondary cavity nester, and older forests typically contain an abundance of snags and lightning-damaged trees with cavities. Old yellow-pine forests (whether pure or mixed with other species) typically form open stands with well-developed grass or shrub understories. These understories support arthropods in a forest layer that is used extensively by fledged owlets and molting adults in late summer. Although the abundances of lepidoptera and other arthropods in, and the extent to which the species are limited to, ponderosa pine and associated tree species are unknown, many are host-plant specific (Munroe 1979). However, there are up to 4 times as many lepidopteran species associated with Douglas-fir and ponderosa pine than other common western conifers (Furniss and Carolin 1977).

In addition, two common foraging tactics, hawk-glean, hover-glean, are used inside of the crown of trees by the owl (Reynolds and Linkhart 1987b). The interior of large, old ponderosa pine and associated species (e.g., Douglas-fir) are open, exposing large limbs and trunks that provide the owls with perches and access to areas where arthropods feed and rest. The openness of these stands also provides space for hawking flying insects between crowns, and for hover-gleaning them from outer needle bunches (Reynolds and Linkhart 1987b).

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Finally, the unique structure of older forests in the northern portion of the owl's range also occurs in pine forests in their winter range (Central America and Mexico). If, in fact, flammulated owls winter in these forests, then the owl may have "fine-tuned" its foraging repertoire to the structure of trees, stands, and foods in these forests through evolutionary time and may have given up the behavioral plasticity required to live in other forests.

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Does the Sacramento Mountain Salamander Require Old-Growth Forests?¹

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Studies of populations of *Aneides hardii* before and after logging disturbance of their mixed-conifer habitat showed no detectable short-term (0.5-3.5 years) effect. The distribution of salamanders among size classes differed on logged and unlogged sites in 1989, but the result may be due to sampling error. Although *Aneides hardii* populations persist through the first intensive cutting, they may not survive the repeated 10-year logging cycle that is planned by the U.S. Forest Service. More frequent cutting may destroy the present subterranean habitat structure which is probably vital to the salamander's survival.

INTRODUCTION

Woodland salamanders are a diverse tribe (Plethodontini, "plethodonines") of lungless salamanders (Plethodontidae) that are characterized by a complete suppression of the larval stage; eggs are laid in terrestrial nests and the hatchlings look like miniature adults (Wake 1966). Being freed from the necessity of breeding in bodies of water, plethodonines have colonized moist forest litter habitats throughout the United States.

Many plethodonine species are small, isolated fragments of former, more widespread distributions (Wake 1966). This fact, combined with their low vagility and susceptibility to heat and desiccation, make the continued existence of many species especially vulnerable to habitat changes, whether they result from long-term climatic trends or from alterations by humans and their agents.

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³Museum Specialist, National Ecology Research Center, U.S. Fish and Wildlife Service, 4512 McMurry Avenue, Fort Collins, CO, 80525. Previous studies of terrestrial salamanders in disturbed areas have concentrated on the effects of logging and fire, which are probably the most pervasive human-mediated disturbances at the present. The majority of these studies were done in the Pacific Northwest, and many of the results were presented in two symposia (Ruggiero et al. 1991, Szaro et al. 1988). Other studies were carried out in Virginia, Alabama, North Carolina, and New York (Ash 1988, Blymyer and McGinnes 1977, Dodd 1991, Petranka et al., in press, Pough et al. 1987). These studies are correlational, i.e., the researchers compared the numbers of salamanders or burrows observed on forest lands that were in different stages of recovery from disturbance.

We feel that the reliability and generality of the detailed conclusions reached in most or all of these studies suffer from two important drawbacks. One is the bias introduced by sampling methods. All of the studies cited above, except that of burrow counting, depend on the detection of salamanders on or near the surface. Plethodonines are fossorial and an unknown percentage of the population is on the surface at any one time (Dodd 1990). The assumption that this percentage is the same in distinct sampling environments is probably wrong. Because of the unknown effects of this factor, it is probably misleading to compare directly the numbers of salamanders sampled in logged and unlogged habitats. The most reliable conclusions are drawn where species are ubiquitous and abundant in mature forests but absent from areas that have been recently cleared. Such is the case for Plethodon vonahlossee in North Carolina (Petranka et al., in press).

One study has overcome the drawback of unknown population sizes. Using a mark-recapture technique to estimate populations, Ash (1988) succeeded in marking about 80% of the salamanders on forested and clearcut plots during the first, second, and fourth summers after cutting. He clearly documented the disappearance of *P. jordani* from the cut plots.

The second drawback present in all previous studies stems from the fact that plethodonine salamander populations are often patchy, even in relatively uniform habitats (pers. obs.). If no prelogging studies are done, the absence of salamanders on a disturbed plot can be interpreted in three ways: the sampling is inadequate, they were eliminated by the disturbance, or they were not there in the first place. In this study, we examined plots before and after logging in an experimental approach that evaluated the effects of logging on the Sacramento Mountain salamander, *Aneides hardii*.

The Sacramento Mountain salamander is restricted to three disjunct areas of the high mountains of southcentral New Mexico (Wake 1965). The northernmost population is found in the Capitan Mountains of Lincoln County. Towards the southwest, two other populations inhabit the Sacramento Mountains; one is centered on Sierra Blanca Peak, Lincoln County, in the central part of the mountain chain, and the other occurs from Cloudcroft, Otero County, southward to the southern end of the mountain range. Salamanders are found from about 2,400 m to the top of Sierra Blanca Peak (3,570 m; Moir and Smith 1970). Most of the salamander's mixed-conifer forest habitat occurs within the Lincoln National Forest, with small amounts on the Mescalero Apache Indian Reservation and on private lands. The distribution is a fragmented relict of one that was continuous in cooler and moister periods during the Pleistocene (Lowe 1950, Murray 1957, Pope and Highton 1980).

Although much of the range of *A. hardii* has been subject to logging for about 100 years, the Forest Service has recently adopted a plan that will increase the intensity and geographic scope of logging beyond historic levels (U.S. Forest Service 1986a). During the current 10-year plan, logging will only take place within the range of the southernmost population enclave of the salamander (U.S. Forest Service 1986b), but future plans may include logging of the Sierra Blanca and Capitan Mountains habitats.

Logging is the primary threat to the Red Hills salamander, *Phaeognathus hubrichti*, one of six

plethodontid species on the U.S. List of Threatened and Endangered Species (Dodd 1991, Greenwalt 1976, U.S. Fish and Wildlife Service 1991), and timber harvest is implicated in the declines of many of the 29 other species of woodland salamanders, including *A. hardii*, that are either under review or proposed for listing by the U.S. Fish and Wildlife Service (Drewry 1991, Jacobs 1988). *Aneides hardii* is currently listed as endangered by the New Mexico Department of Game and Fish.

In response to the expressed concerns of environmentalists and government agencies, the Lincoln National Forest funded a series of studies designed to measure the impact of logging on populations of the Sacramento Mountain salamander. The research described here was a part of these studies.

DESCRIPTION OF THE HABITAT

The mixed-conifer forest inhabited by A. hardii is found above 2,400 m. Selective and clearcut logging has been extensive during the last 100 years on slopes less than 40%, but the study areas were all mature forests with some characteristics of old-growth (downed logs, snags, large trees). Dominant overstory species include white fir (Abies concolor) and Douglas-fir (Pseudotsuga taxifolia) with lesser amounts of Engelmann spruce (Picea engelmanni) and southwestern white pine (Pinus strobiformis). Rocky Mountain maple (Acer glabrum), gooseberry (Ribes spp.), and oceanspray (Holodiscus dumosus) share the open understory with seedling conifers and downed logs in various stages of decay.

Prior to the present logging cycle, ground cover was predominantly litter (conifer needles and twigs) in all sites except one, where the dominant cover was loose rocks. Herbs, woody debris (branches, logs, and bark), and moss were other common components of the ground cover. Limestone rocks and boulders are exposed on the slopes.

Ramotnik and Scott (1988) showed by multivariate analysis that the salamander was more common in areas at higher elevations with Engelmann spruce, large white fir and Douglas-fir trees, and large downed logs. Salamander presence was negatively correlated with the presence of white and ponderosa pine (*Pinus ponderosa*). Salamander populations were ubiquitous above 2,800 m, but they were scarce and patchy at lower elevations.

METHODS

Between 1986 and 1990, we sampled 21 sites inhabited by salamanders in mature mixed-conifer forest on or near four timber sales in the Lincoln National Forest, Otero County, New Mexico (2,700-2,900 m elevation). Sixteen of the sites were experimental and scheduled to be logged, and five sites served as unlogged controls. At an arbitrary spot near the center of each site on a 20 by 50 m plot, we recorded the species and diameters of the trunks of trees greater than 2 m tall. We measured ground cover, woody debris, percent slope, aspect, and canopy cover on a 2 by 50 m plot that bisected the larger plot parallel to the slope. Five sites were established in 1986, seven more were added in 1987, four in 1988, and five in 1989.

Almost half of the sites had a northern aspect (315°-45°), but aspects of the other sites included all of the remaining cardinal points. Slopes varied from level to 70%, but most were between 25% and 40%. Canopy cover was 50% to 91%.

Salamander populations were assessed during wet weather by time-constrained searches (TCS; Bury and Raphael 1983, Campbell and Christman 1982, Corn and Bury 1990, Raphael and Rosenberg 1983) in the immediate vicinity of the vegetation sites. Searches were 1 person-hour in duration in 1986 and 2 person-hour thereafter. During the searches, one to four workers turned cover objects and tore apart rotted logs. Salamanders were counted and usually measured from the tip of the snout to the posterior margin of the vent. All sites were not surveyed each year. In order to evaluate the technique, TCS were repeated two to four times on 18 unlogged sites, nine of which were sites not associated with this logging study.

Two sites were logged between the 1986 and 1987 salamander activity seasons, six were logged between the 1987 and 1988 seasons, one plot was logged before the 1989 season, and seven sites were logged before the 1990 season. Logging methods and intensity varied among the sites, but the final result was a very open woodland where sunshine penetrated to the surface litter (fig. 1). Slash was either left in place or piled. Three of the sites (BR 1-3) were logged by cable and the other 13 were tractor logged. Salamander populations were evaluated again by TCS after logging.

The results of TCS are very dependent on the sampling environment (Corn and Bury 1990). The unlogged forests that we sampled are structurally very similar, but the habitat is very different after they are

logged. For this reason, it is unrealistic to compare directly the number of salamanders in unlogged and logged sites. However, long-term trends can probably be detected by repeated TCS sampling in the same habitat through several years.

Salamanders are long-lived, and populations could persist for many years even though reproduction may be inadequate to permanently maintain the population (Hairston 1987). Therefore, the success or failure of reproduction and juvenile survival may be one of the first clues to the future trajectory of the population. We studied the size class distributions of salamanders in the 1990 samples for insight into the question. Sixteen logged and five unlogged sites were compared by the Chi-square test (Siegel 1956). Differences in sample distributions were considered significant when P < 0.05.





Figure 1.--Mixed conifer forest plots before (above) and after (below) tractor logging, Lincoln National Forest, Otero County, New Mexico. The logged forest is a result of the least intensive type of logging practiced in this area.

RESULTS

Counts of the number of salamanders in repeated TCS on the same unlogged sites differed by as much as a factor of almost 6, but differences were usually less than 50% (table 1). The use of the TCS technique before and after logging yielded results that are reliable enough to evaluate the immediate question of whether or not *Aneides* populations survived through the actual logging process. However, because of their variability, TCS results must be used conservatively, and long-term population trends can only be detected in samples repeated over several years.

Aneides hardii was present in our samples on all sites except one before and after logging (table 2). In 1990, two sites had been cut for 3.5 years, six had been cut for 2.5 years, one had been cut for about 1.5 years, and seven had been cut for about 6 months.

The distribution of size classes of salamanders in logged and unlogged sites differed in 1990 (P < 0.01, fig. 2).

DISCUSSION

Time-constrained searches are subject to biases that are not usually explicitly recognized by workers who use them (Aubry et al. 1988, Bury 1983, Ramotnik and Scott 1988, Raphael 1984, 1988, Raphael and Barrett 1984, Welsh 1987, Welsh and Lind 1988, 1991) although Bury and Corn (1988) and Corn and Bury (1990) discussed some of the problems, and Bury and Raphael (1983) and Raphael and Rosenberg (1983) compared the efficiency of TCS with other sampling techniques.

There are several possible sources of bias and inconsistency in TCS. Salamanders move both horizontally and vertically in the soil column, depending on the weather and the season (Fraser 1976, Heatwole 1962 and references therein, Jaeger 1979, 1980). Different sexes and ages migrate differently. For instance, we observed that brooding *Aneides* females stay with their nests, resulting in fewer adult females on the surface during most of the summer. Salamanders are differentially vulnerable to TCS in different habitats.

Table 1.--Validation of the time-constrained search (TCS) method for *Aneides hardii*, Lincoln National Forest, Otero County, New Mexico. Numbers are salamanders found during TCS for 1 person-hour (1986) or 2 person-hour (1987-1990). All sites were unlogged and some were searched twice in 1 year. All searches were between 1 June and 1 September, and unusually dry periods were avoided. Dashed lines indicate that searches were not conducted.

Site no. Median			Year			
	1986	1987	1988	1989	1990	
BR 6	9.5		9	10	20	7
BR 7	35		10	28	41	57
TU 4	28		31	25		
TU 5	88			38	88	92
SS 1			23-22			
T 2		0	0			
T 3		0	0-2			
T 10		0	0			
T 20		0	0-0			
T 21		0	0-0			
T 30		0	0			
T 45		0	0-0			
HA 1	36			31	41	
HA 2	27			24	29	
HA 3	36			36	43	17
HA 4	39		33		44	
MO 4	2.5				3	2
SA 4	12		7			17

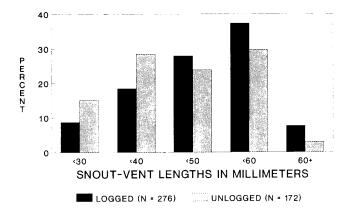
Table 2.--Numbers of *Aneides hardii* found on permanent study sites before and after logging, Lincoln National Forest, Otero County, New Mexico. LC indicates when the site was cable logged, and LT indicates when the site was tractor logged. Dashed lines indicate that searches were not conducted. Numbers of salamanders found before and after logging should not be compared because of differing search environments.

					Year				
Site no.	1986		1987		1988		1989		1990
BR 1	20*			LC	9		19		16
BR 2	26*			LC	15		15		8
BR 3	52*			LC	41		31		23
BR 4	13*	LT	14		15		34		57
BR 5	8*	LT	6		24		34		12
BR 6 (control)			9		10		20		7
BR 7 (control)			10		28		41		55
TU 1			14	LT	20		19		41
TU 2			28	LT	14		23		34
TU 3			10	LT	9		24		8
TU 4			31		25	LT	34		20
TU 5 (control)					38		88		92
HA 1					31		41	LT	12
HA 2					24		29	LT	6
HA 3 (control)					36		43		17
HA 4			33				44	LT	15
HA 5							49	LT	27
MO 1							0	LT	0
MO 2							5	LT	1
MO 3							9	LT	1
MO 4 (control)							3		2

^{*} Number of salamanders extrapolated to 2-hour equivalent based on a 1-hour search.

DISTRIBUTION OF SALAMANDER SIZES 1990

Figure 2.--Distribution among size classes of *Aneides hardii* in samples from logged and unlogged sites in 1990, Lincoln National Forest, Otero County, New Mexico. Salamanders were collected from 16 logged sites and 5 unlogged sites. Differences are significant ($\chi^2 = 15.2$, 4 d.f., P < 0.01).



Aneides is most often found in forested areas with deep surface litter and many large decayed logs; during dry weather salamanders can still be found in the hearts of moist rotted logs. However, salamanders also occur on sparsely vegetated rocky slopes, where they are abundant under rocks in damp weather, but they disappear entirely during extended dry spells.

Another problem that TCS shares with other sampling methods is that we have very little idea about the relation between the numbers sampled and actual population density. This is especially serious when making comparisons between species that might be expected to be differentially vulnerable to sampling (Welsh and Lind 1988). The solution to this problem requires a large number of species-specific markrecapture studies, such as those carried out by Hairston (1987) and Ash (1988).

The destructiveness of TCS is a drawback to its use in some studies. Where space is limited, repeated TCS would rapidly modify or destroy much of the surface structure. In these cases, a less destructive method such as nighttime lantern searches is needed (Gordon et al. 1962, Pough et al. 1987), although *A. hardii* does not seem to be active in large numbers on the surface at night (pers. obs.).

There are no clear trends in the numbers of salamanders taken on either the experimental or the control sites (table 3). Although searches in the logged sites consistently yielded fewer salamanders than in the unlogged sites, the discrepancy could be simply a

Table 3.--Trends in salamander abundance in timeconstrained searches, Lincoln National Forest, Otero County, New Mexico. Numbers of salamanders taken on logged and unlogged sites should not be compared because of differing search environments.

	1986	1987	1988	1989	1990
UNLOGGED SITES Number of searches Salamanders/search	5 23.8	7 19.3	7 27.4	12 31.0	5 34.6
LOGGED SITES Number of searches Salamanders/search	 	2 10.0	8 18.4	9 25.9	16 17.6

consequence of differing search conditions and not necessarily a reflection of differences in total salamander numbers.

The significant difference between the size distributions of salamanders on the control and experimental sites in the 1990 surveys is perhaps indicative of incipient long-term population trends, although it may be merely a sampling artifact. With respect to the control sites, the logged sites had relatively fewer juvenile salamanders (<40 mm snoutvent length, SVL) and more adults (SVL >50 mm; fig. 2). If this pattern continues, it may signify reduced reproduction or survivorship among young salamanders in logged sites.

Removal of canopy cover can increase insolation, ground temperatures, and evaporative water loss (Geiger 1971). Diurnal, and probably annual, fluctuations are also greater after deforestation (Blymyer and McGinnes 1977, Bury 1983), and heavy machinery compacts the soil which may destroy subterranean passages (Buhlmann et al. 1988, Scott, pers. obs.). The important observation is that *Aneides* populations have survived these disturbances, at least for the short term.

Long-term survival is another question. It is still too early to determine if the *Aneides* in logged areas are reproducing at a rate that will sustain the populations, or if they will slowly disappear. The present Forest Service plan calls for a 10-year cutting cycle; that is, each logging sale will be evaluated every 10 years to determine if there is a merchantable amount of timber (U.S. Forest Service 1986b). The effects of almost continuous disturbance on salamanders cannot be predicted because this type of intensive management has not been attempted before in this forest.

Salamander populations may not be so resilient to repeated perturbations at lower, warmer elevations. Ash (1988) and Petranka et al. (in press) documented the disappearance of plethodonines after logging at lower elevations in the Appalachian Mountains. *Aneides* becomes scarce near their lower elevational limits (2,400-2,700 m), populations are restricted to mesic microhabitats, and they are absent from many sites that appear to be suitable. Logging in these areas could have an entirely different effect than at higher elevations. Postlogging studies of sites now in place at lower elevations are planned to examine this question.

A key factor in *Aneides* biology is the subterranean habitat; salamanders spend about 8 months below the

soil surface. Very few egg masses have been found, indicating that the bulk of nesting takes place underground. The soil is compact and it freezes to at least 10 cm deep. Observations made in soil pits indicate that the only apparent routes to these depths are through rotted-out root channels. Under the new cutting regime, it remains to be seen if trees cut at smaller diameters can produce the large, deeply penetrating roots that allow salamanders access to subterranean nesting and hibernating chambers.

Other species of plethodontid salamanders in different types of forests, at lower elevations, and in different structural habitats will respond to forest disturbance in different ways. Generalizations about the effects of logging on plethodontid salamanders will have to wait until we know much more about how salamanders use the habitat and how this use is modified by different logging practices (F.H. Pough, in litt.).

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Black Bear Damage to Old-Growth Trees Around Middens of Mount Graham Red Squirrels¹

Andrew A. Smith,² R. William Mannan,² and Russell Davis³

Abstract.—We surveyed black bear (*Ursus americanus*) damage to living and dead trees (snags) around 215 middens of Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in the Pinaleno Mountains of southeastern Arizona. One hundred midden sites in spruce/fir forest were compared to 58 spruce/fir random sites, and 115 midden sites in transition-zone forest were compared to 143 transition-zone random sites. Black bear damage occurred almost exclusively on trees ≥ 18 cm dbh (diameter at breast height) of three species: Engelmann spruce (*Picea engelmanii*), corkbark fir (*Abies lasiocarpa* var. *arizonica*), and white fir (*Abies concolor*). In both forest types, approximately 70% of the midden sites had ≥ 1 damaged tree. The frequency of damage found at random sites was 33% in the spruce/fir forest and 39% in the transition-zone forest. Nine percent of all spruce and fir trees were damaged at spruce/fir midden sites, and 24% were damaged at transition-zone midden sites. The frequency of damage to individual trees at midden sites was more than double that at random sites. Twenty-nine percent of snags in decay classes 1 and 2 were damaged at spruce/fir midden sites, and 39% were damaged at transition-zone midden sites.

INTRODUCTION

The highest elevations of the Pinaleno Mountains in southeastern Arizona support relict stands of coniferous forest and associated wildlife. These stands are over 250 years old on average, contain dense multi-layered canopies, and produce large amounts of decaying wood in the form of logs and snags (Mannan and Smith 1991). These attributes are indicative of old-growth forests (Thomas et al. 1988). The montane ecosystems of which these stands are a part are presumed to have been isolated at least since the end of the Pleistocene, 11,000 years ago (Spicer et al. 1985).

The Mount Graham red squirrel, found only in the Pinaleno Mountains (Hoffmeister 1986), occupies high elevation stands of Engelmann spruce and corkbark fir, as well as mixed-conifer stands at lower elevations (Spicer et al. 1985, Warshall 1986). The U.S. Fish and

Wildlife Service listed the Mount Graham red squirrel as endangered in 1987 because its population was small and declining, its range restricted, its habitat altered by man, and its remaining habitat was threatened by planned human activities (U.S. Fish and Wildlife Service 1987).

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Red squirrels rely on conifer cones stored in caches for winter food supplies (Smith 1968, Rusch and Reeder 1978, Gurnell 1983, Halvorson 1986). Primary caches, or middens, are typically used by a single animal and defended vigorously (Clarke 1939, Kilham 1954, Streubel 1968). Middens must remain cool and moist so that stored cones do not dry, open, and lose their seeds (Finley 1969). Adequate sites for storing cones may be particularly limited in the Pinaleno Mountains because this range is on the southern edge of the geographic distribution of red squirrels, and is hotter and drier than red squirrel habitat at higher latitudes.

The Pinaleno Mountains also support a large population of black bears (Waddell and Brown 1984). Black bears in the Pinaleno Mountains commonly strip bark from the base of trees, apparently to feed on the cambium. Stripping by black bears has been observed in many areas of North America (Zeedyk 1957, Fritz 1951, Lutz 1951, Maser 1967, Giusti 1990), and can cause significant damage to stands of trees (Glover 1955, Mason and Adams 1989). Black bear damage to conifer trees in the Pinaleno Mountains undoubtedly influences the rate of production of snags and logs and the degree of canopy closure in old-growth stands, and thus could potentially effect the habitat of the endangered Mount Graham red souirrel.

We surveyed black bear damage to trees around middens of Mount Graham red squirrels in the coniferous forests of the Pinaleno Mountains. We then compared the frequency of damage to trees at midden sites to the frequency of damage to trees at randomly selected sites scattered throughout the forest.

METHODS

The study area was located in approximately 1,400 ha of the higher elevations (2,680 m - 3,267 m) of the Pinaleno Mountains, 25 km southwest of Safford in southeastern Arizona (approx. 32 N latitude). Mean annual precipitation is estimated to be greater than 63 cm above 3,110 m (Martin and Fletcher 1943). Almost half of the annual precipitation falls as rain in July and August, although snowfall in winter months contributes significantly to this total.

We randomly selected 215 of 324 Mount Graham red squirrel middens located as of October 1989. We categorized midden sites by forest type based on elevation (Stromberg and Patten 1989). Stands above 3,110 m were classified as spruce/fir forest and were dominated by Engelmann spruce and cork-bark fir. Stands below 3,110 m were classified as transition-zone forest and were dominated by various combinations of Engelmann spruce, cork-bark fir, Douglas-fir (Pseudotsuga menziesii), white fir, and aspen (Populus tremuloides). One hundred of the selected middens were located in the spruce/fir forest and 115 in the transition-zone forest. Data on midden sites were collected in 1989 and 1990.

We centered circular plots (radius = 10 m, area = 0.03 ha) on these selected middens. We then recorded the species and dbh of living and dead trees (snags) ≥3 cm dbh, the presence of bear damage on each tree or snag, and the decay class of the snags occurring within each plot. Snag decay class estimates were based on criteria developed by Cline et al. (1980) and Horton and Mannan (1988): class 1 – branches, twigs. and possibly needles present, top of bole pointed, nearly all bark remaining, sapwood intact; class 2 branches present but broken, bole broken near top, most bark remaining on bole, sapwood decaying; class 3 – branches broken near bole, bole broken, little bark remaining, sapwood friable, heartwood decaying but firm; class 4 - branches gone, bole broken at less than half original height, bark gone, sapwood mostly gone, heartwood soft; class 5 - branches gone, bole broken close to breast height, bark gone, sapwood gone, heartwood friable.

A grid system placed over a map of areas surveyed for red squirrel middens through October 1989 was used to select 201 random sites. We located each site in the field by pacing a distance and direction from a known landmark (e.g., a bend in a road, a trail junction). Plots at random sites were characterized in a manner identical to that described above for midden sites, and categorized as occurring in spruce/fir forest (n = 58) or transition-zone forest (n = 143) based on elevation. The combined total area of all random sites was 6.31 ha, or 0.5% of the total study area. We collected data at all random sites in 1990.

Data from midden and random sites in each forest type were summarized into percentages of plots, trees, and snags with bear damage. Percentages were compared using a chi-square test for homogeneity (Ott 1988).

RESULTS

Black bear damage in the Pinaleno Mountains occurred almost exclusively on trees ≥ 18 cm dbh (fig. 1). In the spruce/fir forest, Engelmann spruce and cork-bark fir were the only species damaged by black bears. In the transition-zone forest bears also damaged significant numbers of white fir trees. The following analysis is limited to these 3 species, and to trees and snags ≥ 18 cm dbh.

In both forest types, approximately 70% of the midden sites had ≥ 1 tree with bark stripped at the base (fig. 2). Among random sites, the occurrence of such damage ranged from 32% in the spruce/fir forest to 38% in the transition-zone forest. Overall, 9% of the trees within midden plots were damaged in the spruce/fir forest (fig. 3) and 24% in the transitionzone forest (fig. 4) - in each case >2 times the percentage of damaged trees at random sites. The average number of trees damaged per plot was 1.85 and 0.66 at spruce/fir midden and random sites, and 3.18 and 0.79 at transition-zone midden and random sites, respectively. Most of the trees damaged by black bears at midden sites in both forest types were cork-bark firs: 119 of 185 (64%) damaged trees in the spruce/fir forest (fig. 3) and 311 of 366 (85%) in the transition-zone forest were cork-bark firs (fig. 4).

We could reliably determine black bear damage only on snags in decay classes 1 and 2, because the evidence is obscured in later stages of decay with the deterioration of bark and sapwood. In both forest types, there were significantly more snags in decay classes 1 and 2 with bear damage at midden sites than at random sites (fig. 5).

DISCUSSION

Black bears in the old-growth forests of the Pinaleno Mountains damaged more trees, particularly cork-bark fir, adjacent to middens of Mount Graham red squirrels than at random locations throughout the forest. There are several potential explanations for this relationship. For example, bears may select trees for food for the same reasons red squirrels use them. If red squirrels choose highly productive sites where trees supply more or more nutritious cones or buds, these same trees are likely also to have cambiums rich in nutrients or moisture and be more attractive to bears. Or, it may be that bears prefer to feed on trees in dense stands, such as those occurring near red squirrel middens (Mannan and Smith 1991), because such sites satisfy the cover requirements of bears.

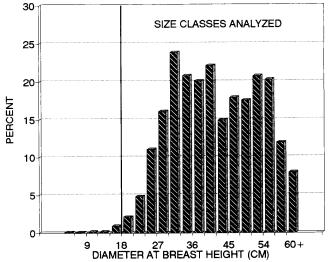


Figure 1. Percent of trees with black bear damage in 3 cm dbh increments at midden sites of Mount Graham red squirrels and random sites (combined) in the spruce/fir and transition-zone forests of the Pinaleno Mountains, Arizona, 1989-1990. Vertical line marks trees that were included in this study (to the right) and those that were not (to the left).

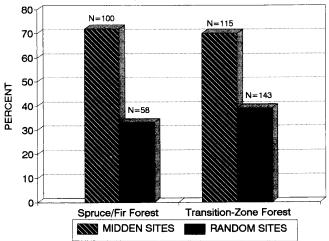


Figure 2. Percent of plots at midden sites of Mount Graham red squirrels and random sites with ³ 1 tree with black bear damage in the spruce/fir and transition-zone forests of the Pinaleno Mountains, Arizona, 1989-1990 (spruce/fir: X² = 23.13, 1 d.f.; transition-zone: X² = 23.69, 1 d.f.)

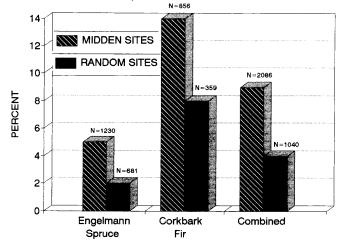


Figure 3. Percent of trees at midden sites of Mount Graham red squirrels and random sites in the spruce/fir forest, Pinaleno Mountains, Arizona, 1989-1990 (Engelmann spruce: X² = 15.88, 1 d.f.; corkbark fir: X² = 9.69, 1 d.f.; combined: X² = 28.51, 1 d.f.).

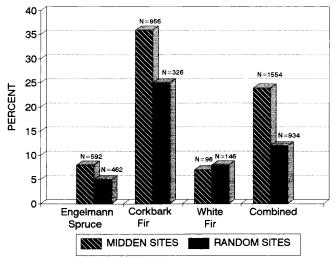


Figure 4. Percent of trees at midden sites of Mount Graham red squirrels and random sites in the transition-zone forest, Pinaleno Mountains, Arizona, 1989-1990 (Engelmann spruce: X² = 4.72, 1 d.f.; corkbark fir: X² = 13.86, 1 d.f.; white fir: X² = 0.003, 1 d.f.; combined:

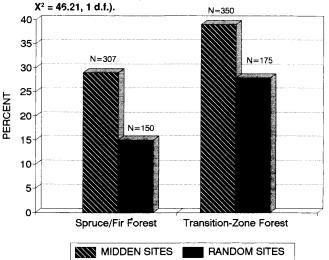


Figure 5. Percent of snags in decay classes 1 and 2 at midden sites of Mount Graham red squirrels and random sites in the spruce/fir and transition-zone forests, Pinaleno Mountairis, Arizona, 1989-1990 (spruce/fir: X² = 10.21, 1 d.f.; transition-zone: X² = 6.62, 1 d.f.).

Black bear damage frequently kills the trees on which it occurs (Glover 1955, Mason and Adams 1989), and potentially influences the habitat of the endangered red squirrel. Mount Graham red squirrels choose unusually dense, closed-canopy stands in which to forage and place their middens (Froehlich 1990, Mannan and Smith 1991). Significant damage by bears to these areas, as observed in the current study, eventually could have a negative influence by opening the canopy and making these sites less suitable for middens. In addition, the loss of trees from bear damage must surely result in the loss of sources of food or cover for red squirrels. However, Mannan and Smith (1991) also found that midden sites occurred in areas with large amounts of decaying wood in the form of snags and downed logs - both of which are important for red squirrel survival. Therefore, bear damage also may provide a significant positive influence by contributing to the dead

wood component required of sites used by red squirrels. We believe that both the negative and positive processes described above are occurring in the Pinaleno Mountains.

The complexity of the situation is magnified when one considers that the frequency at which new bear damage occurs undoubtedly varies over time. When bear populations are high, the probability of new tree damage increases. This correlation is probably intensified in years of low precipitation, when spring forage for the bears is scarce and tree cambium then becomes an important food supply.

Such annual and seasonal variability in new bear damage may partly explain why the ratios of snags and trees with and without bear damage were similar in our study. This similarity could be interpreted as evidence that bear damage was not an important factor in the production of snags. Such an interpretation would require the assumption that if bear damage did kill many trees the ratio of snags with damage to those without would be higher than the ratio of trees with damage to those without. However, if relatively few trees were damaged by bears in years just prior to our study compared to the damage occurring during our study, then the ratios of snags and trees with and without bear damage could be similar.

If the frequency of bear damage is variable over time, we can envision 3 resulting scenarios. (1) In some years very little damage occurs and thus there is very little effect on red squirrel habitat; (2) when bear damage reaches a certain minimum level, snags are created without significantly disturbing the forest canopy, thus enhancing the suitability of sites for midden storage (after a time lag of several years for the damaged trees to die and decay); and (3) when bear damage is high, the forest canopy is significantly disturbed after the trees die, and the number of potential midden sites decreases. The degree and sequence of these scenarios from year to year could greatly influence red squirrel numbers in a limited area such as the Pinaleno Mountains.

Whatever the nature of the interaction of black bear damage to old-growth trees and red squirrels in the Pinaleno Mountains, it is evident that such a relationship does exist. The damage that black bears inflict on trees certainly influences processes that affect the structure of old-growth forests, particularly where red squirrels middens are located. Because we are dealing here with two sensitive species of mammals isolated together in a sensitive forest type of limited area, we feel strongly that further examination of these interactions is warranted.

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Effects of Moderate Timber Harvesting in an Old-Growth Arizona Mixed Conifer Watershed¹

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Abstract.—There is growing interest in the development of silvicultural prescriptions that will maintain old-growth characteristics while allowing some degree of commercial utilization. A silvicultural prescription based on small patch-clearcut and group-selection openings and single-tree selection in most remaining areas was evaluated in a watershed supporting an old-growth mixed conifer stand. The treatment resulted in increased residual tree growth and in relatively constant stand growth. The stand retained its uneven-aged structure and relative species composition. The watershed has retained many of the desired old-growth attributes although many of the largest trees were harvested. The increased growth rates indicate that the basal area in larger trees should recover relatively rapidly. Tree regeneration also has been satisfactory. In addition, the treatment resulted in significant increases in mean annual water yields and in herbaceous plants for livestock and wildlife use. Nongame birds were generally unaffected by the treatment.

INTRODUCTION

The question of proper management of the remaining old-growth forests of the Southwest, as well as of the rest of the United States, has resulted in heated technical debates among land managers. There are strong arguments for preserving existing old-growth stands to maintain proper habitats for a variety of threatened and common wildlife species; to maintain biological diversity of the forests and genetic diversity of the component species; to provide a living laboratory for numerous ecological investigations; to maintain historical reference areas; and to provide for aesthetic experiences. Even limited harvesting will affect a stand's old-growth status by reducing the basal area in larger trees and eliminating future snags and sources of forest floor debris. However, there are questions whether silvicultural prescriptions can be developed that will maintain old-growth attributes while allowing commercial utilization in some of the stands or that will accelerate the development of old-growth characteristics in older stands which may not currently qualify for this status. In order for managers to make decisions, they must understand how the different forest resources and values, including old-growth, will respond to their activities.

Southwestern mixed conifer forests account for many of the remaining old-growth stands in Arizona, New Mexico, and southwestern Colorado and, therefore, are at the center of much of the current management reevaluation. Mixed conifer stands usually

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are found on moist sites above 2,438 m in elevation. There are about 1.1 million hectares of mixed conifer and associated spruce-fir and aspen forests in Arizona and New Mexico (Choate 1966, Conner et al. 1990). These forests produce a wide range of commercial and noncommercial products. They are important for the timber industry and provide valuable habitat for game and nongame wildlife species as well as forage for livestock. In addition, they provide recreational opportunities for local and nearby urban populations. The forested watersheds, which receive relatively large amounts of precipitation, are the headwaters of most of the major rivers in the Southwest.

In the mid-1970s, prior to the current technical controversy, two mixed conifer watersheds were selected in eastern Arizona as the site of a mixed conifer resource evaluation project. The project was designed to demonstrate and evaluate the existing knowledge of integrated resource management for mixed conifer forests. A new resource allocation procedure developed and described by Brown (1976) indicated that a prescription using patch clearcutting, in conjunction with single-tree and group selection methods, should produce the highest level of return for the mix of timber, watershed, range, and wildlife resources. Harvesting of mixed conifer forests to create small openings has been advocated as a method of increasing water yields from relatively moist forested areas (Hibbert 1979, Rich and Thompson 1974), as well as enhancing other resource values. This prescription is consistent with the silvicultural recommendations of Alexander (1974) and Jones (1974) for southwestern mixed conifer forests; however, such a prescription had not been previously tested in the Southwest. Consequently, several experiments were conducted to evaluate its effects on the different forest resources

such as water yields, stand structure and growth, tree regeneration, herbage production and utilization, and wildlife habitat impacts.

This paper summarizes the impacts of the prescription for initial harvesting in an old-growth stand on stand growth and development, natural and advance regeneration, water yields, herbage production and utilization, and wildlife resources. While the maintenance of old-growth characteristics was not an original concern, we will attempt to show that the stand retained many of the desired stand features associated with old-growth forests following the prescribed harvesting treatment. In addition, accelerated growth of residual trees following treatment should result in a more rapid recovery in the number of larger trees, which is an important characteristic of old-growth stands.

STUDY AREA

The study was conducted on the Thomas Creek watersheds, which are located within the Apache-Sitgreaves National Forests of east-central Arizona, approximately 24 km south of Alpine. The South Fork watershed, which covers 227.4 ha, was treated, while the adjacent 189.0 ha North Fork watershed served as the experimental control area. Elevations on South Fork range from 2,545 to 2,789 m, and those of North Fork range from 2,545 to 2,819 m. The most common soils on the watersheds are Mollic Eutroboralfs and Mollic Cryoboralfs derived from basalt parent materials. Soil depths generally vary from 50 to over 100 cm, except along the channel where deeper soils occur.

Average annual precipitation (with standard error) for the 23 years of record (1964-1986) was 768 ± 36 mm. Approximately 56% of the precipitation occurs during the October through May winter period, mainly as snow, which can remain on the ground into May. July and August receive the most monthly precipitation with respective means of 114 ± 7 mm and 112 ± 9 mm, and May receives the least moisture with an average of 22 ± 5 mm.

Streamflow has been measured on South Fork since the 1963 water year (October through September) and at North Fork since the 1966 water year (Gottfried 1991). Annual runoff during the period prior to treatment in 1978 averaged (with standard error) 82 ± 31 mm on South Fork and 69 ± 29 mm on North Fork. Over 80% of the runoff on both watersheds occurs in March, April, and May.

FOREST STAND CHARACTERISTICS

The two Thomas Creek watersheds originally supported undisturbed, multistoried, southwestern mixed conifer stands. Although a formal old-growth rating system did not exist in the 1970s, the watersheds were considered to support old-growth stands. They met Hunter's (1989) criteria that old-growth stands should not have been harvested and should have scattered dominant trees, which are declining because of old age. The stands should have large amounts of dead and down material. Much of the area probably would also have received high ratings under a system used by the Southwestern Region of the USDA Forest Service4 for evaluating old-growth stands, although such surveys have only recently been conducted. The Forest Service system, which uses a scale with 100 possible points, is based on the patchiness; and the presence of decadent trees, amount of basal area in large trees; variation in tree sizes and spacing; vertical structure; snags, and dead and down material.

The stands consist of mosaics of groups and patches of varying sizes. Patches could be singlestoried or multistoried, but the overall effect was of a multistoried stand (Jones 1974). Composition also was variable, with some areas containing one species and other areas containing up to eight tree species. The major species are Engelmann spruce (Picea engelmannii), blue spruce (P. pungens), Douglas-fir (Pseudotsuga menziesii var. glauca), white fir (Abies concolor), corkbark fir (A. lasiocarpa var. arizonica), ponderosa pine (Pinus ponderosa), southwestern white pine (P. strobiformis), and quaking aspen (Populus tremuloides). Fitzhugh et al. (1987) classified the stands as belonging to the Picea engelmannii / Senecio cardamine habitat type (PIEN/ SECA), Abies concolor phase. Other habitat types appear to occur locally within the watersheds; for example, the Abies concolor/Muhlenbergia virescens (ABCO/MUVI) and the Abies concolor / Quercus gambelii (ABCO/QUGA) habitat types appear to occur on drier sites (Moir 1990, pers. comm.; USDA Forest Service 1986).

The original timber inventory in 1969 measured 41.3 m²/ha of basal area and 1,097 trees/ha on South Fork, and 39.0 m² and 1,878 trees/ha on North Fork. Regressions of the relationship between number of trees per hectare and 5-cm diameter class (Husch et al. 1972) indicated that the two stands exhibited an almost balanced uneven-aged stand structure (Gottfried 1989). Measurements were made at permanent inventory points using standard point sampling procedures based on a 25 BAF gage (Husch et al. 1972)

The initial diameter distribution regressions for both areas had coefficients of determination (R²) values of 0.99, indicating a lack of disturbance (Gottfried 1978). Dieterich (1983) determined that the watersheds have not burned since 1893; but prior to fire suppression activities, the mean fire interval for major or area-wide fires was 22 years. Smaller fires affected limited areas of the watersheds during

⁴U.S. Department of Agriculture, Forest Service, Apache-Sitgreaves National Forests. 1990. Manual for old growth inventories. (Unpublished document)

periods between the major fires. This study also provided evidence of the relatively old age of some of the trees on the watersheds. Dieterich (1983) determined that several ponderosa pine and southwestern white pine trees originated from the early seventeenth century.

Dwarf mistletoes (Arceuthobium spp.) are parasites on many of the tree species present in southwestern mixed conifer forests. Gottfried and Embry (1977), working in an area that included Thomas Creek, found that 21% of the Douglas-fir and 38% of the ponderosa pine trees were infected with these parasites. Dwarf mistletoes also were observed on a small number of spruce and white pine. Dwarf mistletoes accounted for 4% of the mortality in the general area (Gottfried 1978). Wind-related mortality, which is often associated with root or rot-causing diseases, accounted for 17% of the natural mortality, especially on Engelmann spruce, corkbark fir, quaking aspen, and Douglas-fir.

THE TREATMENT

Prescription

South Fork was divided into six land response units (fig. 1) according to Brown (1976) to facilitate

applying the operational resource allocation and utilization procedures. The land response units were divided on the basis of slope, aspect, or unique features such as the stream bottom. The downstream section of the watershed, which contained two and a half units, was not treated because of locally steep slopes; a wet meadow in the upper part of the watershed was also left undisturbed. The selected prescription called for group selection with a 30% reduction in basal area, and single-tree selection in the adiacent stand in Unit 3 (94.3 ha); patch clearcutting of 0.5 to 0.8 ha openings over one-third of the area, and single-tree selection in the adjacent areas in Unit 4 (64.4 ha); and single-tree selection with a 30% reduction in sawtimber basal area in upstream section of Unit 5 (11.3 ha), which included the areas adjacent to the upper stream channel.

The marking guides and rules, which were typical of the 1970s, indicated that groups and individual trees would be selected for harvesting on the basis of poor or high risk, overmaturity, dwarf mistletoe infection, and other defect criteria. Attempts were made to protect poles and advance regeneration within patches. In addition, snags were to be left; squirrel trees and living culls were to be cut only in the patches and groups. Logging slash, generally greater than 20 cm in diameter, was to be skidded to

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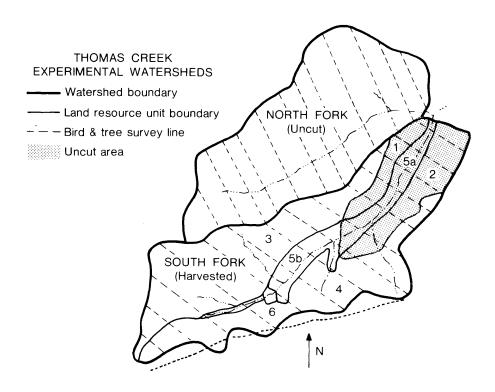


Figure 1. Map of the Thomas Creek Watersheds showing the land response units and inventory lines.

The lower end of South Fork was not harvested because of steep slopes.

Table 1. Stand changes in the Thomas Creek South Fork harvesting unit for trees ≥ 2.5 cm diameter breast high (on a per hectare basis). The 1979 values reflect growth of survivor trees and the reductions associated with harvesting and natural mortality, but not values associated with new ongrowth trees (Gottfried, in press).

1974					1979						
Species	Basal a	a <u>rea</u> (SE)	Trees (no.)	Total tree volume (m³)	Basal a	area (SE)	% change	Trees (no.)	% change	Total tree volume (m³)	% change
Engelmann spruce	2.87	0.30	47.05	16.30	2.20	0.51	23	37.71	20	11.88	27
Blue spruce	1.59	0.56	19.52	10.20	1.04	0.46	35	15.37	21	5.84	43
Douglas-fir	15.20	1.27	303.56	78.73	9.83	1.06	35	233.31	23	45.34	42
White fir	9.22	1.04	127.87	63.72	5.37	0.75	42	68.35	46	33.86	47
Corkbark fir	0.85	0.32	18.66	4.27	0.73	0.28	14	17.32	7	3.07	28
Ponderosa pine	7.02	0.82	100.22	59.28	3.85	0.60	45	84.58	16	29.33	50
S.W. white pine	4.52	0.61	159.35	22.59	3.18	0.55	30	116.33	27	14.40	36
Quaking aspen	4.52	0.82	117.27	17.51	4.03	0.76	11	101.14	<u>14</u>	15.08	<u>14</u>
Total	45.79	1.79	893.50	272.60	30.23	$\frac{-1.85}{1.85}$	34	674.11	$\overline{25}$	158.80	$\overline{42}$

landings, machine-piled and burned, while smaller slash was to be lopped and left.

Harvest

The main harvesting activities began in May 1978 and continued through January 1979, removing approximately 13,924 m³ net volume. The harvest resulted in a significant 34% reduction in the total basal area of the treated area and a 25% reduction in the number of trees (table 1). The 1979 values reflect growth of trees which were present in 1974. The reduction was 30%, to 32.1 m²/ha, on areas that remained stocked with at least 5.7 m²/ha following the harvest. Ninety-four percent of the 94 inventory points remained stocked, a decline from the earlier 100% level. The only two species to show significant declines in stocking were Douglas-fir and ponderosa pine.

Analysis of aerial photographs from the postharvest period indicated 63 patch-clearcut and group-selection openings of 0.2 ha or larger on Thomas Creek. The average size for all openings was 0.5 ha and ranged from about 0.2 to 1.7 ha. The total area in the 63 openings was 30.5 ha, accounting for 18% of the harvested area and 13% of the total watershed area.

EFFECTS ON FOREST PRODUCTIVITY

One of the initial concerns at Thomas Creek was the impact of the prescribed treatment on forest health and productivity for commercial forest products. This evaluation was based on common stand parameters such as species composition, stand structure and stocking, regeneration success, as well as the growth of the residual trees and the overall stand. Gottfried (in press) presents more details about the measurement and statistical techniques used in this study. Statistics were not used to verify all changes; but where mentioned, statistical significance is indicated by values at the 5% level.

Forest Overstory Productivity

While the initial goal of the treatment was to make the stand more productive by removing high risk trees and accelerating growth of the more vigorous residual trees, the Thomas Creek treatment allows for an evaluation of the consequences of the harvesting on an old-growth mixed conifer stand.

Although many of the largest trees were harvested, stand volume growth did not appear to change dramatically during the posttreatment 1979 to 1986 period when compared to growth during the prior 1969 to 1974 period (Gottfried, in press). Periodic annual gross growth dropped only by 2% from 5.01 m³/ ha to 4.90 m³/ha in the posttreatment period. Overall stand basal area had increased significantly to 36.3 m²/ha between 1979 and 1986, with the largest individual species increases occurring in blue spruce, Douglas-fir, and white pine. Stand volume growth should increase as the residual trees move into larger size classes.

However, periodic annual net postharvest growth did decline from 4.02 m³/ha to 3.28 m³/ha, but this change is influenced by mortality following the harvest (Gottfried, in press). Mortality increased from 0.98 m³/ha/year prior to harvesting to 1.63 m³/ha/year afterwards. Much of the mortality in terms of trees/ha was the result of injuries caused by logging or road construction, especially in the smaller size classes, while most mortality in terms of basal area per hectare was attributed to miscellaneous, multiple, or unknown causes. It often is difficult to determine the exact cause of death. Mortality related to disease, poor vigor, and logging damage should have declined in the present stand and, therefore, net growth should be increasing.

The relative lack of change of the gross volume growth and basal area per hectare values for the stand are an indication that average tree growth has accelerated following treatment. Tree growth in the South Fork treated area was compared to growth in the undisturbed North Fork stand. Evaluations of mean tree growth for all species combined showed

significant increases in diameter and basal area increments for all diameter classes below 58 cm breast height when compared to the sample trees on the control area (Gottfried, in press). Adjusted mean annual growth in the treated area ranged from 0.447 cm for white fir to 0.165 cm for ponderosa pine; the overall average was 0.345 cm. Douglas-fir and white fir showed significant growth for some of the five composite size classes used in the analysis (Gottfried, in press). Significant overall increases were noted for aspen, white pine, and Engelmann spruce, while ponderosa pine did not respond to treatment. Periodic mean tree basal area growth ranged from 0.0036 m² for white fir to 0.0013 m² for ponderosa pine, with an overall average of 0.0024 m². Significant increases in periodic annual basal area growth were noted for all species, except ponderosa pine. Additional information on the growth of the South Fork and the undisturbed North Fork stands has been presented in Gottfried (1989) and Gottfried (in press).

Regeneration

A main concern was with the ability to maintain or obtain adequate conifer and aspen regeneration, particularly in the patch-clearcut areas. Natural regeneration appears satisfactory to maintain most undisturbed stands. However, previous regeneration problems following conventional harvesting in mixed conifer stands (Gottfried 1983, Jones 1967) had led to some apprehension. Ffolliott and Gottfried (1991) intensively studied natural regeneration in nine representative patch-clearcut openings and in the adjacent partially harvested forest. By 1989, eleven years after harvesting, there were over 2,500 trees/ha in the openings and over 7,600 trees/ha within the forest. Tree densities, while significantly different, were satisfactory in both areas. However, stocking was similar, averaging 45% in the openings and 61% in the forest. Most of the seedlings in the openings were growing next to the edges, but center areas

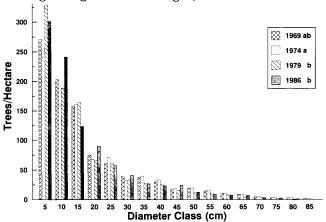


Figure 2. The diameter class-density distributions show changes in stand structure over the time period from 1969 to 1986. Different letters indicate significant differences (alpha = 0.05) between inventories according to the Kolmogorov-Smirnov Test (Gottfried, in press). The pretreatment period includes the 1969 and 1974 inventories and the posttreatment period includes the 1979 and 1986 inventories.

should become stocked as the surrounding regeneration grows and further modifies the microclimate. In addition to new seedlings and suckers, advance regeneration survived the treatment in good condition. Gottfried (1987) found that most of the Thomas Creek sale area, outside of landings and road zones, contained an average of 5,466 established trees/ha and that 89% of the area was stocked with at least one healthy tree. The new and advance regeneration are satisfactory to maintain a healthy and productive stand.

EFFECTS ON OLD-GROWTH CHARACTERISTICS

Old-growth Rating

Old-growth characteristics were not evaluated prior to treatment. The Forest Service4 rating system is influenced heavily by the amount of basal area in trees equal to or larger than 46 cm in diameter. This parameter receives 55 out of 100 possible points. The basal area value has obviously declined because of treatment and so has the rating. In 1991, the Alpine Ranger District conducted an old-growth inventory of the Thomas Creek watersheds (Rugg 1991, pers. comm.). Much of the harvested area was rated in the 25 to 40 category, while some areas in the middle of the watershed received a lower score because of the lack of larger trees. This finding does not mean that larger trees were absent, however. The 1986 inventory indicated an average of 68 trees/ha in the desired diameter classes, which is equivalent to 16.8 m²/ ha. A greater number of larger trees could have been retained to enhance old-growth characteristics. However, accelerated growth should result in relatively rapid ingrowth into the 46 cm diameter class. A simple stand projection (Ffolliott 1965) found that this size class should gain 0.49 trees/ha/year on South Fork compared to 0.37 trees/ha/year on North Fork. While this difference was not compared statistically, it represents a 32% increase over North Fork conditions.

It should be noted that scores in most of the control watershed were in the 50- to 75-point category; but some undisturbed areas received lower ratings in spite of the presence of large, old ponderosa pine and Douglas-fir trees. The importance of basal area in the rating system may result in some old-growth stands being scored low, and possibly, being eliminated from further consideration for appropriate management.

Stand Structure

The distribution of size classes and canopy levels is another important parameter of old-growth condition. The maintenance of uneven-aged structure was an important consideration during planning. Stand changes resulting from the harvest and from natural stand dynamics can be compared using the four inventories between 1969 and 1986 and statistical differences identified using the Kolmogorov-Smirnov (K-S) test (Gottfried, in press). (It should be noted that all values in this and subsequent paragraphs, except those related to table 1, include new ongrowth trees. These are trees of any size that were too small to be tallied in one inventory but have grown sufficiently to be included in later inventories.) In 1969, the sale area contained 958.60 trees/ha and 44.0 m²/ ha of basal area. Stand structure, based on the diameter distributions by 5-cm diameter classes, and composition were relatively constant between 1969 and 1974 (fig. 2), but changed after the harvest. However, overall diameter distribution in 1979, when the stand with ongrowth contained 954.32 trees/ha and 33.4 m²/ha, and in 1986 were similar to those of the original 1969 stand. The K-S tests were next conducted on sets of data that excluded the three smallest size classes (5, 10, and 15 cm). The results showed no differences in the distribution of tree density by size classes between any of the inventories. The analyses indicated that harvesting did not alter the stand's basic diameter distribution and its uneven-aged structure.

The q-values (Husch et al. 1972) indicated small shifts over the study period (Gottfried, in press). In 1986, the q-values for the sale area, and for the stand on North Fork, were both 1.47. The 1986 regressions for the South Fork treated area and the North Fork had coefficients of determination of 0.94 and 0.98, respectively. This is another indication that the almost balanced uneven-aged structure had been maintained on South Fork.

Composition

The maintenance of species diversity is another important factor used to evaluate old-growth. The relative species composition of the stand did not change because of treatment, although ponderosa pine, Douglas-fir, and white fir were heavily harvested (table 1). Relative stand composition has fluctuated over the entire study period, but the relative changes generally have been less than 5% of the total trees/ha. The main exception is white fir, which increased over 9% between 1969 and 1986. This species currently accounts for 24% of the composition. The change appears to be due to a steady increase in the number of trees less than 18 cm d.b.h.--79 trees/ha in 1974 to 188 trees in 1986. White fir and ponderosa pine showed increases between 1979 and 1986, while the relative composition of Douglas-fir declined. The increase in ponderosa pine can be related to ingrowth into the 5-cm d.b.h. class; however, the generally low growth rates and vigor of many ponderosa pine has created some concern.

Other Old-Growth Parameters

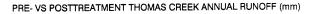
There are several other parameters used in oldgrowth evaluations, such as patchiness and the presence of snags and larger woody debris. The stand's natural patchiness should be enhanced by the

patch-clearcut and group-selection openings. The number of snags was not measured but the marking guides generally called for their retention as well as the retention of living cull trees. A relatively healthy residual stand would indicate fewer new snags in the future. The amount of larger material on the forest floor was also not inventoried after logging, although levels were initially high (Sackett 1979). The requirement to haul larger slash to landings for disposal has compromised this characteristic. The current opinion is that this material should be left to contribute to nutrient cycling, particularly nitrogen fixation, and provide protection for regeneration and habitat for small mammals. However, not all slash was hauled and new material is being added by natural mortality. Additional snags or quantities of dead and down material could be created through management intervention in the future.

Future Considerations

What are we going to do in the future? This problem is common to the goal of enhanced forest productivity and health as well as to the development of oldgrowth characteristics. The amount of basal area in larger trees was the main old-growth attribute to decline because of the harvest. Increasing the length of the rotation from 120 to 180 years, for example, would allow trees to grow to larger sizes. This change could be associated with increasing the cutting cycle from 20 to 30 years which would allow a longer growth and recovery period between entries. This would have less of an impact on the site and on animals which are sensitive to disturbances.

The exact prescription is also in question. Can maximizing growth and maintaining old-growth characteristics be continued following future harvests? What compromises will have to be considered? One option would be to adhere to the original plan for the second entry (harvest) which was to continue the patch clearcutting and group selection methods. The objective in the selection areas was to reduce the



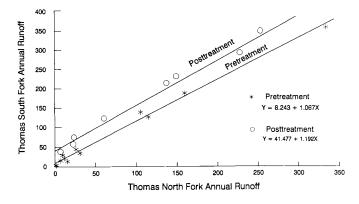


Figure 3. The relationship between the watersheds changed after treatment, indicating significant increases in annual streamflow (Gottfried 1991).

basal area to 23.0 m²/ha with the constraint that no more than 35% of the existing basal area would be removed (Brown 1976). This plan could be modified slightly to emphasize group selection throughout the area with the eventual goal of maintaining one-sixth of the area in old-growth groups. The impacts on the growth of residual trees would depend on the nature of further removals in the areas between groups. The proposal would enhance patchiness but could reduce the overall basal area and size class requirements for mixed conifer old-growth. An alternative could create fewer openings and retain higher basal area levels. The control of dwarf mistletoe in the residual stand would have to be considered in the creation of new openings or the enlargement of existing openings. The group shelterwood method could also be prescribed to regenerate some areas; old-growth values would be enhanced if the final removal harvest were not conducted. However, this could impact regeneration of some seral, shade-intolerant species such as ponderosa pine. A possible choice is to concentrate on single-tree selection and have old-growth trees scattered throughout the area although this would modify the stand's natural patchiness. Other options would be to limit the second entry to light sanitation and improvement harvesting in the middle size classes and defer a regeneration cut for 10 more years, or if maintaining the existing old-growth characteristics is selected as the paramount objective, to withdraw the area from further harvesting.

STREAMFLOW AND SEDIMENT RESPONSES

Streamflow

One of the major objectives for the South Fork experiment was to evaluate the effects of relatively moderate timber harvesting on water yield responses. Earlier watershed experiments (Baker 1986, Rich and Thompson 1974) had demonstrated that water yield increases usually resulted from creating relatively large forest openings or from heavy reductions in stand basal area. Gottfried (1991) found that the Thomas Creek treatment produced statistically significant average annual water yield increases (with standard error) of 44 ± 11 mm ($44.8\% \pm 11.7\%$) (fig. 3). The comparison of the estimated annual runoff for the two periods indicated that runoff increases were significant for each of the eight posttreatment years. The yearly streamflow increases that occurred during the posttreatment period were generated by winter snowmelt or rain storms. Close to 80% of the annual runoff still occurs in March. April, and May. Summer runoff increased slightly (3) ± 3 mm) but the change was not statistically signifi-

The increases in average annual water yields have been attributed to increased snowpack accumulations (Plasencia et al. 1984) and reduced evapotranspiration in the group-selection and patch-clearcut openings (Gottfried 1991). The change in evapotranspiration occurs because generally deep rooted, mature trees have been replaced by shallower rooted tree regeneration and herbaceous species. Consequently, it takes less precipitation to recharge the soil and any further increments are available for movement into the stream channels. Gottfried (1991) indicated that it appears that the partially harvested areas, which represent 82% of the cut area, are also contributing to the increased flows during average and wet years because the residual trees are not using all of the soil water. Trees use most of the available water during dry years. Troendle (1987) found a relationship between basal area and soil water for a Colorado lodgepole pine (P. contorta) stand which tends to support this explanation. Troendle and King (1987) determined that partial harvesting in a Colorado subalpine forest resulted in significant increases in snow water equivalents that would augment runoff. However, a similar effect was not confirmed on Thomas Creek (Gottfried 1991).

Sedimentation

Changes in sedimentation and channel dynamics related to the Thomas Creek treatment were studied by Heede and King (1990). These authors determined that overland flow and sediment delivery from severely disturbed and undisturbed sites were inconsequential. However, sediment deliveries from severely disturbed areas (41 kg/ha/year) were significantly higher than from undisturbed sites (6 kg/ha/year). Little erosion was caused by logging. The natural channel adjustment process accelerated after treatment because of the increased streamflows (Heede and King 1990), but the impacts on downstream areas is unknown.

EFFECTS ON HERBAGE PRODUCTION AND UTILIZATION

Patch Clearcuts and Other Openings

As might be expected, more herbage was produced in the patch clearcuts than in the adjacent forests. In the 8-year period after the treatment on Thomas Creek, annual production of herbaceous plants ranged from 233 to 398 kg/ha in nine representative patch clearcut openings, while the production under the adjacent partially harvested forest ranged from 44 to 103 kg/ha (Ffolliott and Gottfried 1989). The average annual herbage production for the three herbaceous plant inventories at Thomas Creek was 303 kg/ha in the patch clearcut areas, an increase of 249 kg/ha over the level of production estimated to have been present before treatment. Herbage production has remained consistently higher in these openings since treatment, which is an important management consideration because of the low levels of production associated with the normally dense mixed conifer forests (Hungerford 1970; Patton 1974, 1976; Patton and Judd 1970; Reynolds 1969a, 1969b; Thill et al. 1983).

Utilization of forage plants by livestock and big game species was higher in the representative patch clearcuts than in the adjacent forest for two of the three sampling dates (Ffolliott and Gottfried 1989). Some of the patch clearcuts experienced greater levels of utilization than others, possibly the result of different animal species feeding in different sites, as has been observed elsewhere (Ffolliott et al. 1977, Patton 1974). Nevertheless, the patch clearcut openings on Thomas Creek should benefit livestock, mule deer (Odocoileus hemionus), and elk (Cervus elaphus).

Single-Tree Selection Areas

Most undisturbed mixed conifer forests are dense and do not produce large amounts of herbage production. Therefore, it is not surprising that the reductions in forest density levels by the single-tree selection treatment on Thomas Creek resulted in an increase in herbage. Annual herbage production in the forests adjacent to the patch clearcuts averaged 76 kg/ha for the three inventories, an increase of 22 kg/ha in comparison to the amounts estimated for undisturbed conditions (Ffolliott and Gottfried 1989). The increase likely would have been larger if the reductions in stand density had been greater. Nevertheless, it is apparent that even small reductions in forest density can influence herbage production. The relationship between reductions in mixed conifer stand densities and increased herbage production was substantiated by Thill et al. (1983) who studied this relationship with respect to forage production for deer and elk in several areas in the vicinity of Thomas Creek.

WILDLIFE RESPONSES

The effects of the Thomas Creek treatment on wildlife were varied. Some species benefited because of increased forage production and enhanced habitat diversities. However, other wildlife species could have been impacted detrimentally, especially those species that are dependent upon habitats consisting of undisturbed forest conditions. Studies concentrated on three groups or species of animals: deer and elk, red squirrels, and nongame birds. The increased production of forage and the creation of a more diversified habitat, due largely to an increase in edge surrounding the patch-clearcut and group-selection openings, was beneficial to mule deer and elk. Several other studies have demonstrated increased levels of use in these habitats (Patton 1974, 1976; Reynolds 1966, 1969a; Severson and Medina 1983). Equally important, a protective cover also has been maintained through the distribution of residual trees in the surrounding multistoried stand. The duration of the increased use of the improved habitat is unknown, although it is possible that the impacts of treatment could only exist for a relatively short

period of time. The amount of forage in the openings should decline as tree regeneration increases in size while the amount under the residual stand will decline as the canopy closes again. However, placement of Thomas Creek and the surrounding mixed conifer forests into a rotational system of timber harvesting might prolong the beneficial effects of the small openings and single-tree selection on mule deer and elk. Interactions of these big game animals and cattle also could influence the sustainability of the treatment effects.

Studies in Thomas Creek prior to treatment have shown that the best habitat for red squirrels (Tamiasciurus hudsonicus) consists of multistoried mixed conifer stands with trees from 30 to 36 cm d.b.h. in dense groups of 0.04 ha or less (Patton and Vahle 1986, Vahle and Patton 1983). One or more cone-bearing trees 46 cm d.b.h. or larger should be included in the group. This habitat is represented mostly by undisturbed forest conditions. Therefore, to the degree that the treatment altered these conditions, the habitat of red squirrel was affected correspondingly.

Although the effects of the timber harvesting on red squirrels was not evaluated directly, efforts were made to minimize the impacts. Group selection is one form of silviculture that is used to maintain the desired multistoried character of mixed conifer stands (Alexander 1974, Jones 1974). Furthermore, the retention of tree groups around active food cache sites in which cones are stored in accumulations of feeding debris, potential cache sites, and nesting sites should minimize the detrimental effects of timber harvesting on red squirrel habitat (Patton and Vahle 1986, Vahle and Patton 1983). Such a requirement was part of the Thomas Creek prescription.

The treatment on Thomas Creek resulted in only minor, short-term changes in the bird populations. Total estimated bird numbers dropped slightly (12%) after the timber harvest, but the number of species present increased from 28 to 35 (Scott and Gottfried 1983). House wrens (Troglodytes aedon), American robins (Turdus migratorius), and pine siskins (Cardeulis pinus) were additions to the bird population following the treatment. There were no significant differences in bird numbers when analyzed by either nesting or feeding guilds. The ruby-crowned kinglet (Regulus calendula) was the only major species to show a significant decline.

It was concluded, therefore, that a moderate timber harvesting operation that removes about 30% of the basal area of a stand, whether for multiresource benefits or primarily for timber production, will not affect bird populations adversely (Scott and Gottfried 1983). However, more severe reductions in basal area, such as the diameter limit removals in the mixed conifer stands on the nearby Willow Creek watershed (Gottfried 1983, Rich and Thompson 1974), could result in lower total numbers of birds (Franzreb 1977). The relationship between bird populations and timber harvesting practices observed in the White Mountains of Arizona tend to

be consistent with those found in southwestern ponderosa pine forests (Szaro and Balda 1979, 1982).

The effects of harvesting old-growth on endemic wildlife species requires further research, especially since some species are largely dependent on this condition. The deer and elk and red squirrel conclusions were drawn from our knowledge of their preferred habitats; only birds were observed directly. A data base does exist for additional studies on these and other species. In addition to wildlife studies, Thomas Creek provides a potential area for further research on other topics related to old-growth such as nutrient cycling, growth and yield, fire management, regeneration dynamics, and the hydrologic cycle.

CONCLUSION

There is considerable interest in the future management of the remaining old-growth forests and woodlands of the Southwest. Areas of old-growth should certainly be maintained without intervening management; old-growth is too valuable. Hopefully, common criteria can be developed to identify prime old-growth areas. The question is whether a compromise can be achieved in other areas between oldgrowth goals and some degree of management for traditional forest resources. Can silvicultural approaches be developed which will maintain oldgrowth attributes or accelerate their development in stands which do not currently qualify? The Thomas Creek experiment was established in the 1970s to develop and evaluate a planning procedure for integrated resource management in a southwestern mixed conifer stand. Experiments were established to evaluate the impacts of this initial entry on forest productivity, water yields, herbage production and utilization, and wildlife resources. While the impacts on old-growth were not initially considered in the Thomas Creek study, it is possible to gain some important insights into the effects of timber harvesting activities on the response of different parameters related to old-growth forests in the Southwest.

The treatment has enhanced and sustained forest productivity by accelerating growth of most residual trees and a rapid recovery of stand volume and basal area. High densities of new regeneration in the openings and under the partially harvested forest, in addition to satisfactory survival of advance regeneration, should serve as the foundation for a healthy and productive stand in the next rotation.

Although the overall old-growth rating has declined because of the harvesting of many of the largest trees, the stand has maintained many old-growth characteristics, especially its uneven-aged structure and tree species diversity. In fact, the treatment retained many large trees; 46% of the basal area in 1986 consisted of trees in the largest size classes. The significant increases in tree growth which occurred following treatment should result in a more rapid recruitment into the desired size classes. Reducing the number of entries and extending the

planned rotation from 120 to 180 years would also allow for the growth of more large trees. Modification of slash disposal activities would benefit the forest ecosystem and also enhance the ratings.

The Thomas Creek treatment resulted in significant water yield increases, demonstrating that large clearings or removing large numbers of trees is not necessary to generate increased runoff from forested watersheds. The increases were achieved with more moderate treatments. The fact that the partially harvested areas appear to have contributed to the runoff increases is another benefit to be considered when evaluating the potential for uneven-aged management in these forests. The small clearings and, to a lesser extent, the partially harvested stand also were beneficial for herbage production and wildlife and range resources. Nongame bird populations generally were unaffected by the harvest.

The prescribed treatment has produced a wide range of benefits while retaining many of the old-growth characteristics of the stand. Some old-growth attributes are impacted during any harvesting operation but these should recover in the future. Thomas Creek is only a small section of the south-western mixed conifer forest, and additional evaluations of the prescription should be conducted before general recommendations can be made. However, the prescribed treatment is a viable option for similar old-growth stands where harvesting is acceptable.

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A Computer Graphics Technique for Visualizing Spatial Disturbance and Succession in Old-Growth Forests¹

Wayne D. Shepperd²

Techniques are described for collecting and processing spatially explicit data from fixed-area inventory plots to produce graphical schematics illustrating the composition, structure, and development of the inventoried forest. An application of these techniques in two forested subalpine watersheds in the central Rockies is presented. Plot schematics produced from this data reveal patterns of species composition, stand structure, succession, and mortality that are not apparent from conventional tabular summaries of inventory data.

Introduction

One of the major frustrations in describing old-growth forests is finding a way to convey to others a mental image of the forest we are discussing. We all see things differently when we think of an old-growth forest. Our attempts to describe them are invariably influenced by our own experiences and priorities, and the values that old-growth forests have in our particular discipline.

Collecting quantitative information in mature forests, summing it on a per-unit-area basis, and presenting it in a tabular format does not capture the essence of an old-growth forest. This is especially true when we are trying to use such information to describe old-growth forests to people who are not familiar with the concepts and jargon of basal area, cubic volume, MAI, etc. Traditional summaries of inventory data can present an unrealistic view of old-growth forests because they do not provide any useful information about the spatial variability of species and/or size classes in the population.

Oblique photos taken within the forest help somewhat, but are hard to obtain in the poor light conditions in the interior of mature forests. Species composition is difficult to see in some forest types, vertical canopy structure is distorted from a forest floor perspective, and some trees may be hidden. (大学教育などのようななどのなったがある。

This paper describes an effort to provide a solution to these problems by developing computer software to graphically process quantitative field inventory data in a manner that provides a true depiction of the spatial integrity and structure of the forest. The objective was not to produce a virtual image of the forest, but to develop schematic diagrams--analogous to the blueprints of a house or a wiring circuit--that would enable users to easily visualize the structure and spatial arrangement of trees that had been measured on inventory plots.

Methods

The Deadhorse Creek and Lexen Creek Research Watersheds on the Fraser Experimental Forest in central Colorado were used as a source of data to develop the graphic system described here. These watersheds both contain mature, undisturbed forests of Engelmann spruce, subalpine fir, and lodgepole pine, portions of which have many oldgrowth characteristics. Both watersheds are typical of mature subalpine forest ecosystems in the central and southern Rockies.

Data Collection and Summary

Producing a graphical image of a forest requires spatially explicit inventory data not provided by traditional stand-exam cruising techniques.

Variable radius, or nested sampling techniques that do not measure all trees in a plot, are often used to

¹Paper presented at Old-growth Forests in the Rocky Mountains and Southwest Conference (Portal, AZ, March 9-13, 1992).

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collect this traditional data. Graphically reconstructing a stand requires measurements of the height, diameter, crown dimensions, and location of each tree within a plot of fixed area. The size and shape of plot used to collect data for graphic visualization needs to be large enough to represent the variability of stocking and structure within the stand, and be economically feasible over a large area. Circular, 1/50-acre (0.008-ha) plots were selected for use in this study after trying several plot sizes within the study watersheds. Circular plots were chosen because they were easy to lay out using a single center stake. The 33-foot (10.05m) diameter of these plots provided adequate representation of the spatial variation of forests within these watersheds, sampling between 1 and 16 trees per plot with an average sample of 6 trees.

Forty-nine plots were sampled within the two watersheds. The azimuth and distance to each tree within 16.65 feet (5.025 m) of plot center was recorded, along with the tree's species, bole diameter at breast height, total height, live crown length, and average crown diameter. All stems greater than 1 inch diameter breast height (dbh) were measured, including standing dead and down dead originating within the plot. Similar data were also collected for smaller stems in a 3-foot wide strip through plot center. Increment cores were collected for one tree in each overstory crown class in each plot to measure tree ages. Two cores to measure 10-year radial growth were also obtained from all trees in the plot over an inch in diameter. At least two dominant trees were measured within, or near, each plot for determination of site index.

Two ASCII data files were created from the data collected from the 49 inventory plots. The first consisted of the measured tree data collected from each plot. Each line of the file contained data collected from a single tree, including the plot, tree number, azimuth, and distance from plot center to the center of the tree, species and size class codes (which also identified live and dead trees), stem and crown dimensions, and the age of the tree if it was cored. These data were processed in a computer program to calculate cubic and Scribner volumes for each tree, which were added to the original data file. Accumulated summaries of each plot's data on a unit-area basis were also saved in a second file, to which physiographic and site index information were then added.

The Graphics Program

The graphic visualization program is written in GWBASIC and will run on any IBM compatible PC with a VGA color monitor. It utilizes information from both of the tree data and plot summary files to reproduce a visual representation of a selected plot and a summary of plot data on a single screen frame (fig. 1). Side and overhead projections of the plot are presented, along with a quantitative summary of the plot measurements and other site data. All trees are diagrammed to scale and placed in the proper position on the plot. Open "wire frame" diagrams are used so no trees are hidden from view. Species are identified by crown shape in the illustrations here, and in different colors on a computer monitor. Standing dead trees are shown as stems without crowns. Dead stems that have fallen are represented as filled circles scaled to the tree's diameter and drawn at the position in the plot where the tree once stood. The ages of cored trees are shown at the right side of the screen, with connecting lines to the tip of the diagrammed tree in the side view of the plot.

The user starts the program by displaying an introduction to the program, then viewing either a description of the plot or a summarized plot data file to choose a plot to view. After a plot number has been entered, the graphic template is drawn and the tree data file searched until the first tree in the requested plot is encountered. At this point, a subroutine is called to draw the tree based on its species and whether it is live, dead, or down dead. A separate subroutine is used for each species, dead trees, and down dead. Only the shape of the crown and color of the diagram are controlled by the subroutine. Height, diameter, crown width, crown length, and location of the tree on the plot are all determined by actual tree data and are correctly scaled. If the tree was cored for an age determination, a line is drawn from the tip of the tree to its age, displayed at the right of the screen. After all trees in a plot (including seedlings) have been diagrammed, the plot summary file is again called to obtain physiographic and quantitative data to complete the display. (A separate file was used in lieu of computing the summaries from the raw tree data to speed up program execution.)

Results

Diagrams produced by the computer program greatly facilitated interpretation of inventory data

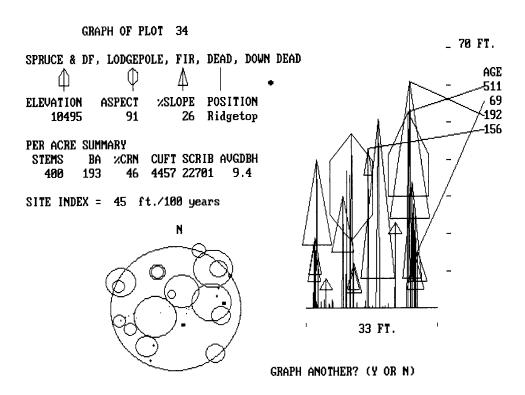


Figure 1.--Side and overhead plot projections with all trees drawn to scale using a different crown shape for each species. Ages of cored trees are shown at right.

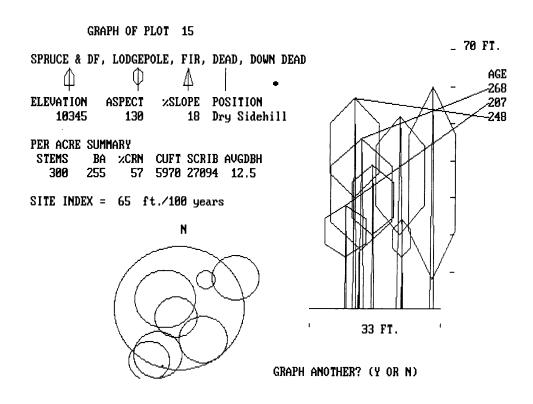


Figure 2.--A plot containing only lodgepole pine. Older pine trees were not very large in the study watersheds.

from the Lexen and Deadhorse Watersheds. Because only trees within the plot were projected, crown positions, tree heights, and size differences could be clearly seen.

Species composition was perhaps the easiest characteristic to discern in the graphs (fig. 1). Most of the plots in these watersheds contain at least two species, but a few contained only lodgepole pine (fig. 2). Size and crown development were also readily apparent. The full, well proportioned crowns of overstory trees that are not crowded were distinctly different from the small crowns of suppressed trees in the understory. The irregularity of stocking in the inventoried plots was clearly visible in the graphs. Trees throughout both watersheds tended to be clumped together in groups with intertwined crowns. Gaps in the canopy above the forest floor were evident in nearly all plots.

Patterns of past disturbance and successional trends could also be interpreted using the graphs. Shade tolerant subalpine fir predominated in the understories of many plots. Young, small spruce were rare, and lodgepole pine were almost nonexistent in the understory. Although tree age data were incomplete, many of these plots contain very old trees. Seeing the ages of a subsample of trees on the graphs made it very clear that these stands are anything but even-aged (fig. 1). Small trees that were older than larger ones illustrate the effects of past suppression. Other incongruities such as a lodgepole pine in the overstory that was younger than nearby spruce suggest a more open forest existed in the past. On other plots, older trees that were not very large illustrate the harsh growing conditions at higher elevations, on poor sites, or in some lodgepole pine stands in these watersheds (fig. 2).

The condition of some plots appeared to be very stable, with no standing dead trees and few dead stems on the ground (fig. 1). Other plots seemed to be in transition, with a mixture of species, size, age, and mortality classes present (fig. 3). Still others appeared to be quite unstable, with many standing dead and down trees present (fig. 4). Disturbance and mortality have been a sporadic process in these stands for some time, as evidenced by the canopy gaps in many plots that once contained trees.

Although not an original objective, one of the best uses for these graphs is to screen data for errors. They are especially useful in locating erroneous tree dimensions that somehow slip through other screening processes. Several strangely shaped trees in the original diagrams of these plots resulted from erroneous data in the input file. Such discrepancies can be easily spotted and corrected before further analysis is done. For example, a 36-year-old dominant prompted me to locate and correct several mistakes in recording tree ages on one plot.

Interpretation of the Graphs

A number of observations can be made after studying the graphs from the Deadhorse and Lexen Watersheds. Stand structure is quite variable from plot to plot across elevation and aspect gradients within these watersheds. Old spruce and lodgepole trees do not exist in distinct stands in these two watersheds, but rather appear as small, discontinuous groups of older trees that are surrounded by and contain younger cohorts. The absence of large-scale disturbances in these mature forests does not mean they are absolutely stable, either. Numerous small-gap disturbances have occurred in these watersheds in the past and continue today.

The intensive sampling done in this study indicates that delineation of old-growth within these watersheds would be strongly dependent upon physiography and the ability to adequately survey age class structure throughout the entire area. Some plots undeniably meet the descriptive criteria for old-growth spruce-fir and lodgepole pine stands in the central and southern Rockies. However, others containing ancient trees might score low because the trees are small or other descriptive attributes are not present. Old-growth rating criteria and delineation must recognize the small-scale dynamic processes that occur in mature subalpine forests, and adjust for the natural variability in these ecosystems.

A comparison of graphic visualization, stand exam, and walk-through scorecard surveys is planned within these watersheds to analyze their effectiveness in delineating old growth.

³See paper by Mel Mehl in this report.

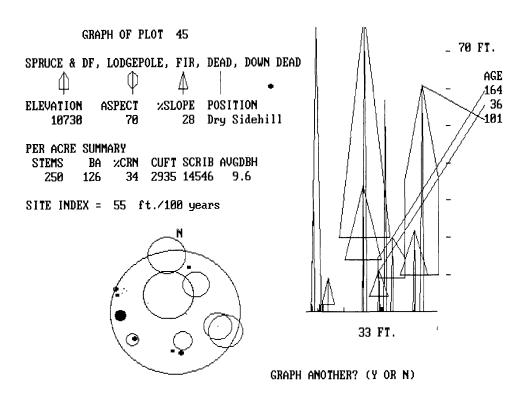


Figure 3.--Diagram of a plot containing a mixture of species, size, age, and mortality classes, indicating a gradual transition to subalpine fir.

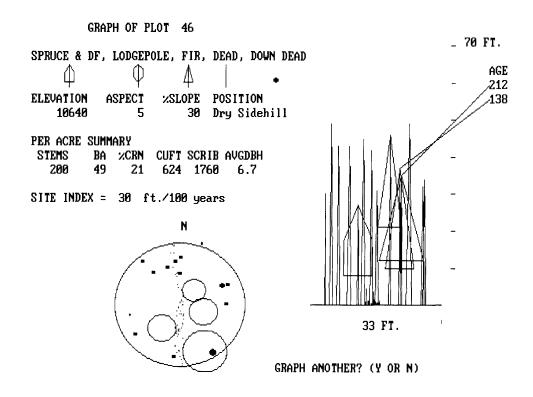


Figure 4.--Diagram of a plot with many standing dead and down trees, indicating stand breakup.

Conclusions

Graphical visualization procedures provide an alternative means for resource professionals and interested publics to examine and interpret field data from areas being considered for old-growth status. The schematic plotting techniques used here require a relatively small investment in data acquisition and computer hardware, but allow the user to easily discern patterns of disturbance and successional trends in mature or old-growth forests. Having a means to systematically view stand structure and species composition from a variety of sites and growing conditions may allow further development of quantitative tools that can be used to identify and classify old-growth forests.

The field procedures and computer program used here can be easily modified for use in other forest types, or with different sized inventory plots. Copies of the GWBASIC language code used to produce the graphs used in this paper are available by sending a blank diskette to the author.

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