Chapter 14

Management Strategies for Bark Beetles in Conifer Forests

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1. INTRODUCTION

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are important disturbance agents in conifer forests. The genera Dendroctonus, Ips, and Scolytus are well recognized in this regard (Table 14.1). For example, in western North America, the mountain pine beetle (Dendroctonus ponderosae Hopkins) colonizes several tree species, most notably lodgepole pine (Pinus contorta Dougl. ex Loud.), ponderosa pine (Pinus ponderosa Dougl. ex Laws.), and whitebark pine (Pinus albicaulis Engelm.). Recent outbreaks have been severe, long lasting, and well documented, with over 27 million hectares impacted (BC Ministry of Forests, Lands and Natural Resource Operations, 2012; USDA Forest Service, 2012). In British Columbia, Canada, alone 710 million m³ of timber have been killed (BC Ministry of Forests, Lands and Natural Resource Operations, 2012). In Europe, the European spruce beetle (Ips typographus (L.)) is regarded as the most important pest of Norway spruce (Picea abies (L.) Karst.) (Christiansen and Bakke, 1988; Schelhaas et al., 2003), an indigenous species also widely planted for commercial timber production outside its native range. It is estimated that 8% of all tree mortality that occurred in Europe between 1850 and 2000 was caused by bark beetles, primarily I. typographus (Schelhaas et al., 2003). In Asia, the red turpentine beetle (Dendroctonus valens LeConte), an exotic invasive introduced from North America, has caused significant levels of tree mortality since being detected in China in 1998 (Yan et al., 2005). Although considered a minor pest in its native range, more than 10 million Chinese red pine (Pinus tabuliformis Carr.), China's most widely planted pine species, have been killed by D. valens.

Over the last century, substantial basic and applied research has been devoted to the development of effective tools and tactics for mitigating undesirable levels of tree mortality attributed to bark beetles. There are two basic approaches. *Direct control* involves short-term tactics designed to address current infestations by manipulating beetle populations, and often includes the use of fire, insecticides, semiochemicals (i.e., chemicals released by one organism that elicit a response, usually behavior, in another organism), sanitation harvests, or a combination of these treatments. *Indirect control* is preventive, and designed to reduce the probability and severity of future bark beetle infestations within treated areas by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and altering age classes and species composition. Unlike direct control, the focus of indirect control is on the susceptibility of residual forest structure and composition to future infestations.

The purpose of this chapter is to synthesize information related to the management of bark beetles in conifer forests, and to present a case study on the management of I. typographus in central Europe. We concentrate on what some authors commonly refer to as *aggressive* species (i.e., they are capable of causing large amounts of tree mortality during certain circumstances) (Table 14.1), and draw heavily from research conducted and practical experience gained while working in North America and Europe. Our hope is that this synthesis provides a basic understanding of current and evolving strategies for reducing the negative impacts of bark beetles on forests. However, we stress that in most cases we concentrate on native species important to the proper functioning of forest ecosystems as they regulate certain aspects of primary production, nutrient cycling, and ecological succession (Romme et al., 1986). In this context, some level of tree mortality is desirable and often results in a mosaic of age classes and species compositions that increases resilience to bark beetles and other disturbances. This differs from the negative impacts associated with outbreaks, which often merit intervention. We encourage the reader to delve deeper into the literature cited for more detailed information on specific bark beetle-host complexes.

TABLE 14.1 Bark Beetle Species Notable for Causing Substantial Levels of Tree Mortality in Conifer Forests

 within their Native Ranges

Common Name	Scientific Name	Common Host(s)
Arizona fivespined ips	Ips lecontei	P. ponderosa
California fivespined ips	lps paraconfusus	P. contorta, Pinus lambertiana, P. ponderosa
Douglas-fir beetle	Dendroctonus pseudotsugae	Pseudotsuga menziesii
eastern fivespined ips	Ips grandicollis	Pinus echinata, Pinus elliottii, Pinus taeda, Pinus virginiana
eastern larch beetle	Dendroctonus simplex	Larix laricina
eastern six-spined engraver	Ips calligraphus	P. echinata, P. elliotti, P. ponderosa, P. taeda, P. virginiana
European spruce beetle	lps typographus	Pi. abies, Picea orientalis, Picea yezoensis, occasionally Pinus sylvestris
fir engraver	Scolytus ventralis	Abies concolor, Abies grandis, Abies magnifica
Jeffrey pine beetle	Dendroctonus jeffreyi	Pinus jeffreyi
larger Mexican pine beetle	Dendroctonus approximatus	P. ponderosa
mountain pine beetle	Dendroctonus ponderosae	P. albicaulis, P. contorta, Pinus flexilis, P. lambertiana, Pinus monticola, P. ponderosa
northern spruce engraver	lps perturbatus	Picea glauca, Picea x lutzii
pine engraver	lps pini	P. contorta, P. jeffreyi, P. lambertiana, P. ponderosa, Pinus resinosa
pinyon ips	lps confusus	Pinus edulis, Pinus monophylla
roundheaded pine beetle	Dendroctonus adjunctus	Pinus arizonica, Pinus engelmannii, P. flexilis, Pinus leiophylla, P. ponderosa, Pinus strobiformis
six-toothed bark beetle	lps sexdentatus	Pinus heldreichii, Pinus nigra, Pinus pinaster, P. sylvestris, Pi. orientalis
southern pine beetle	Dendroctonus frontalis	P. echinata, P. engelmannii, P. leiophylla, P. ponderosa, Pinus rigida, P. taeda, P. virginiana
spruce beetle	Dendroctonus micans	P. sylvestris, Pi. abies
spruce beetle	Dendroctonus rufipennis	Picea engelmannii, Pi. glauca, Picea pungens, Picea sitchensis
western balsam bark beetle	Dryocoetes confusus	Abies lasiocarpa
western pine beetle	Dendroctonus brevicomis	Pinus coulteri, P. ponderosa

1.1 Bark Beetle Ecology

Some knowledge of bark beetle ecology and physiology is important to understanding the utility and proper implementation of control strategies. In brief, adult bark beetles maintain limited energy reserves (Atkins, 1966), and are highly susceptible to predation, starvation, and adverse weather conditions when searching for hosts. Beetles therefore must detect and locate the correct habitat, correct tree species, and the most susceptible trees within these species with efficiency (Byers, 1995; Borden, 1997; Schlyter and Birgersson, 1999). For example, the dominant theory of host finding and selection in *D. ponderosae* suggests pioneering females use a combination of random landings and visual orientations followed by direct assessment of hosts based on olfactory and/or gustatory cues (Raffa and Berryman, 1982, 1983; Wood, 1982). Given the cues received during this process and other factors, such as the beetle's internal physiology (Wallin and Raffa, 2000), the host is either rejected or accepted. If the host is accepted, gallery construction is initiated upon which many species release aggregation pheromones that enhance attraction of conspecifics to the target tree (Borden, 1985; Byers, 1995; Zhang and Schlyter, 2004) as successful colonization requires overcoming host tree defenses (Wood, 1972; Hodges *et al.*, 1979, 1985; Raffa *et al.*, 1993; Franceschi *et al.*, 2005). This can only be accomplished by recruitment of a critical minimum number of beetles to *mass attack* the tree and overwhelm its defenses.

Most conifers are capable of mobilizing large amounts of oleoresin following wounding, which constitutes their primary defense against bark beetle attack (Vité, 1961, Reid et al., 1967, Franceschi et al., 2005) (see Chapter 5); however, resin chemistry also plays an important role (Smith, 1966; Cook and Hain, 1988; Reid and Purcell, 2011). The development of a hypersensitive response, consisting mainly of secondary metabolites around points of attack, has also been demonstrated to be important (Lieutier, 2004). Beetles that initiate host selection are often killed by drowning or immobilization in resin (termed *pitch out*) especially when adequate moisture, flow, and oleoresin exudation pressure exist, such as in the case of vigorous hosts (Raffa and Berryman, 1983) or when beetle populations are low (Figure 14.1). The presence of pitch tubes and/or boring dust is commonly used to identify trees that have been attacked by bark beetles. Monoterpenes released from pitch tubes may enhance attraction to the host tree. However, for most aggressive species attraction to host volatiles has not been demonstrated in the absence of aggregation pheromone components (Borden, 1997). Many bark beetles introduce a variety of microbes into the tree upon colonization (see Chapter 6), which may have deleterious effects on tree health, but mortality occurs primarily through girdling of the phloem and cambium tissues. The resultant tree mortality may impact timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, real estate values, biodiversity, carbon storage, endangered species, and cultural resources (Coulson and Stephen, 2006), among other factors.

Following pupation, adult beetles of the next generation tunnel outward through the bark and initiate flight in search of new hosts. The life cycle may be repeated once every several years (e.g., the spruce beetle, *Dendroctonus rufipennis* Kirby) or several times a year (e.g., the western pine beetle, *Dendoctonus brevicomis* LeConte), which has obvious implications to their management. For example, mechanical fuel treatments (e.g., thinning of small-diameter trees) are commonly implemented in the western United



FIGURE 14.1 Beetles that initiate host colonization are often killed by drowning or immobilization in resin when hosts are vigorous, as depicted by this *Dendroctonus brevicomis*. This is usually considered the primary defense of conifers against bark beetle attack. Management strategies exist to increase tree vigor, and thus reduce the susceptibility of trees and forests to bark beetles. *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

States to reduce the risk, severity, and extent of wildfires (Stephens *et al.*, 2012). However, much of the biomass removed is unmerchantable, and therefore cut and lopped (i.e., the boles are severed into short lengths and limbs removed) or chipped and redistributed on site. Chipping has been demonstrated to increase levels of tree mortality attributed to bark beetles, presumably due to the plumes of monoterpenes released, but conducting chipping operations in autumn (as compared to spring/early summer) after most species have become relatively inactive results in fewer trees being attacked and killed (Fettig *et al.*, 2006a; DeGomez *et al.*, 2008).

1.2 Development of Outbreaks

Mechanisms contributing to bark beetle outbreaks are complex and include density-dependent and density-independent factors (see Chapters 1, 4, and 7), but two requirements must be met for an outbreak to occur: (1) there must be several years of favorable weather conducive to beetle survival and population growth; and (2) there must be an abundance of susceptible host trees. In many cases, age–class structure and tree species composition will be dominant factors influencing the severity of outbreaks. However, many experts agree that anthropogenic-induced climate change has also contributed to some outbreaks due to shifts in temperature and precipitation that influence both the beetles and their hosts (Bentz *et al.*, 2010; Sambaraju *et al.*, 2012).

During endemic bark beetle populations, trees weakened or damaged by other agents (e.g., pathogens) are often colonized and killed by bark beetles. For example, endemic populations of northern spruce engraver (*Ips*

perturbatus (Eichhoff)) infest forest debris, widely scattered individual trees or small groups of trees. However, natural (e.g., flooding, wildfire, and wind storms) and anthropogenic-induced (e.g., road building, construction of utility rights-of-way, and logging) disturbances may produce large quantities of damaged, dead, or dying spruce that serve as ideal hosts. If favorable climatic conditions coincide with large quantities of suitable host material, populations may erupt resulting in the mortality of apparently healthy trees over extensive areas (Holsten and Werner, 1987). Similarly, outbreaks of *I. typographus* in central Europe are often precipitated by large-scale blowdown events associated with severe storms (see Section 6). In the absence of such large-scale disturbances, damage to individual hosts from subcortical insects (Boone et al., 2011), defoliators (Wallin and Raffa, 2001), drought (Fettig et al., 2013a), lightning strikes (Hodges and Pickard, 1971), and root pathogens (Klepzig et al., 1991) may reduce host resistance and facilitate successful colonization by bark beetles. Such hosts are thought to be important in maintaining localized populations between outbreaks.

Individual bark beetle species generally exhibit a preference for trees of certain sizes. For example, it is well established that D. ponderosae initially colonizes the largest trees within P. contorta forests (Shepherd, 1966; Rasmussen, 1972), with progressively smaller trees being attacked over time (Klein et al., 1978; Cole and Amman, 1980; Amman and Cole, 1983). This is despite largerdiameter P. contorta having more pronounced defenses (Shrimpton, 1973; Boone et al., 2011), but provide for a higher reproductive potential and probability of beetle survival (Amman, 1969, 1975; Reid and Purcell, 2011; Graf et al., 2012) because of the greater quantity of food (phloem) available on which larvae feed. To that end, Safranyik et al. (1974) reported that P. contorta <25 cm dbh (diameter at breast height) (diameter at 1.37 m in height) serve as D. ponderosae sinks, whereas trees >25 cm dbh serve as sources producing more D. ponderosae than required to overcome host defenses. This has obvious implications to the population dynamics of D. ponderosae. In other species, a preference for smaller-diameter trees may be exhibited. For example, the pine engraver (Ips pini (Say)) most frequently colonizes trees 5-20 cm dbh, and attack rates are negatively correlated with tree diameter (Kolb et al., 2006). Understanding host preferences and how these influence outbreak dynamics is critical to the proper implementation of management strategies.

A considerable amount of effort has been devoted to the identification of tree, stand, and landscape conditions associated with bark beetle infestations. Most aggressive species exhibit a preference for larger-diameter trees growing in high-density stands with a high percentage of host type (reviewed by Fettig *et al.*, 2007a for North

America) (see Section 3). Furthermore, forested landscapes that contain little heterogeneity may result in large contiguous areas susceptible to bark beetles. It is clear that efforts to prevent undesirable levels of tree mortality attributed to bark beetles must account for these variables (see Section 5).

2. DETECTION AND SURVEY

Information on the intensity and extent of bark beetle infestations adequate to plan appropriate control strategies requires accurate detection and survey methods. Many methods have been developed to address different bark beetle species, host species, and spatial scales. These range from trapping programs to monitor populations, to simple ground-based surveys, to a broad array of aerial surveys using methods such as sketch mapping, to more sophisticated methods using remotely sensed data obtained from satellites (Wulder *et al.*, 2006a, b; Meigs *et al.*, 2011).

2.1 Aerial Survey

Research concerning the application of remote sensing methods for detection and survey was initiated in the mid-20th century. Aerial photography was frequently used in the 1970-1980s, including both true color and colorinfrared photography (Puritch, 1981; Gimbarzevsky, 1984). Usually, these surveys were limited to detection of infestations followed by more detailed surveys to identify currently infested trees. Infestations were manually drawn (sketched) on maps, but such techniques have largely been replaced by more sophisticated methods, particularly in North America. For example, surveys using helicopters and/or fixed-wing aircraft with global positioning systems (GPS) and digital sketch-mapping equipment is one of the most precise and widely used methods today (Wulder et al., 2005a) (Figure 14.2). In addition to showing your position on a digital map, sketch mapping allows real-time acquisition of geographic information system (GIS) data without being at the corresponding physical location, and is relatively inexpensive compared to other survey methods (often < \$US1/ha). It also allows for quick processing of data and reporting compared to waiting weeks or months for quality aerial or satellite imagery. However, flying presents unique risks, and considerable variability has been observed in data reported from different observers (Figure 14.2).

The landscape scale of aerial survey (1:10,000– 1:50,000) is often considered sufficient for control planning purposes (Wulder *et al.*, 2004), but requires survey methods that are accurate and provide spatially distinct data. Landsat data, as those derived from the analysis of enhanced wetness difference index (EWDI), are sufficient to detect



FIGURE 14.2 Digital sketch-mapping systems are now commonly used during aerial survey. The system, consisting of a tablet PC, external GPS receiver, and stylus, has the capability to display multiple types of background images for navigation and mapping (aerial imagery, topographic maps, etc.) and vector data (e.g., administrative and political boundaries, aerial hazards, etc.). *Photo credit: D. Wittwer, Forest Health Protection, USDA Forest Service.*

larger groups of trees, but not small or low-density infestations (Skakun et al., 2003). However, it is hard to achieve sufficient accuracy within large areas, especially when infested trees or groups of trees are scattered across the landscape (Wulder et al., 2006a, b). Some methods provide quite precise data on individual trees through imagery collected on multiple dates or spatial high resolution, but are expensive (Bone et al., 2005). These methods enable detection of trees during the later stages of infestation when their foliage is fading and distinctly different from that of healthy trees or those previously killed by bark beetles or other agents (Figure 14.3). During surveys, a common method of estimating when trees died uses needle color and retention. For example, for D. ponderosae in P. contorta these stages are commonly referred to as the green stage (within 1 year of attack; green foliage or foliage just beginning to fade), red stage (1-3 years since death; red foliage), and gray stage (>3 years since death; gray, limited or no foliage). However, relationships between foliage characteristics and time since tree death vary considerably by bark beetle species and host species, among other factors. It is also important to emphasize that these are crude

estimates that may vary by several years from the actual time since tree death.

The identification of currently infested trees is critical to maximizing the effectiveness of direct control strategies such as sanitation (Niemann and Visintini, 2005) (see Section 4.3.1). As indicated, trees that have been dead for 1 or more years and which the beetles have vacated are detected based on patterns of crown fade, and currently infested trees (i.e., which exhibit little or no crown fade) are then detected by their proximity to faded trees (Wulder et al., 2006a, 2009) and confirmed by the presence of pitch tubes and/or boring dust during ground-based surveys. Some experiments have shown that detection of currently infested trees (green stage) is possible with the use of thermal scanners (Heller, 1968), and on aerial photographs with the use of color-infrared film to improve contrasts between infested and uninfested trees (Arnberg and Wastenson, 1973). However, neither method has been widely adopted. At the local scale, detailed surveys of red stage trees can be performed with aerial photography or high-resolution satellite imagery such as IKONOS (White et al., 2004).

2.2 Ground-based Surveys

Methods for identifying currently infested trees depend primarily on ground-based surveys. In North America, these surveys are supported by data from aerial surveys focused on detection of red-stage trees. In many European countries, currently infested trees are detected by trained field observers called *sawdusters* (see Section 6). During outbreaks, sawdusters are actively employed searching for currently infested trees on a systematic basis throughout the year. In well-organized management units, where one sawduster is operating on a scale of ≈ 1000 ha, the effectiveness of infested tree detections is very close to 100%. Once identified, infested trees are marked, numbered, and mapped.



FIGURE 14.3 An outbreak of *Dendroctonus ponderosae* in *Pinus albicaulis* forests in California, United States. During aerial survey, host and bark beetle signatures are often differentiated by crown color and pattern of mortality. *Photo credit: D. Cluck, Forest Health Protection, USDA Forest Service.*

Sometimes the date of detection is also placed on the tree. Usually after several days, these trees are cut and removed or debarked (see Section 6). During a recent outbreak of *I. typographus* in southern Poland, 1.5 million currently infested trees were identified during ground-based surveys and harvested (Szabla, 2013). In Europe, ground-based surveys using well-trained dogs to detect infested trees have been demonstrated to be effective, even when visible signs of attack were not evident on tree boles (Feicht, 2006).

Ground-based surveys may also be conducted to quantify the impact of bark beetles on forests. Sample designs vary widely depending on variables of interest, but often include collection of standard forest mensuration data. For example, in France infestations of the six-toothed bark beetle (*Ips sexdentatus* (Boern)) were located using color-infrared aerial photography and validated by ground-based survey. Assessments then concentrated on counting all dead and dying trees sighted within a fixed distance of roads (Samalens *et al.*, 2007). In the United States, the USDA Forest Service has installed a large network of plots in the Rocky Mountains to quantify the impacts of *D. ponderosae* outbreaks on forest fuels and other attributes (Fettig *et al.*, unpubl. data).

3. RISK AND HAZARD RATING

Risk and hazard rating systems have been developed for several species of bark beetles to provide land managers and others with means of identifying stands or forests that foster initiation and/or spread of infestations. In general, rating systems that estimate the probability of stand infestation define "risk," while those that predict the extent of tree mortality define "hazard," although conventions vary among authors resulting in confusion between differences in these systems. Some authors have reserved "risk" solely for rating systems in which measures of insect population pressure are included (Waters, 1985). Risk and hazard rating systems represent a critical step in forest planning, especially where bark beetles are known to cause significant levels of tree mortality.

As indicate earlier, most bark beetle species capable of causing extensive levels of tree mortality exhibit a preference for larger diameter trees (often with declining radial growth) growing in high-density stands with a high percentage of host type (Table 14.2), and therefore such variables serve as a foundation for many risk and hazard rating systems (Table 14.3). In western North America, among the most commonly used is that of Shore and Safranyik (1992) for D. ponderosae in P. contorta. Susceptibility is calculated based on four factors: (1) percentage of susceptible basal area (trees \geq 15 cm dbh); (2) average stand age of dominant and co-dominant trees; (3) stand density of all trees >7.5 cm dbh; and (4) the geographic location of the stand in terms of latitude, longitude, and elevation. Dendroctonus ponderosae population data, referred to as a beetle pressure index, incorporates the proximity and size of D. ponderosae populations (Table 14.4). The stand susceptibility index and beetle pressure index are then used to compute an overall stand risk index (Shore and Safranyik, 1992; Shore et al., 2000). Due to the unique ability of D. ponderosae to cause extensive levels of tree mortality in several hosts, numerous risk and hazard rating systems have been developed for this species (reviewed by Fettig et al., 2014a), but also for other bark beetle-host systems, particularly for the more aggressive bark beetle species. For example, several models have been developed to predict tree losses attributed to Douglas-fir beetle (Dendroctonus pseudotsugae Hopkins) (Weatherby and Thier, 1993; Negrón, 1998; Shore *et al.*, 1999); roundheaded pine beetle (Dendroctonus adjunctus Blandford) (Negrón, 1997); spruce beetle (Schmid and Frye, 1976; Reynolds and Holsten, 1994, 1996; Steele et al., 1996); southern pine beetle (Dendroctonus frontalis Zimmermann) (Billings and Hynum, 1980; Reed et al., 1981; Hedden, 1985; Stephen and Lih, 1985), most recently using GIS-based three-dimensional platforms (Chou et al., 2013); D. brevicomis (Liebhold et al., 1986; Steele et al., 1996; Hayes

TABLE 14.2 Factors Characteristic of Stands Susceptible to Dendroctonus frontalis in Three Physiographic Regions of the Southern United Sates

Coastal Plain	Piedmont	Appalachian Mountains
Dense stocking	Dense stocking	Dense stocking, natural regeneration
Declining radial growth	Declining radial growth	Declining radial growth
Poorly drained soils	High clay content	Southern aspects
High proportion of Pinus echinata and P. taeda	High percentage of P. echinata	High percentage of P. echinata and/or P. rigida
(Modified from Belanger and Malac, 1980.)		

in the Black Hills of South Dakot	a and Wyoming, United S	tates	
	Probability on Infestation	Classes	
Variables	Low=1	Moderate=2	High=3
Stand structure		Two-storied	Single-storied
Mean dbh ¹ (cm)	<15.2	15.2–25.4	>25.4
Basal area (m²/ha)	<18.4	18.4–34.4	>34.4
Stand Value		Overall Rating	
2–6		Low	
8–12		Moderate	
18–27		High	

TABLE 14.3 Rating the Probability of *Pinus ponderosa* Stands becoming Infested by *Dendroctonus ponderosae* in the Black Hills of South Dakota and Wyoming, United States

¹Diameter at breast height, 1.37 m.

A number of rating systems use similar approaches of assigning values to model variables which are then multiplied (or added) to obtain an overall rating. (Modified from Stevens et al., 1980.)

TABLE 14.4 Determination of the Relative Size of a *Dendroctonus ponderosae* Infestation (Small to Large, Top) and then the Bark Beetle Index (0.06–1.0, Bottom) based on the Relative Size of the Infestation

Number of Infested Trees outs	ide Stand (within 3	km)	Number of I	nfested	Trees wi	thin Stand	
			<10		10–100		>100
<900			Small		Medium	ı	Large
900–9000			Medium		Medium	ı	Large
>9000			Large		Large		Large
Distance to Nearest Infestation (k	am)						
Relative infestation size	In stand	0–1	1–2	2–3		3–4	>4
Beetle Pressure Index (B)							
Small	0.6	0.5	0.4	0.3		0.1	0.06
Medium	0.8	0.7	0.6	0.4		0.2	0.08
Large	1.0	0.9	0.7	0.5		0.2	0.1

Once the beetle pressure index (B) and stand susceptibility index (not presented here) are known, these values are used to compute an overall stand risk index. (Modified from Shore and Safranyik, 1992.)

et al., 2009); and I. typographus (see Section 6), among others.

Risk and hazard rating systems are influenced by geographic location, site quality, and tree-diameter distributions. Measures of density are usually stand-level means, while differences in microtopography may create localized differences in productivity important to determining risk and hazard (Fettig, 2012), specifically in reference to the probability of infestation. As such, rating systems should primarily be used to identify areas most susceptible to bark beetles, as actual predictions may not be very accurate. Bentz et al. (1993) evaluated several *D. ponderosae* rating systems in *P. contorta* forests in Montana, and reported that none provided adequate predictions of tree losses. Alternatively, Shore et al. (2000) evaluated the Shore and Safranyik (1992) rating system in *P. contorta* forests in British Columbia, and reported most stands fell within the 95% prediction interval of the original model data. Finally, it is likely climate change will affect the predictive capacities of some systems due to the effects of projected changes on host-tree vigor, and on the temperaturedependent life history traits of bark beetles. We expect that the threshold values identified in many rating systems will require revision in the future (e.g., reductions in existing tree density thresholds associated with highly susceptible stands).

Other methods have been developed to predict tree losses attributed to bark beetles based on trap catches. For example, Billings (1988) developed a practical system for predicting risk of D. frontalis infestations in the southern United States based on captures of D. frontalis in attractantbaited multiple-funnel traps and the ratio of D. frontalis to one of its major predators, Thanasimus dubius (Fabricius) (Coleoptera: Cleridae). Traps are deployed on a county basis and monitored for several weeks in spring. Since its inception, this system has received widespread use and is generally regarded as an accurate means of forecasting D. frontalis population trends (i.e., increasing, declining, or static) and infestation levels (i.e., low, moderate, high, or outbreak). Similarly, Hansen et al. (2006) developed an effective method using attractant-baited multiple-funnel traps to estimate relative levels of tree mortality attributed to D. rufipennis in the central Rocky Mountain region. However, trap catches are regarded as poor indicators of future levels of tree mortality in some bark beetle-host systems. For example, Hayes et al. (2009) showed that monitoring of D. brevicomis populations through the use of attractant-baited multiple-funnel traps was ineffective for predicting levels of *D. brevicomis*-caused tree mortality. However, levels of tree mortality could be effectively predicted at large spatial scales (forests; 3000 to 14,000 hectares of contiguous host) by simply measuring stand density.

4. DIRECT CONTROL

Bark beetles have been the focus of direct control dating back to the 1700s. For example, in central Europe the Royal Society of Sciences at Göttingen, Germany, established an award to recognize the best proposal for bark beetle control in response to large-scale outbreaks of *I. typographus* in the mid-18th century. In response, Gmelin (1787) described two treatments, sanitation and burning of infested host material, that are still used today. In North America, the first documented use of large-scale direct control occurred in response to outbreaks of D. ponderosae in the Black Hills of South Dakota and Wyoming (Hopkins, 1905). Significant efforts have been undertaken since to develop effective direct control strategies for several species of bark beetles. Most target reducing localized populations, slowing the rate of infestation spread, and protecting individual trees or stands.

A successful direct control program requires prompt and thorough applications of the most appropriate strategies at a magnitude dictated by the bark beetle population and the spatial extent of the infested area. Treatments applied to areas adjacent to untreated areas where elevated populations occur are likely to be less successful due to immigration from untreated to treated areas. Coggins et al. (2011) found that mitigation rates of >50% (sanitation harvests) coupled with ongoing detection, monitoring, and treatment of infested trees within treated sites in British Columbia was sufficient to control D. ponderosae infestations. Alternatively, others have stressed that many large-scale, well-funded, and well-coordinated direct control programs (sanitation harvests) were largely ineffective (Wickman, 1987), and that resources would be better allocated to indirect control. Direct control is an expensive endeavor, and therefore decisions regarding its use and implementation are often dictated by more practical concerns such as resource availability (e.g., budget, time, personnel, and equipment), market conditions, logistical constraints (e.g., accessibility and ownership patterns), and environmental concerns.

4.1 Acoustics

Bark beetles use acoustics in a variety of behaviors, including territoriality (Rudinsky *et al.*, 1976), mate recognition (Rudinsky and Michael, 1973), and predator escape (Lewis and Cane, 1990). While applied research is in its infancy, Hofstetter *et al.* (2014) reported that applications of biologically derived acoustical signals disrupted behaviors in *D. frontalis* important to their reproductive performance, and therefore may have utility in the future management of this and other bark beetle species.

4.2 Biological Control

Natural enemies, such as predators and parasitoids, are important in regulating bark beetle populations at endemic levels, and have potential utility in biological control programs. In portions of China, successful classical biological control has been implemented in response to the introduction of *D. valens* by mass rearing and release of *Rhizophagus grandis* Gyllenhal (Coleoptera: Rhizophagidae), a predatory beetle native to Eurasia (Yang *et al.*, 2014). The use of *R. grandis* is also a common strategy for control of the great spruce beetle (*Dendroctonus micans* (Kugelann)). Native to Siberia, *D. micans* invaded Europe in the 19th century and its range is still expanding. Successful classical biological control efforts have been implemented using *R. grandis* in France (Grégoire *et al.*, 1985), Georgia (Kobakhidze *et al.*, 1970), the United Kingdom

(Fielding *et al.*, 1991), and Turkey (Yüksel, 1996). A common approach is to inundate stands with *R. grandis* at the leading edge of infested areas. Other research has indicated that conservation and supplemental feeding may be useful to enhance the effect of native biological control agents (Stephen *et al.*, 1997). For example, the parasitoid complex of *D. frontalis* in the southern United States consists of several species that may be important in regulating small infestations. Supplemental feedings of parasitoids in the laboratory and field with EliminadeTM (Entopath Inc., Easton, PA), an artificial diet consisting largely of sucrose, has been shown to increase longevity and fecundity (Mathews and Stephen, 1997, 1999; Stephen and Browne, 2000), but is not used operationally.

Synthetic formulations of entomopathogenic microorganisms, such as fungi, bacteria, and viruses, may also be useful for managing bark beetle populations. Efforts have focused largely on the fungus Beauveria bassiana (Bals.) Vuill. (Ascomycota: Hypocreales), which has been demonstrated to cause high levels of mortality in several species of bark beetles, including I. typographus (Wegensteiner, 1992, 1996; Kreutz et al., 2000, 2004). One tactic being developed includes contaminating beetles collected in attractant-baited traps, and then releasing these individuals back into the field to contaminate the pest population (Vaupel and Zimmermann, 1996; Kreutz et al., 2000). While this method has potential, additional research is needed to develop more practical methods of release and spread of *B. bassiana* in bark beetle populations as field studies have provided less conclusive evidence of mycosis than under laboratory conditions (Safranyik et al., 2002). Related research is being conducted in the western United States to developed B. bassiana as a tool for protecting trees from colonization by bark beetles (Fettig et al., unpubl. data). Other research has focused on bacteria. For example, Sevim et al. (2012) showed that strains of Pseudomonas fluorescens Flügge can be modified to express insecticidal toxins, and may represent a new method of control for I. sexdentatus, and perhaps other bark beetles. Chapter 7 presents detailed information on natural enemies of bark beetles.

4.3 Cultural

4.3.1 Sanitation

Sanitation involves the identification of trees infested by bark beetles, and subsequent felling and removal or treatment to destroy adults and brood beneath the bark, thereby reducing their populations. Where it is economically feasible, trees may be harvested and transported to mills where broods will be killed during processing. Otherwise, felled trees are burned, chipped, peeled, and



FIGURE 14.4 Log WizardTM being used to peel bark from *Picea engel-mannii* infested with *Dendroctonus rufipennis* in Utah, United States. This and other similar methods are often used in conjunction with sanitation and trap tree methods to destroy brood and adults beneath the bark. *Photo credit: S. Munson, Forest Health Protection, USDA Forest Service.*

debarked (Figure 14.4) or treated by solarization (i.e., placement of infested material in the direct sun, which is often sufficient to kill brood beneath the bark in warmer climates). In some cases, an emphasis is placed on sanitation of newly infested trees during the very early stages of colonization in order to also reduce the quantity of attractive semiochemicals (e.g., aggregation pheromones) released into the stand (see Section 4.6). However, reducing the level of attractive semiochemicals is difficult due to complications regarding the identification of newly attacked trees and the level of responsiveness required in their prompt removal. Identifying susceptible stands (see Section 3), coupled with the ability to address the infestation and resource values adversely affected, will determine where sanitation is most effective. Synthetic attractants may be used to concentrate existing infestations within small groups of trees prior to sanitation.

Sanitation, one of the oldest D. frontalis control tactics (St. George and Beal, 1929), continues to be the most recommended. Harvesting and utilizing currently infested trees, plus a buffer strip of uninfested trees, can halt infestation growth. Dendroctonus frontalis infests concentrated groups of trees (spots) creating infestations that can expand over time without intervention. These groups may range in size from a few trees to several thousand hectares. Timely sanitation is often not possible during large-scale outbreaks of D. frontalis due to limitations in labor, but in this case cut-and-leave (i.e., felling all freshly attacked and currently infested trees toward the center of an infestation) may be employed (Figure 14.5). Similar, sanitation is considered the most effective direct control method for *I. typographus*, and is widely implemented throughout central Europe (see Section 6). Depending on the scale and extent, sanitation

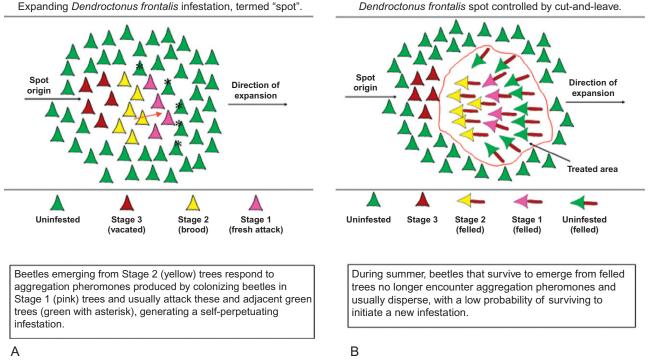


FIGURE 14.5 Illustrations of an expanding *Dendroctonus frontalis* "spot" (A) and one that has been controlled by cut-and-leave tactics (B). *Modified from Fettig et al.* (2007a).

may have the added benefit of reducing stand risk and hazard by influencing structure and composition.

4.3.2 Salvage

Salvage involves the harvest and removal of dead trees in order to recover some economic value that would otherwise be lost. Technically, salvage is not a direct control method as its implementation has no immediate effect on bark beetle populations (i.e., beetles have already vacated the trees). However, the term commonly appears in the bark beetle literature, particularly in Europe (see Section 6). In some cases, thinning (see Section 5) may be combined with sanitation and salvage in order to manipulate stand structure to reduce risk and hazard. Salvage or other treatment of hazardous trees may be necessary for safety concerns prior to accessing forests where high levels of tree mortality have occurred.

4.4 Insecticides

Insecticides are highly regulated by federal, provincial, state, and local governments, and therefore their use for protecting trees from mortality attributed to bark beetles varies accordingly. For example, hundreds of thousands of trees may be treated with insecticides during outbreaks of *D. ponderosae* in the western United States, yet their use for control of *I. typographus* is banned in most European

countries. A list of insecticides registered for protecting trees from bark beetle attack can usually be obtained online from regulatory agencies and/or cooperative extension offices, and should be consulted prior to implementing any treatment. It is important to note whether the product is registered for ornamental and/or forest settings, and to limit applications to appropriate sites using suitable application rates while carefully following label restrictions. Generally, only high-value, individual trees growing in unique environments are treated (e.g., developed campgrounds and wildland-urban environments). Tree losses in these environments result in undesirable impacts such as reduced shade, screening, aesthetics, and increased fire risk. Dead trees also pose potential hazards to public safety requiring routine inspection, maintenance, and eventual removal. In addition, trees growing in progeny tests, seed orchards, or those genetically resistant to forest diseases may be treated, especially when epidemic populations of bark beetles exist. Applied correctly, failures in insecticide efficacy are rare and often associated with inadequate coverage, improper mixing, improper storage, and/or improper timing (i.e., applying insecticides to trees already attacked). Remedial applications to kill adults and brood beneath the bark of infested trees are rarely used today (Fettig et al., 2013b).

Most insecticide treatments involve topical sprays applied to the tree bole from the root collar to the mid-crown until runoff (Figure 14.6). It is important that all parts of the tree that are likely to be attacked are



FIGURE 14.6 A common method of protecting conifers from bark beetle attack in the United States is to saturate all surfaces of the tree bole with an insecticide. Bole sprays are typically applied in late spring prior to initiation of the adult flight period for the target bark beetle species. Usually only high-value, individual trees growing in unique environments or under unique circumstances are treated. *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

adequately protected. For some bark beetle species, such as *Ips*, this may require coverage of small limbs and branches. The amount of insecticide (product + carrier, usually water) applied varies considerably with tree species, bark beetle species, tree size, bark and tree architecture, equipment and applicator, among other factors (Fettig et al., 2013b). However, application efficiency (i.e., the percentage of material applied that is retained on trees) is surprisingly high, generally ranging between 80 and 90% (Haverty et al., 1983; Fettig et al., 2008). Bole sprays are usually applied in late spring prior to initiation of the adult flight period for the target bark beetle species. Length of residual activity varies by active ingredient, formulation, bark beetle species, tree species, and location. In most cases, a minimum of one field season of efficacy is expected, but two field seasons is common in some bark beetle-host systems (Fettig et al., 2013b). In rare cases, more than one application per year may be recommended, but this is usually not supported by the scientific literature (Fettig et al., 2006b).

Researchers attempting to find safer, more portable and longer lasting alternatives to bole sprays have evaluated the



FIGURE 14.7 Experimental injections of emamectin benzoate for protecting *Pinus ponderosa* from mortality attributed to *Dendroctonus brevicomis*. Small quantities [usually <500 ml tree (total volume) based on tree size] were injected with the Arborjet Tree IVTM microinfusion system (Arborjet Inc., Woburn, MA), and later trees were challenged by baiting. A single injection provided adequate protection for three field seasons spurring additional research and later registration of a commercial formulation. *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

effectiveness of injecting small quantities of systemic insecticides directly into the tree bole with pressurized systems (Figure 14.7). These systems push adequate volumes of product (i.e., generally less than several hundred milliliters for even large trees) into the small vesicles of the sapwood. Following injection, the product is transported throughout the tree to the target tissue (i.e., the phloem where bark beetle feeding occurs). Injections can be applied at any time of year when the tree is actively translocating, but time is needed to allow for full distribution of the active ingredient within the tree prior to the tree being attacked by bark beetles. This takes at least several weeks (Fettig et al., 2014b). Tree injections represent essentially closed systems that eliminate drift, and reduce non-target effects and applicator exposure. With the advent of systemic formulations specifically for tree injection, tree injections may become more common tools for protecting conifers from bark beetle attack (Fettig et al., 2013b), particularly in areas where bole sprays are not practical.

4.5 Fire

Burning of infested host material may cause significant beetle mortality and provide some level of direct control (DeGomez *et al.*, 2008); however, attempts to burn standing infested trees have produced mixed results and are seldom used. The application of prescribed fire and/or broadcast burns to suppress bark beetle populations is largely ineffective and rarely practiced (Carroll *et al.*, 2006), but may be appropriate for some species. For example, the use of prescribed fire in the late summer and early autumn in interior Alaska is becoming more common to reduce hazardous fuels and improve wildlife habitat. Such burns may have the added benefit of killing adult *I. perturbatus* that overwinter in the litter layer (Burnside *et al.*, 2011), yet the effectiveness of this treatment has not been adequately explored.

4.6 Semiochemicals

After discovery of the first bark beetle pheromone in the mid-1960s (Silverstein *et al.*, 1966), several bark beetle species were among the first organisms investigated for pheromones, but it was not until years later that these and other semiochemicals were used in management. Utilization has centered on aggregation pheromones that attract the subject species for purposes of retention and later destruction, and antiaggregation pheromones that inhibit host finding and colonization success. The primary semiochemicals associated with most aggressive bark beetle species have been isolated and identified (Wood, 1982; Borden, 1997; Zhang and Schlyter, 2004), and combined with an integrated understanding of their context in the chemical ecology of forests have led to the development of several direct control strategies.

4.6.1 Attractants

The use of attractants in traps to detect or monitor bark beetles is common (Figure 14.8), and often used to survey for exotic, invasive species. For example, the United States Cooperative Agricultural Pest Survey (CAPS) for I. typographus includes use of cis-verbenol, ipsdienol and 2-methyl-3-buten-2-ol in multi-funnel traps. As mentioned earlier, attractants are also used in trapping programs to monitor population trends and to predict levels of tree mortality attributed to bark beetles (see Section 3), as well as to time deployment of direct control tactics with peak emergence or flight activity patterns. However, some caution should be exerted when interpreting trap catches. For example, Bentz (2006) showed that emergence of D. ponderosae from naturally infested trees occurred during a short period of time (30 days), while beetles were caught in attractant-baited traps over a much longer period (130 days). Furthermore, a large proportion of the total number of beetles caught in traps occurred prior to and following peak emergence from trees. In this case, trap catches were a poor representation of overall activity levels.

Attractants are also used in traps to collect and remove beetles through *mass trapping*, and to a lesser extent are placed on insecticide-treated trees to create *lethal trap trees* that induce mortality of beetles upon contact with the tree.



FIGURE 14.8 An attractant-baited multiple-funnel trap used for monitoring bark beetle populations. *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

The tactic of controlling bark beetle populations by mass trapping has been attempted for several species in Europe (Bakke et al., 1983, Weslien et al., 1989, Hübertz et al., 1991) and North America (Bedard et al., 1979; Bedard and Wood, 1981; Borden and McLean, 1981; Shea and Neustein, 1995; Ross and Daterman, 1997; Bentz and Munson, 2000). Trapping efficiency varies by bait composition, placement and release rate, trap design and placement, stand structure and composition, and abiotic factors. As mentioned earlier, attractants may be used to induce attacks on individual trees or small groups of trees (termed *trap trees*) to induce colonization prior to sanitation (see Section 4.3.1). An alternative, known as push pull, combines the use of mass trapping or trap-tree methods with inhibitors to divert beetles from high-value stands to attractant-baited traps or trees. However, as with any method using attractants, some beetles may infest or *spill* over onto adjacent trees resulting in additional levels of tree mortality, a behavior exhibited in many Dendroctonus species. When using attractant-baited traps, placement in areas of non-host trees or in forest openings should limit spillover. Similarly, baiting trees that are widely separated from other hosts (e.g., by >10 m) should reduce the probability of spillover.

4.6.2 Inhibitors

Inhibitors, such as antiaggregation pheromones, are used to protect individual trees and forest stands. Verbenone has received considerable attention and is the primary antiaggregation pheromone of D. ponderosae, D. frontalis, and D. brevicomis, but also causes inhibition in several other species (Zhang and Schlyter, 2004). Production occurs by the beetles themselves (Byers et al., 1984), by autooxidation of the host monoterpene α -pinene via the intermediary compounds *cis*- and *trans*-verbenol (Hunt *et al.*, 1989; Hunt and Borden, 1990), and by degradation of host material by microorganisms associated with bark beetles (Leufvén et al., 1984). Lindgren et al. (1996) proposed that verbenone is an indicator of host tissue quality and that its quantity is a function of microbial degradation. Verbenone is presumed to reduce intra- and interspecific competition by altering adult beetle behavior to minimize overcrowding of developing brood within the host. Fettig et al. (2007b) showed that Temnochila chlorodia (Mannerheim) (Coleoptera: Trogositidae), a common bark beetle predator in western North America, is attracted to verbenone, and therefore its impact on beetle populations may be enhanced by verbenone treatments.

In North America, verbenone has been demonstrated effective for reducing tree mortality attributed to D. ponderosae and D. frontalis, but not D. brevicomis. During the 1990s, D. frontalis populations were epidemic in many areas of the southern United States, and research there led to the development and registration of a 5-g verbenonereleasing pouch (Clarke et al., 1999). Subsequently, larger capacity pouches (7-g and 7.5-g) were evaluated and registered (Progar et al., 2013). The effectiveness of verbenone varies with time and geographical area (Amman, 1994), outbreak intensity (Progar et al., 2013), dose (Borden and Lindgren, 1988; Gibson et al., 1991), tree species (Negrón et al., 2006), and bark beetle species (Fettig et al., 2009). Failures in efficacy are not uncommon, and have limited more widespread use (Table 14.5). Another antiaggregation pheromone, 3-methylcyclohex-2-en-l-one (MCH), which has been demonstrated effective for reducing colonization of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) by D. pseudotsugae, has yielded more consistent efficacy (Ross et al., 2001). However, research in North America has largely focused on verbenone, presumably due to the substantial impacts of recent outbreaks of D. ponderosae.

Recent research has concentrated on combining verbenone with other inhibitors to increase levels of inhibition (Zhang and Schlyter, 2004). In this context, a diverse array of chemical cues from con- and heterospecifics and nonhosts is likely to disrupt bark beetle searching more than high doses of a single semiochemical (e.g., verbenone) or even mixtures of semiochemicals intended to mimic one **TABLE 14.5** Barriers to Successful Development of Semiochemical-based Tools for Protecting Conifers from Mortality Attributed to Bark Beetles Based Largely on Experiences with Verbenone and *Dendroctonus ponderosae* and *D. brevicomis* in Western North America, but with Wider Applicability

,	· ,
Chemical stability of formulations in the forest environment	Little is known about chemical stability once released into the active airspace.
Complexity of semiochemical signals used in host finding, selection and colonization processes	Bark beetles use a variety of contextual cues during host finding, selection, and colonization. Insufficient reductions in tree mortality may be due, in part, to inadequate chemical or other signaling. For example, synthetic verbenone deployed alone without other beetle-derived or non-host cues may not provide sufficient levels of inhibition.
Costs and small market conditions	These factors are significant barriers to investment in research and development, specifically basic science.
Inconsistent release	Several authors have speculated that failures in effectiveness have resulted from problems associated with passive release, which is largely controlled by ambient temperature.
Levels of inhibition	Sensitivity varies among populations and among individuals within a population thus influencing effectiveness.
Managing expectations	Research is needed to determine what levels of efficacy are acceptable (e.g., based on reductions of negative impacts to forests), and under what conditions inhibitors are likely to be most effective.
Population size	Effectiveness declines with increasing population density. Higher levels of tree mortality are expected during severe infestations and with a declining proportion of preferred hosts when populations still exist at epidemic levels.

Continued

TABLE 14.5 Barriers to Successful Development ofSemiochemical-based Tools for Protecting Conifersfrom Mortality Attributed to Bark Beetles Based Largelyon Experiences with Verbenone and Dendroctonusponderosae and D. brevicomis in Western NorthAmerica, but with Wider Applicability—cont'd

Range of inhibition	Studies show that the maximum range of inhibition is quite limited. Higher densities of small, point- source releasers may provide for better dispersal patterns and greater reductions in tree mortality.
Ratio of inhibitors to attractants	Levels of inhibition vary based on this ratio.
Variation in stand structure, especially tree density	Concentrations of semiochemicals rapidly decrease with increasing distance from a point source, and in low density forests unstable layers and multi- directional traces (eddies) may dilute concentrations and reduce effectiveness.

type of signal (e.g., antiaggregation pheromones), as they represent heterogeneous stand conditions to foraging insects. To that end, a bark beetle encounters several decision nodes during host searching that may be exploited by combining verbenone (or other antiaggregation pheromones) with non-host volatiles, including (1) habitat suitability (e.g., green leaf volatiles and angiosperm bark volatiles), (2) host presence (e.g., green leaf volatiles and angiosperm bark volatiles), and (3) host suitability and susceptibility (e.g., antiaggregation and aggregation pheromone components of con- and heterospecifics, and host volatiles that signal changes in host vigor and/or tissue quality) (Borden, 1997; Schlyter and Birgersson, 1999; Zhang and Schlyter, 2004; Progar *et al.*, 2014).

The most common method of applying inhibitors includes pouch release devices (Figure 14.9) stapled at maximum reach (2 m in height) to individual trees prior to beetle flight, or applied in a gridded pattern to achieve uniform coverage when stand protection is the objective. For some species, such as *D. frontalis*, a unique distribution of release points may be required (Clarke *et al.*, 1999). Bead, flake, and sprayable formulations have been evaluated but are not widely used. The release rates of passive releasers vary with changes in temperature and humidity, and since they dispense semiochemicals through a membrane, are strongly influenced by meteorological conditions making the amount of semiochemical released somewhat



FIGURE 14.9 An example of a 7-g verbenone pouch (Contech Inc., Delta, BC) applied to reduce the amount of mortality attributed to *Dendroctonus ponderosae* in *Pinus contorta* stands. Semiochemical release devices are typically stapled at maximum reach (2 m in height) to individual trees or applied in a gridded pattern to achieve more uniform coverage when stand protection is the objective. *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

unpredictable (Holsten et al., 2002). Puffers are small battery-activated reservoirs that emit frequent, measured puffs of aerosolized liquid, thus overcoming some of the problems associated with passive releasers, but are prohibitively expensive for forestry applications (Progar et al., 2013). However, once the fluid is dispensed from puffers, evaporative properties and thus release rates are still heavily influenced by meteorological conditions. Mafra-Neto et al. (2013) have recently developed a novel matrix impregnated with verbenone (SPLAT[®] Verb, ISCA Technologies Inc., Riverside, CA) that has shown a high degree of efficacy for protecting *P. contorta* from *D. ponderosae*. Rather than a single release device, SPLAT is an amorphous, flowable controlled-release emulsion with chemical and physical properties that can be adjusted by small changes in composition and application. This formulation is also biodegradable, which has been an objective for the development of release devices as significant labor cost savings are achieved by not having to retrieve release devices from the field after use. A formulation of biodegradable flakes and a novel dispenser have also been developed and are being evaluated (Gillette *et al.*, 2012; Fettig, unpubl. data). In all cases, the fate of semiochemicals once released into the active airspace of forests is highly influenced by forest structure and meteorological conditions.

4.6.3 Future Semiochemical Research

Significant advances have been made concerning the molecular biology and biochemistry of pheromone production in bark beetles, the synthesis of semiochemicals in the laboratory, the deployment of semiochemicals in the field, and the fate of semiochemicals once released into the active airspace of forests. Despite this, significant research needs exist, including (1) improving the efficacy and cost effectiveness of blends and delivery systems, (2) redefining selection criteria for target areas where semiochemical-based treatments are likely to be most effective, (3) examining the effects of forest structure and abiotic factors on semiochemical plumes, (4) expansion of related research into understudied forest types, and (5) assessment of semiochemical performance at varied levels of beetle population and host availability (Progar et al., 2014). The results of a recent meta-analysis demonstrating the effectiveness of semiochemicals to reduce levels of tree mortality attributed to bark beetles are encouraging (Schlyter, 2012) and should spur additional research and development.

5. INDIRECT CONTROL

5.1 Thinning

It is widely accepted that thinning is an effective means of increasing the resiliency of forests to bark beetle infestations and other disturbances (Fettig et al., 2007a). However, it is important to stress that prescriptions vary widely and have different effects on structure and composition. For example, in the western United States many thinning treatments are implemented for fuels reduction, which concentrates on reducing surface fuels, increasing the height to live crown, decreasing crown density, and retaining large trees of fire-resistant species (Agee and Skinner, 2005). While such treatments may also reduce the susceptibility of forests to some bark beetle species, related prescriptions vary from those that might be implemented specifically for bark beetles. In the latter case, crown or selection thinning (i.e., removal of larger trees in the dominant and codominant crown classes) may be required to achieve target threshold densities, residual tree spacing, and significant reductions in the abundance of preferred hosts necessary to adequately reduce stand susceptibility (e.g., from D. brevicomis). Furthermore, thinning may have differential

effects among bark beetle species. In many systems, a suite of less aggressive species is attracted to logging residues (e.g., several *Ips* spp. in North America), but depending on the vigor of residual trees may result in little tree mortality. Thinning conducted in a careless manner may result in increases in other subcortical insects and root pathogens (Harrington *et al.*, 1985).

Fettig et al., (2007a) used the concept of growing space as a mechanism to illustrate how changes in host tree vigor, among other factors, influence susceptibility of individual trees and forest stands to bark beetle attack following thinning. Trees utilize growth factors, such as sunlight, water, nutrients, temperature, oxygen, and carbon dioxide, until one or more factors become limiting (Oliver and Larson, 1996). Disturbances can make growing space available to some trees at the expense of others (e.g., herbivory), or alter the amount of growing space available to all trees (e.g., drought). For example, when soil moisture is limited, trees close their stomata to avoid excessive water loss, which inherently leads to reduced productivity as stomatal closure also prohibits uptake of carbon dioxide and therefore photosynthesis. A tree's photosynthates are allocated to different uses in an order of priorities (Oliver and Larson, 1996): (1) maintenance respiration; (2) production of fine roots; (3) reproduction; (4) primary (height) growth; (5) xylem (diameter) growth; and (6) insect and disease resistance mechanisms. While somewhat conceptual, this hierarchy illustrates how production of insect resistance mechanisms is compromised first when growing space becomes limited by one or more factors. Conversely, it demonstrates how cultural practices that release growing space through reductions in tree density influence the susceptibility of individual trees, stands, and forests by strengthening insect resistance mechanisms (Fettig et al., 2007a).

Reductions in tree density also cause changes in microclimate that affect beetle fecundity and fitness, phenology, and voltinism (number of generations per year), as well as that of predators, parasitoids, and competitors. Changes in tree density may also cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during initial phases of host tree colonization. Bartos and Amman (1989) suggested that changes in microclimate were the principal factors associated with reductions in stand susceptibility to D. ponderosae following thinning in P. contorta. Thinning increased light intensity, wind movement, insolation, and temperature in affected stands. Thistle et al. (2004) examined near field canopy dispersion of a tracer gas (SF_6) , as a surrogate for bark beetle pheromones, within the trunk space of trees. They showed that when surface layers of air are stable (e.g., during low wind velocities), the tracer plume remained concentrated and directional because of suppression of turbulent mixing by the forest canopy. Lower density stands result in unstable layers of air and multi-directional traces (eddies) that diluted "pheromone" concentrations (Thistle *et al.*, 2004) and presumably reduce beetle aggregation, thus influencing host finding and colonization successes. Furthermore, the killing of groups of trees is fundamental to expansion of some infestations, and therefore some authors have suggested that residual spacing of leave trees is more important than reductions in overall tree density (Whitehead *et al.*, 2004; Whitehead and Russo, 2005). This is likely not the case in all bark beetle–host systems.

In North America, thinning from above or diameterlimit thinning, and thinning from below (Cole and Cahill, 1976; McGregor et al., 1987) applied to reduce basal area (Amman et al., 1977; Cahill, 1978; Bennett and McGregor, 1980), remove trees with thick phloem (Hamel, 1978), and/or increase residual tree spacing (Whitehead et al., 2004; Whitehead and Russo, 2005; Table 14.6) have all been implemented to reduce the susceptibility of *P. contorta* forests to *D. ponderosae*. Schmidt and Alexander (1985) found that thinning from above was effective until residual trees grew to susceptible sizes; however, it left stands with reduced silvicultural value that were often vulnerable to windthrow or snow damage. Thinning from below may optimize the effects of microclimate, inter-tree spacing, and tree vigor (Whitehead and Russo, 2005; Coops et al., 2008) even though residual trees are of diameter classes considered more susceptible to attack (Waring and Pitman, 1980; Mitchell et al., 1983, but see Ager et al., 2007). However, this practice may not be economically viable since only

smaller diameter trees are removed. Recommended residual conditions include inter-tree spacings of at least 4 m (Whitehead *et al.*, 2004; Whitehead and Russo, 2005) or 400–625 trees/hectare (Whitehead and Russo, 2005). While thinning during endemic populations is most desirable, thinning may also be useful during an outbreak, specifically if combined with sanitation harvests and/or other direct control methods (Waring and Pitman, 1985).

Schmid and Mata (2005) monitored levels of tree mortality attributed to D. ponderosae in 1-hectare plots over a 17-year period in South Dakota. The authors concluded that the effectiveness of thinning P. ponderosa forests to residual densities between 18.4 and 27.6 m²/hectare to reduce susceptibility was questionable. However, they suggested that their results were confounded by small study plots being surrounded by extensive areas of unmanaged forest where D. ponderosae populations were epidemic. Later, Schmid et al. (2007) reported thinning to 18.4 m²/ hectare in susceptible stands may not be sufficient to yield long-term reductions in susceptibility if not followed with subsequent thinning over time to maintain lower tree densities. These publications raise important issues that likely apply to other bark beetle species for which thinning and other management strategies (see Section 4) have been demonstrated effective. That is, it is critical that treatments are applied at a frequency, scale, and intensity dictated by the bark beetle population and the spatial extent of infested areas. Relatedly, Ager et al. (2007) simulated the impacts of thinning over 60 years, coupled with a D. ponderosae outbreak at 30 years, to examine how thinning might influence

3.3

1.2

minnings were Conducted, Britis	sh Columbia, Canada		
Location (Year of Treatment)	Treatment	No. Trees Attacked/ha	Green: Red Attack Ratio ¹
Cranbook (1992)	Untreated	22	1.8
	Spaced to 4 m	2	0.3
	Spaced to 5 m	7	0.5
Parson (1993)	Untreated	56	2.9
	Untreated	15	0.3
	Spaced to 4 m	0	-
	Spaced to 5 m	0	-
Hall Lake (1994)	Untreated	158	1.8
	Thinned to 500 trees/ha	37	1.4

452

167

TABLE 14.6 Cumulative Number of *Pinus contorta* Killed by *Dendroctonus ponderosae* 9–12 years after Thinnings were Conducted, British Columbia, Canada

Untreated

Spaced to 4 m

¹*Ratios* > 1.0 *indicate that infestations are building.* (Modified from Whitehead *et al.*, 2004.)

Quesnel (1991)

bark beetle impacts in a 16,000-hectare landscape in eastern Oregon. They employed the Forest Vegetation Simulator and Westwide Pine Beetle Model (WPBM). The latter simulates beetle populations in terms of a "beetle kill potential" (BKP), where one unit of BKP is sufficient to kill 0.0929 m² of host tree basal area (Smith *et al.*, 2005). While not widely adopted, the model assumes that beetles emerge and disperse, and choose stands to attack based on distance and certain stand attributes. The authors reported that contrary to expectations, WPBM predicted higher levels of tree mortality from an outbreak in thinned versus unthinned scenarios. In this case, thinning favored retention of early seral tree species (e.g., *P. ponderosa*), leading to increases in the proportion and average diameter of preferred hosts.

5.2 Landscape Heterogeneity

Efforts to prevent undesirable levels of tree mortality must also account for the spatial distribution of cover types. In many areas, treatments should be implemented to increase heterogeneity (e.g., of age, size, and species compositions) as homogeneous forested landscapes promote creation of large contiguous areas susceptible to similar disturbances (Fettig et al., 2007a). Studies have shown that insects tend to focus host searching in patches of high host concentrations (Root, 1973), which increases the probability of encounters with suitable hosts. In heterogeneous stands or landscapes this occurs with less efficiency (Jactel and Brockerhoff, 2007). For example, in North America several authors have suggested that shorter rotations and promotion of multiple age classes will minimize levels of tree mortality attributed to D. ponderosae (Safranyik et al., 1974; Taylor and Carroll, 2004; Whitehead et al., 2004).

5.3 Prescribed Fire

Prescribed fire is primarily used to reduce surface and ladders fuels in fire prone forests. Tree mortality resulting from prescribed fire may be immediate due to consumption of living tissue and heating of critical plant tissues, or can be delayed occurring over the course of several years. Levels of delayed tree mortality are difficult to predict, and depend on numerous factors including tree species, tree size, phenology, degree of fire-related injuries, initial and post-fire levels of tree vigor, the post-fire environment, and the frequency and severity of other predisposing, inciting, and contributing factors. Following prescribed fire, short-term increases in levels of bark beetle-caused tree mortality are often reported, primarily in the smaller-diameter classes (Stephens et al., 2012). However, in the longer term burned areas may benefit from the positive impacts of prescribed fire on growing space and other factors that reduce forest susceptibility to bark beetles (Fettig et al., 2006a; Fettig and McKelvey, 2010).

5.4 Social Acceptance of Management Strategies

Although public opinion is an important factor influencing the management of bark beetles (Wellstead et al., 2006), few contemporary studies have evaluated the social acceptance of various direct and indirect control strategies. McFarlane et al. (2006) examined public attitudes relevant to management preferences for D. ponderosae in Banff and Kootenay National Parks, Canada. Data were collected by mail survey from a large pool of residents living in or near the parks. All groups agreed that "allowing the outbreak to follow its course without intervention" was not an acceptable option. Preferred options included "sanitation cutting to remove infested trees from small areas" and the "use of pheromones to attract beetles to one area." Other acceptable options included the use of prescribed burning, sanitation of large areas, and "thinning the forest to remove some of the uninfested but susceptible trees." Visitors to these parks had similar attitudes to the local residents in support of direct and indirect control (McFarlane and Watson, 2008). This differs from tourists' perception of an I. typographus outbreak in Bavarian Forest National Park, Germany, where respondents showed a neutral attitude toward the bark beetle, and were somewhat disinclined to support control measures within the park (Müller and Job, 2009). In Virginia, a survey of landowners indicated that those that were college educated were more willing to participate in the state's Southern Pine Beetle Prevention Program (Watson et al., 2013), which concentrates on pre-commercial thinning to reduce forest susceptibility to D. frontalis. A better understanding of public perceptions towards outbreaks and proposed management strategies may help managers to better inform the public of the usefulness and consequences of different treatments.

6. CASE STUDY—MANAGEMENT OF *IPS TYPOGRAPHUS* IN CENTRAL EUROPE

As previously discussed, *I. typographus* is one of the most important forest insects in Europe due to its role in the dynamics of forest ecosystems and the profound impact of outbreaks on ecosystem goods and services (Grégoire and Evans, 2004; Stadelmann *et al.*, 2013). Outbreaks are usually precipitated by other disturbances such as windstorms, severe drought, or weakening of trees by pathogenic fungi (Wermelinger, 2004). Such trees attract beetles by releasing host volatiles (Lindelöw *et al.*, 1992), and provide abundant host material. In recent years, spectacular storms such as Vivian (1990), Lothar (1999), Gudrun (2005), and Kirill (2007) impacted huge areas of Europe and destroyed millions of trees, creating large quantities of susceptible host material and subsequently *I. typographus* outbreaks (Komonen *et al.*, 2011). Furthermore, the frequency and severity of outbreaks is expected to increase as a result of climate change (Schlyter *et al.*, 2006). During outbreaks, thousands of trees are attacked and killed within several weeks prompting large and well-coordinated direct control efforts. For example, during 1940–1951 one of the largest outbreaks in central Europe resulted in sanitation of 30 million m³ of infested trees. In northeastern Poland alone,

100,000 hectares of infested spruce forest were harvested during 1945–1948, and decreased spruce inventories there by 50% (Puchniarski, 2008).

Several thousand scientific and popular papers have been published on various aspects of the biology, ecology, and management of *I. typographus*. In this regard, the species ranks among the best studied of forest insects. Since publication of the first forestry text that addressed bark beetles (Ratzeburg, 1839), control methods and strategies have been systematically developed based on the practical experiences of foresters and research executed by scientists. In many European countries, several methods of control are regularly implemented in response to outbreaks of *I. typographus*.

6.1 Sanitation Salvage

As previously discussed, salvage involves the harvest and removal of dead trees, but in the context of *I. typographus* has the added benefit of removing attractive host material that facilitates rapid population growth. In central Europe, "salvage" is traditionally regarded by foresters and other practitioners as removal of infested trees (sanitation) combined with the salvage of previously infested trees or those impacted by other disturbances, termed here sanitation salvage. This is considered the most effective direct control strategy for reducing levels of tree mortality attributed to I. typographus in Europe (Wermelinger, 2004). It is common practice that a large number of infested and susceptible downed, damaged, and standing trees are treated during outbreaks, especially in countries where responding agencies are well organized and technically prepared for such large and logistically complicated operations (Szabla, 2013) (Table 14.7).

The first step in sanitation-salvage operations is to locate and mark trees to be removed. While selection of such trees is obvious in some cases (e.g., on the basis of crown fade), the process is much more difficult in the case of newly infested trees. Infested trees are systematically marked by experienced and trained sawdusters, who are usually very adept at finding trees attacked by *I. typographus* (Table 14.7). Conducting sanitation salvage during proper periods is an important factor (Figure 14.10). In the case of infested trees, treatment is critical before emergence of the next generation of beetles (Jönsson *et al.*, 2012; Stadelmann *et al.*, 2013). Trees recently damaged by windstorms or other disturbances should be salvaged before

mid-summer (Göthlin *et al.*, 2000) or may be used as trap trees (Wichmann and Ravn, 2001). Unfortunately, timely sanitation salvage is often not possible during large-scale outbreaks due to limitations in labor and logistical constraints, but delay to after the flight activity period of the following year makes these tactics ineffective and perhaps even harmful. By mid-summer, infested trees are usually heavily colonized by a rich community of natural enemies that may be adversely impacted by sanitation salvage, particularly during latter stages of an outbreak. Furthermore, retention of some dead trees is beneficial for a variety of organisms including predators and parasitoids of *I. typographus*, and several endangered species (Weslien, 1992a; Siitonen, 2001; Jonsell and Weslien, 2003).

During large-scale outbreaks, sanitation-salvage operations may be carried into winter, but is rarely implemented simply because weather conditions and snow loads often preclude access. During winter, the role of *winter sawdusters* is also very important, and the method is highly effective for limiting numbers of attacked trees the following spring and summer (Kolk and Grodzki, 2013). However, winter operations may have a stronger negative impact on natural enemy communities than sanitationsalvage implemented during the spring and summer as many species overwinter in high numbers in and under the bark of trees colonized by *I. typographus* (Weslien, 1992a). Most cluster in the bottoms of trees beneath the snow, which enhances overwintering survival (Hilszczański, 2008).

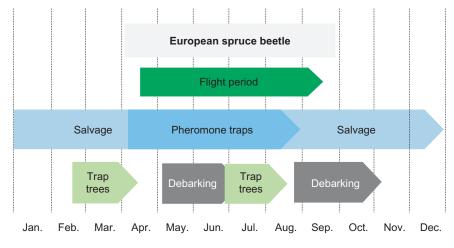
6.2 Trap Trees

It is common practice to use broken and windthrown trees as trap trees for *I. typographus*. Such trees are attractive for at least two seasons, and have limited defensive mechanisms to deter attack (Eriksson et al., 2005). Covering downed logs with the branches and foliage of spruce, while labor intensive, is supposed to protect them from rapid desiccation and is recommended in the Czech and Slovak Republics (Zahradník et al., 1996). The idea of preparing special trap trees in the form of logs for control I. typographus and other bark beetles dates back to the first half of the 19th century (Skuhravý, 2002). Trap trees are often prepared a few times per year, usually twice, to adequately cover the most important generations of *I. typographus* (Figure 14.10). It is important to debark or otherwise destroy trap trees in a timely manner after oviposition otherwise a high proportion of adults may leave (emerge), colonize adjacent trees, and establish a sister generation (Bakke, 1983). In some countries, standing live trees are used as trap trees. In these cases, trees are usually baited with synthetic pheromones and are often several times more effective at trapping *I. typographus* than pheromone-baited traps (Raty et al., 1995). For example, a study in Belgium

(Based on Szabla, 2013)					
Method	2007	2008	2009	2010	Total
Trap trees (thousands)	8.4	5.2	4.4	3.7	21.7
Baited-trap trees (thousands m ³)	17.5	30.9	31.7	16.2	96.3
Marked "sawdust" trees (thousands)	510	424	272	158	1364
Sanitation (thousands m ³)	803	798	466	231	2298
Debarked-infested trees (thousands m ³)	297	254	17	23	591
Pheromone-baited traps (thousands)	11.6	12.2	11.8	10.6	46.2

TABLE 14.7 Methods of Control for *Ips typographus* during Outbreaks in Southern Poland, 2007–2010(Based on Szabla, 2013)

FIGURE 14.10 Annual timing of direct control strategies used for management of *Ips typographus* in central Europe. Here, "salvage" is synonymous with sanitation or sanitation salvage (see Section 4).



reported trap trees were 14 times more efficient than artificial traps (Drumont *et al.*, 1992). However, efficiency varies with population densities and during endemic populations more beetles are often collected in pheromonebaited traps (Król and Bakke, 1986). On the contrary, trap trees are more effective during outbreaks (Grodzki *et al.*, 2008).

6.3 Pheromone-baited Traps

Pheromone-baited traps were initially used for monitoring of *I. typographus*, but were quickly recognized as a cheaper alternative to trap trees. The number of *I. typographus* collected depends on many factors, including bait composition, placement and release rate, trap design and placement, stand structure and composition, competition from accessible host material such as windthrown trees, harvested logs and damaged trees, and abiotic factors (Bakke, 1992; Lobinger, 1995; Mezei *et al.*, 2012). For example, traps located on southern aspects are often several times more effective at capturing *I. typographus* than those on northern aspects (Lobinger and Skatulla, 1996), presumably due to solar inputs. Mass trapping is regarded as an effective method for protecting stands of wind-damaged spruce (Grégoire et al., 1997), but is considered rather ineffective during large-scale outbreaks (Dmitri et al., 1992; Wichmann and Ravn, 2001). Estimates concerning the effectiveness of traps for reducing I. typographus populations range from 0.2 to 80% (Zahradník et al., 1993), but most studies have shown that only a minor portion is captured (Weslien and Lindelow, 1990; Lobinger and Skatulla, 1996) despite substantial numbers being collected (Szabla, 2013) (Table 14.8). Mass trapping has been implemented during large-scale outbreaks in Sweden (270,000 traps; Weslien, 1992b), and Poland (50,000 traps; Szabla, 2013), but in the latter case was just one of several direct control methods employed (Table 14.7). Generally, high trap catches are not well correlated with activity on trees, but low catches usually coincided with little beetle activity (Weslien, 1992b; Lindelöw and Schroeder, 2001). Mass trapping could be effective as an additional method of control during outbreaks, especially in the context of

TABLE 14.8 Numbers of Individuals (in Millions) Collected at the Time of Mass Trapping Efforts for Ips typographus	
during Outbreaks in Southern Poland, 2007–2010 (Based on Szabla, 2013)	

<i>Ips typographus</i> 194 189	170	72	625
Pityogenes chalcographus (l.) 156 122	162	72	512
<i>Trypodendron lineatum</i> (Olivier) 6 3	5	1	15

protecting living trees rather than reducing *I. typographus* populations (Dubbel *et al.*, 1995; Jakuš, 2001).

A potentially negative impact of mass trapping is that several members of the natural enemy community may be collected and killed. This is of specific concern for the European red-bellied clerid (*Thanasimus formicarius* (L.)) an important predator of *I. typographus* and other bark beetles. However, the proportion of trap catches represented by *T. formicarius* is usually <4% (Babuder *et al.*, 1996; Valkama *et al.*, 1997; Grodzki, 2007).

6.4 Push Pull

Advanced methods of semiochemical-based control have not been widely implemented for *I. typographus* despite numerous experiments being conducted. In the Slovak Republic, the use of verbenone and aggregation pheromones of *I. typographus* were ineffective (Jakuš and Dudova, 1999). Verbenone and non-host volatiles have been tested in several different countries with variable results. Promising results were obtained in the Šumava Mountains of the Czech Republic where push pull significantly decreased the probability of *I. typographus* attack on standing healthy trees by 60–80% (Jakuš *et al.*, 2003).

6.5 Debarking of Infested Host Material

Debarking has been implemented in response to concerns of transporting infested logs as beetles could emerge prior to processing (Drumont *et al.*, 1992). While debarking has been demonstrated to kill up to 93% of *I. typographus* beneath the bark, this may still be insufficient to achieve adequate levels of control during outbreaks (Dubbel, 1993). Furthermore, the method is time consuming and relatively expensive. Occasionally infested trees are cut and left untreated for conservation of biodiversity (Jonasova and Matejkova, 2007).

6.6 Biological Control

Several natural enemies of *I. typographus* have been extensively studied (see Chapter 7), specifically insect parasitoids and predators (Kenis *et al.*, 2004; Wermelinger,

2004), pathogens (Wegensteiner, 2004), and to a lesser extent woodpeckers (Fayt et al., 2005). Ips typographus parasitoids and predators exhibit clear habitat preferences. Some species prefer standing trees or high stumps while others prefer open areas or shady conditions (Hedgren, 2004; Hilszczański et al., 2005). Similarly, woodpeckers that commonly feed on *I. typo*graphus, such as the three-toed woodpecker (Picoides tridactylus (L.)), require certain habitat features such as dead standing trees for cavity nesting (Fayt et al., 2005). In that context, habitat manipulation and forestry practice modification could be implemented as measures of natural enemy control enhancement. To date, biological control efforts have not been formally implemented for I. typographus (Wermelinger, 2004), but some recent experiments involving B. bassiana have proven promising (Vaupel and Zimmermann, 1996; Kreutz et al., 2004; Landa et al., 2008; Jakuš and Blaženec, 2011).

6.7 Insecticides

The use of insecticides for management of *I. typographus* is banned in most European countries. Treatments were more widely used in the late 20th century usually in the context of baited trap trees or as a means to protect timber (Drumont *et al.*, 1992; Lubojacký and Holuša, 2011).

6.8 Risk and Hazard Rating and Silviculture

Risk and hazard rating represents critical elements in the management of *I. typographus*. Optimally, both direct and indirect control strategies are prioritized, planned, and implemented based on predicted risks. In most countries where *I. typographus* creates serious problems, estimation of the dynamics of pest activity is based on monitoring of the volume of infested trees (Cech and Krehan, 1997; Knížek and Lubojacký, 2012) (Figure 14.11). Unfortunately, this method provides very little information about potential risks. Moreover the interpretation of other monitoring techniques, such as the use of pheromone-baited traps, is also difficult since the effectiveness of traps depends on so many environmental and technical factors

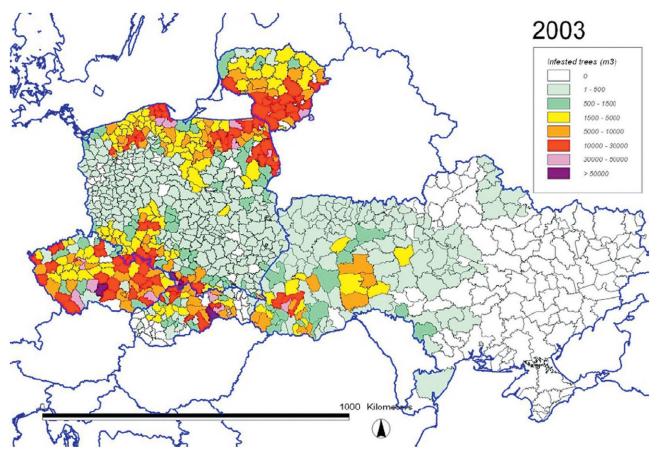


FIGURE 14.11 Distribution of bark beetle-killed trees in *Picea abies* stands of central Europe in 2003, expressed as the volume of infested trees cut in individual territorial units. *From Grodzki* (2005).

(Bakke, 1992; Lobinger, 1995; Grodzki, 2007; Mezei et al., 2012). Nevertheless some tree, stand, and other environmental characteristics related to site, exposure (aspect), water supply, temperature, and co-occurring pathogens, among others, are known to have strong effects on the probability of *I. typographus* attack. Since the first study by Annila (1969), several attempts to develop models of I. typographus development and risk assessment have been made (Zumr, 1982; Schopf, 1985; Anderbrant, 1986; Coeln et al., 1996; Wermelinger and Seifert, 1999; Netherer and Nopp-Mayr, 2005). More sophisticated models, such as PHENIPS, provide a tool for hazard rating at local and regional scales (Baier et al., 2007). Implementation of the TANABBO model enables prediction of stand susceptibility to attack based on select environmental factors and their influence on I. typographus population density (Kissiyar et al., 2005). Additionally, GIS techniques provide useful visualizations of outbreak dynamics (Jakuš et al., 2005).

Stand characteristics that can be manipulated by silvicultural treatment to reduce the susceptibility of forests to *I. typographus* include age class diversity, stand density, host density, and stand composition (Wermelinger, 2004).

Key characteristics positively correlated with the severity of outbreaks include the proportion (density) and age of spruce trees (Becker and Schröter, 2000; Gilbert et al., 2005; Hilszczański et al., 2006; Grodzki, 2010). Susceptibility to I. typographus attack also increases with the socalled "edge effect" and sudden "opening" of the forest (Göthlin et al., 2000; Grodzki et al., 2006; Hilszczański et al., 2006). Others factors affecting the susceptibility of trees include crown length, which is often related to stand density, and tree size, specifically diameter, which is relevant to both standing and downed trees (Lekander, 1972; Weslien and Regnander, 1990; Zolubas, 2003; Eriksson et al., 2005). Silvicultural activities (e.g., thinning) that reduce the susceptibility of trees, stands, and forests to I. typographus in central Europe are for the long term the most acceptable both for environmental and economic reasons.

7. CONCLUSIONS

Bark beetle infestations will continue to occur as long as susceptible forests and favorable climatic conditions coincide. As discussed above, there are a wide variety of tactics available to reduce their severity and extent when properly applied at appropriate scales. However, the only long-term solution is to change forest structure and composition to increase resiliency. Experience has shown that even a course of no action is not without consequence, although this alternative may be the most appropriate under some circumstances. Several assessments have concluded that forests are increasingly vulnerable to tree mortality as a result of the direct and indirect effects of climate change (Fettig et al., 2013a), and that the use of sound, ecologically appropriate management strategies, and prioritization of their application to enhance resiliency is critical. Gillette et al. (2014) examined the various D. ponderosae treatment options available to land managers in North America, and described their long-term consequences in terms of risk of future outbreaks, wildfire, invasion by exotic weeds, loss of hydrological values, and carbon sequestration. They, like us, argue for the increased use of science-based indirect control, specifically thinning, to increase resiliency of forests to multiple stressors including bark beetle infestations.

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