Logging to Control Insects: The Science and Myths Behind Managing Forest Insect “Pests”

A Synthesis of Independently Reviewed Research

Scott Hoffman Black

The Xerces Society for Invertebrate Conservation, Portland, Oregon

About the Author

Scott Hoffman Black, executive director of the Xerces Society, has degrees in ecology, horticultural plant science, and entomology from Colorado State University. As a researcher, conservationist, and teacher, he has worked with both small issues groups and large coalitions advocating science-based conservation and has extensive experience in addressing timber issues in the West. Scott has written many scientific and popular publications and co-authored several reports on forest management, including *Ensuring the Ecological Integrity of the National Forests in the Sierra Nevada* and *Restoring the Tahoe Basin Forest Ecosystem.* His work has also been featured in newspaper, magazines, and books, and on radio and television.

About the Xerces Society for Invertebrate Conservation

The Xerces Society is a nonprofit organization dedicated to protecting the diversity of life through the conservation of invertebrates. Though they are indisputably the most important creatures on earth, invertebrates are an overlooked segment of our ecosystems. Many people can identify an endangered Bengal tiger, but few can identify an endangered Salt Creek Tiger *beetle*. The Society works to change that. For three decades, Xerces has been at the forefront of invertebrate conservation, harnessing the knowledge of highly regarded scientists and the enthusiasm of citizens to implement conservation and education programs across the globe.

Xerces' programs focus on the conservation of pollinator insects, the protection of endangered invertebrates, aquatic invertebrate monitoring, and the conservation of invertebrates on public lands. The Xerces Society also has produced many publications that help the public take direct action to protect and restore habitat supporting invertebrates and other wildlife.

Please cite as: Black, S.H. 2005. *Logging to Control Insects: The Science and Myths Behind Managing Forest Insect "Pests." A Synthesis of Independently Reviewed Research*. The Xerces Society for Invertebrate Conservation, Portland, OR.

For additional copies: Please send $15.00 to the Xerces Society at 4828 SE Hawthorne Boulevard, Portland, OR 97215. Or, download this document from our website at www.xerces.org.

The Xerces Society for Invertebrate Conservation
4828 Southeast Hawthorne Blvd., Portland, Oregon 97215
Tel 503-232-6639 Fax 503-233-6794 www.xerces.org

ISBN 0-9744475-4-4

Preface

PURPOSE OF THIS SYNTHESIS

The purpose of this paper is twofold. The primary goal of this research compilation is to bring together pertinent, peer-reviewed information for use by forest conservationists, managers, media personnel, and scientists regarding the management of insect pests in the temperate forests of western North America. Second, this paper dispels many commonly held misconceptions about forest insect pests.

This document has three parts. **Section One** is a summary of relevant studies on the importance of insects to forest function and the methods used to control forest "pest" insects. **Section Two** is a collection of citations of peer-reviewed journal articles and Forest Service documents organized by topic area. **Section Three** is a compilation of summaries of over 150 scientific papers and Forest Service documents.

ACKNOWLEDGEMENTS

This document could not have been completed without the help of Caitlyn Howell-Walte, Abigail Hyduke, Mace Vaughan, and Matthew Shepherd of the Xerces Society. Thanks also goes to Scot Waring for his help early on. A special thanks goes to Jack Williams, former supervisor of the Rogue-Siskiyou National Forest and currently Chief Scientist for Trout Unlimited, for his thoughtful comments. Thanks also to Brian Nowicki from the Center for Biological Diversity and Steve Holmer from the United Forests Defense Campaign. The contribution made by each of these people improved this document significantly. Any mistakes that remain are the responsibility of the author.

Publication of this document was made possible by the generous support of the Bullitt Foundation, The New Land Foundation, The Maki Foundation, The Lazar Foundation, and the members of the Xerces Society for Invertebrate Conservation.

Table of Contents

Section One: Research Summary

EXECUTIVE SUMMARY

Insects, including those that feed on and sometimes kill trees, are integral components of healthy forest ecosystems. They help decompose and recycle nutrients, build soils, maintain genetic diversity within tree species, generate snags and down logs that wildlife and fish rely on, and provide food for birds and small mammals. Although insects have been a part of the ecology of temperate forests for millennia, many in the timber industry see them only as agents of destruction. A century of fire suppression, clear-cut logging, road-building, grazing, urban encroachment, and the selective removal of large trees has upset the ecological balance in forests across North America, often making them more vulnerable to insect infestations. Some foresters believe the solution to the problem is increased logging. A review of over three hundred papers on the subject reveals that there is little or no evidence to support this assumption. There is an urgent need for federal and state agencies and land managers to reevaluate their current strategy for managing forest insects—which often relies on intensive logging—and to adopt a perspective that manages for forest ecosystem integrity.

*The mountain pine beetle (*Dendroctonus ponderosae*) has been an integral part of lodgepole pine ecosystems almost as long as the ecosystems have existed. Photograph by Dave Powell, USDA Forest Service (www.forestryimages.org).*

Key findings include:

- Native forest pests have been part of our forests for millennia and function as nutrient recyclers; agents of disturbance; members of food chains; and regulators of productivity, diversity, and density.
- Fire suppression and logging have led to simplified forests that may increase the risk of insect outbreaks.
- Forests with diverse tree species and age classes are less likely to develop large insect outbreaks.
- There is no evidence that logging can control bark beetles or forest defoliators once an outbreak has started.
- Although thinning has been touted as a long-term solution to controlling bark beetles, the evidence is mixed as to its effectiveness.

INSECTS AND ECOSYSTEM FUNCTION

When people think about bark beetles or forest defoliators such as the tussock moth—if they think of them at all—they likely picture insects that are destructive pests of trees. What most people do not realize is that the vast conifer forests of temperate North America evolved in concert with these organisms. In fact, these small insects could be termed keystone species, species that play such a vital role in an ecosystem that their removal would have a profound effect on the overall community.

Bark beetles belong to a subfamily of weevils called Scolytinae. They are small (1 mm to 9 mm) and usually cylindrical. The subfamily is very diverse, with the more than six thousand species known worldwide having a wide variety of life histories. Most species of bark beetles cause little or no economic damage, as they normally infest branches, stumps, and stems of standing dead or severely weakened trees, or downed woody material. A few species will attack and kill living, apparently healthy trees. For instance, members of the bark beetle genus *Dendroctonus* can cause severe outbreaks, resulting in high levels of tree mortality.

Other wood-boring beetles include ambrosia beetles (*Platypus* spp.), which feed on a kind of fungus known as ambrosia that they grow in their tunnels; and longhorn beetles (family Cerambycidae) and metallic wood-boring beetles (family Buprestidae), which do not cause tree mortality and infest only dead and already dying trees.

A small fraction of the moth species present in forests also can cause significant damage to forest trees through defoliation. Two important examples are the Douglas-fir tussock moth (*Orgyia pseudotsugata*) and spruce budworm (*Choristoneura* spp.). These moths can defoliate large areas and cause significant tree mortality.

Native forest pests have been part of our forests for millennia and have played an important role in the overall evolution of these ecosystems. As a case in point, one ancient stand of Douglas-fir (*Pseudotsuga menziesii*) over 700 years old revealed that budworms and overstory trees can coexist for centuries (Swetnam and Lynch 1993). Native insects, including those that attack and sometimes kill patches of trees, are integral components of healthy forest ecosystems. These native insects evolved with their host trees over thousands of years; they function as nutrient recyclers, agents of disturbance, members of food chains, and regulators of productivity, diversity, and density (Clancy 1993).

Even large outbreaks of insects and disease organisms that irregularly reach epidemic levels are known to have beneficial effects on the forest ecosystem (Alfaro et al. 1982). Epidemics of forest insects and pathogens have always occurred, and the selective killing of susceptible trees tends to increase overall stand fitness (Haack and Byler 1993). Spruce budworm, for example, may help maintain ecosystem health by selectively killing weaker, genetically inferior trees and thus increasing resistance to future outbreaks (Alfaro et al. 1982). Insects and other invertebrates contribute significantly to biomass decomposition, carbon cycling, nutrient cycling, and energy flow in forest ecosystems and are thus pivotal to maintaining soil fertility and long-term forest health (Haack and Byler 1993).

*In many forest ecosystems bark beetles and defoliators such as western spruce budworm (*Choristoneura occidentalis*), pictured here, reduce the density of trees, improving the overall condition of the forest. Photograph by Dave Powell, USDA Forest Service (www.forestryimages.org).*

Role of mountain pine beetle in lodgepole pine stands

Lodgepole pines (*Pinus contorta*) of the inland West can form large, even-aged stands across vast landscapes. These stands provide a prime habitat for beetles to develop large populations. The mountain pine beetle (*Dendroctonus ponderosae*), considered one of the main insect pests of western forests, can cause significant mortality to lodgepole and, to a lesser extent, ponderosa pines (*Pinus ponderosa*). The mountain pine beetle has been an integral part of lodgepole pine ecosystems almost as long as the ecosystems have existed, with beetle epidemics playing an integral role in the structure and dynamics of these communities (Fuchs 1999).

Mountain pine beetle epidemics are part of a natural boom-and-bust cycle (Amman 1977). Large populations of beetles selectively kill large numbers of the most susceptible trees. Killing these trees facilitates the development of a forest that is structurally, genetically, and compositionally more diverse and therefore less prone to beetle attack in the long run (Amman 1977). Even massive epidemics, in which hundreds or thousands of trees die, are a natural part of forest ecology. Such infestations, which may seem devastating from one person's point of view, play a critical role in the ecosystem (Berryman 1982).

The presence of large numbers of dead trees immediately following an outbreak may lead to fires, which in turn create favorable conditions for the lodgepole pines to regenerate. Beetles attack the stands when the trees are at an age at which the accumulation of seeds is optimal for regeneration of the new stand (Berryman 1982). These pine trees have serotinous cones, pinecones that require heat from a fire in order to open and release the seed. By indirectly increasing the likelihood of beneficial fires, the bark beetles interact with the lodgepole pines in such a way that optimizes the fitness of both species (Berryman 1982).

Maintaining diversity

In many forest types, bark beetles and defoliators reduce the density of trees and cull weak individuals, which relieves the stress on the survivors and improves the overall condition of the forest (Schowalter 1994). In many cases the prime beneficiaries are the non-eaten tree species (Schowalter and Withgott 2001). For instance, the Douglas-fir beetle (*Dendroctonus pseudotsugae*) may help maintain the ponderosa pine—the species that dominated many of these forest stands prior to the human-aided rise of fire-tolerant species—by thinning out individual Douglas-fir trees. At the community level, outbreaks of these insects can help keep a system healthy, and insect outbreaks can be corrective over the long term by increasing tree diversity (Schowalter 1994), which promotes the functional stability and recovery of the forest ecosystem. The turnover of plant parts through mortality and decomposition maintains the nutrient-cycling processes that are essential to soil fertility, thus reallocating resources (Schowalter 1994).

Many bark beetles make distinctive gallery patterns. Photograph © Edward Ross.

Food webs

Bark beetles are also important parts of many forest food webs. A salient feature of bark beetle communities is the staggering number of organisms associated with them (Dahlsten 1982). These insects are hosts for parasites and are prey for a variety of animals, including spiders, birds, and other beetles. Over seventy natural insect enemies and associates have been recorded for the Western pine beetle (*Dendroctonus brevicomis*) and over sixty species for the mountain pine beetle (Dahlsten 1982).

Bark beetle outbreaks can help create habitat and resources for a variety of species. By feeding upon dead or dying trees, bark beetles provide food to insect-gleaning species of birds such as woodpeckers (Koplin and Baldwin 1970) and create snags that may be utilized by birds such as woodpeckers, owls, hawks, wrens, and warblers, as well as many mammals, including bats, squirrels, American marten, Pacific fisher, and lynx. Standing dead and dying trees provide important habitat for approximately one-quarter of all wildlife species in British Columbia (Machmer and Steeger 1995). Epidemics of bark beetles increase the availability of plant material for foraging, browsing, and nesting for wildlife such as small mammals and birds (Stone and Wolfe 1996). In a study of ponderosa pine forests, herbaceous biomass was fifty to a hundred times as great in stands five years after an infestation of mountain pine beetles than in uninfested stands (Kovacic et al. 1985). Forest insects ultimately contribute to large-wood recruitment into riparian areas and stream systems, which is very important for building pools that provide habitat for salmon and trout. Compared to historic conditions, these large, deep pools are lacking in many streams today (Williams and Williams 2004).

FOREST SIMPLIFICATION AND INSECT OUTBREAKS

Contrary to popular belief, bark beetles do not threaten forest resources unless changes in forest conditions facilitate an increase in beetle populations. Although these insects have always been a part of forest ecosystems, forest management may have made bark beetles more prevalent. It is commonly accepted that fire suppression and logging have led to simplified forests that may be at an increased risk of insect outbreaks (Anderson et al. 1987, Ferrell 1996, Filip et al. 1996, Hessburg et al. 1994, Maloney and Rizzo 2002, McCullough et al. 1998, Mitchell 1990, Schowalter and Withgott 2001, Stephen et al. 1996, Swetnam and Lynch 1993).

The spread of native and exotic pests and pathogens in many forest systems can be linked to the simplification and fragmentation of the forest (Aber et al. 2000). The fact that managed landscapes tend to have less tree diversity and more homogeneity of forest structure makes outbreaks of many pathogens—including insects—more likely. Clear-cut logging produces large areas of even-aged stands that are more vulnerable to future outbreaks. Mortality tends to be greatest in overly dense stands, which are susceptible to insects, pathogens, fire, and drought (Ferrell 1996). High-grade logging increases the relative abundance of shade-tolerant trees, which are more vulnerable to insects (Langston 1995).

Contrary to numerous assertions, late successional and old-growth forests are highly productive and remarkably resistant to potential pests. Photograph of old-growth forest in Olympic National Park. © 1992 Gary Braasch.

Reduced frequency of fires has resulted in extensive, continuous areas of forests that are susceptible to western spruce budworm outbreaks (Anderson et al. 1987). Harvesting practices that removed the ponderosa pine and western larch aggravated the problem. Fire suppression, sometimes in combination with logging practices, has resulted in profound changes in the species composition and structure of forests. Associated with these changes is an increased vulnerability of forest stands to damage during insect outbreaks (McCullough et al. 1998).

Swetnam and Lynch (1993) looked at tree-ring chronologies from twenty-four mixed conifer stands to reconstruct the long-term history of western spruce budworm (*Choristoneura occidentalis*) in northern New Mexico. Their results showed that logging and fire suppression created a dense, continuous conifer forest with an elevated proportion of suitable budworm hosts.

Some foresters have put forward a view that old-growth reserves and roadless areas may harbor unwanted insects that can then invade managed stands, but there is no evidence to support such a view. Contrary to numerous assertions, old-growth forests are highly productive and remarkably resistant to potential pests (Showalter 1990). Martikainen et al. (1996) compared population levels of bark beetles between intensively managed forests in Finland and across the border in the less-intensively managed forests in Russia. They assert that foresters are often concerned that areas of natural forest may harbor large numbers of pests and act as dispersal centers to other areas. However, the available information does not support this hypothesis (Martikainen et al. 1996).

Indeed, there is evidence that natural systems may be more resistant than managed ones (Aber et al. 2000) because they have higher species diversity (both floral and faunal) and are therefore less likely to face widespread insect outbreaks. Pre-settlement outbreaks of the western spruce budworm were less severe because of the spatial and temporal heterogeneity of these forests (Swetnam and Lynch 1993). Bergeron et al. (1995) looked at mortality caused by a spruce budworm outbreak at 624 sites in northwest Quebec. They found that coniferous stands that were intermixed with deciduous stands appeared to be less vulnerable than large stands dominated by conifers. Similarly, Cappuccino et al. (1998) investigated the effect of forest diversity on the impact of the spruce budworm and found that mortality of balsam fir caused by budworm was greater in extensive conifer stands than in habitat islands of fir that were surrounded by deciduous forest.

Franklin et al. (1989) suggest that old-growth forests have a greater diversity of insect predators, which may in turn limit pest insect populations. Nowak and Berisford (2000) monitored the differences in growth and insect infestation levels related to management activities in loblolly pine and reported higher insect pests in plantation-style timber stands, particularly after intense management activities. They concluded that intensive management (regular thinning followed by herbicide treatments) may disrupt the balance between common insect pests, such as the tip moth, and their natural enemies.

Similarly, Schowalter (1995) compared arthropod community structure in replicate Douglas-fir and western hemlock canopies in western Oregon in intact old growth; partially harvested old-growth stands; natural mature stands; and regenerating plantations. Species diversity and abundance for several taxa, especially predators and detritivores, were significantly lower in plantations than in older forests (Schowalter 1995). He concludes that the recent conversion of large portions of old-growth and mature forests to young plantations (in Oregon's Willamette National Forest) likely has reduced regional populations of many predator and detritivore species.

There is no evidence that logging can control insects once an outbreak starts. Photograph of logging of mountain pine beetle infested trees by Dave Powell, USDA Forest Service (www.forestryimages.org).

Reduced predator diversity increases the likelihood of pest outbreaks. Forest stand structure, coupled with current forest management strategies, is the primary reason why natural enemies, especially parasitoids, are not effective in regulating southern pine beetle populations (Stephen et al. 1996).

Diverse forests with no fire suppression may have less incidence of insects and disease. Maloney and Rizzo (2002) surveyed a large area of unmanaged forest dominated by pines and white fir for cause of mortality in the Sierra San Pedro Mártir, Baja, Mexico. They concluded that the relative importance of fire and pest organisms appears different between this forest and similar mixed-conifer forests of the Sierra Nevada, California, USA. They found that insects and diseases, in association with periodic droughts, have largely replaced fire in the Sierra Nevada as the main agents of stand replacement. In the Sierra San Pedro Mártir, natural fire, insect, and disease outbreaks help maintain tree diversity. Shouse (2003) also presented evidence that a fire-adapted, natural matrix of this forest could resist drought and beetle threats without management.

It is commonly accepted that fire suppression and logging have led to simplified forests that may be at an increased risk of insect outbreaks. Photograph of clearcut in the Willamette National Forest, Oregon. © Steve Holmer.

From an ecological standpoint, the strategy with the greatest probability of long-term success in protecting forests against pests and pathogens is one that encourages the maintenance of a diverse set of controls, such as occurs in nature (Aber et al. 2000).

LOGGING TO CONTROL BARK BEETLES

There are very few peer-reviewed papers on the effect of logging on bark beetle populations and thus very little evidence that traditional silvicultural practices can solve pest problems. Cronin et al. (1999) cited the paucity of studies that have examined the consequences of human intervention on pest movement patterns, stating: "*We know of no studies that have experimentally evaluated the effects of management strategies on the dispersal of insect pests in forest systems.*"

A variety of silvicultural techniques have been suggested for managing forest-defoliating insects, but the theoretical foundations of many approaches have been built upon observation and correlation, rather than causative studies. Very little reliable empirical evidence exists to support silvicultural manipulations as a way to control insect pests (Muzika and Liebhold 2000). Despite nearly one hundred years of active forest management to control the mountain pine beetle, evidence for the efficacy of control is scant and contradictory (Wood et al. 1985). This publication, *Logging to Control Insects*, summarizes a review of over three hundred papers on bark beetles and other perceived forest pests and finds no evidence to support the claim that logging can control insects once an outbreak starts. Citing several sources, Hughes and Drever (2001) assert that the weight of opinion is that most control efforts to date have had little effect on the final size of outbreaks, although they may have slowed beetle progress in some cases and prolonged outbreaks in others. They also suggest that management interventions have never before controlled a large-scale outbreak. The control of outbreaks is theoretically possible, but would require treatment of almost all of the infected trees (Hughes and Drever 2001).

Bark beetles are always widespread and quite common. Even if we could control them in a stand of trees, this would likely have little impact on infestation at the landscape scale. In some situations, the removal of infested trees prior to the emergence of brood is recommended in an attempt to protect surrounding trees. However, the overall effectiveness of this strategy is unproven (Wilson and Celaya 1998). Further, in most forest situations, it is not feasible to locate and remove all trees prior to the emergence of the adult beetles (Wilson and Celaya 1998).

Amman and Logan (1998) point to failed attempts to use direct control measures, such as pesticides and logging, after an infestation starts. They suggest that by the early 1970s it had become apparent that controlling mountain pine beetle outbreaks by directly killing the beetles was not working.

Wickman (1990) detailed the effort to control the mountain pine beetle (*Dendroctonus ponderosae*) at Crater Lake National Park, Oregon, from 1925 to 1934. Over 48,000 trees were "treated" (cut down and then burned) in the last three years (1931 to 1934) alone. The main lesson learned was that once a mountain pine beetle population has erupted over a large area of susceptible forest type, and as long as environmental conditions remain favorable, there really is no way to stop the beetles until almost all the susceptible trees are either killed or removed by logging. Treating trees perhaps slows the progress of the outbreak, but the outcome is inevitable (Wickman 1990). The report goes on to state: *"The depletion of susceptible trees ended the outbreak, rather than the annual control efforts for ten years."*

The Crater Lake experience is not an isolated one, as control efforts have been standard practice across the West. Klein (1978) traced several mountain pine beetle epidemics from beginning to end and detailed the control efforts. More than 30,000 infested ponderosa pines and 20,000 infested lodgepole pines were treated in 1910 and 1911 on the Wallowa-Whitman National Forest in Oregon. The treatments included felling and peeling, felling and scoring the top, and felling and burning. Chemical methods were employed in the 1940s and 1950s. DDT and other toxic chemicals, such as lindane, were sprayed on thousands of acres in control attempts across the inter-mountain West. In Operation Pushover, more than 1,800 acres of lodgepole pine in the Wasatch National Forest in Utah were literally mowed down by heavy tractors linked together, and the surrounding stands were sprayed with chemicals. In spite of these myriad control attempts, mountain pine beetle outbreaks occurred with increasing frequency and even more damaging results (Klein 1978). Klein (1978) ultimately suggests that doing nothing and letting infestations run their course may be a viable option.

Pine beetle suppression projects often fail because the basic underlying cause for the population outbreak has not changed (DeMars and Roettgering 1982). Typically, if a habitat favorable to high populations of western pine beetle persists, suppression—by whatever means—will probably fail. In summary, once bark beetles reach epidemic levels and cause extensive tree mortality, treatments aimed at reducing densities of the beetles are futile (Wood et al. 1985).

Logging can also lead to heightened insect activity. Soil and roots can be compacted following logging, leading to greater water stress. Soil damage resulting from logging with heavy equipment can increase the susceptibility of future forests to insects and disease (Hagle and Schmitz 1993, Hughes and Drever 2001). Salvage logging after insect outbreaks also can make matters worse by removing snags, parasites, and predators from the forest system (Nebeker 1989). Outbreaks could then be prolonged because of a reduction in the effectiveness of natural enemies (Nebeker 1989). Standing dead trees are important for several birds that feed on mountain pine beetles; these birds are important regulators of endemic beetle populations that keep the risk of epidemics down (Steeger et al. 1998). Widespread removal of dead and dying trees eliminates the habitat required by bird species that feed on those insects attacking living trees, with the result that outbreaks of pests may increase in size or frequency (Torgerson et al. 1990).

Logged stands have less diverse architecture and overall lower seed production than untouched stands. Consequently, logged stands have lower arthropod and small mammal diversity than undisturbed stands (Simard and Fryxell 2003). Mass annihilation of wood-decaying macrofungi and insect microhabitats from logging has an extremely detrimental effect on arthropod diversity (Komonen 2003), including on the natural enemies of pest insects. Sanitation and salvage logging differ from natural disturbance in their effects and tend to decrease habitat complexity and diversity, which can lead to an increase in insect activity (Hughes and Drever 2001).

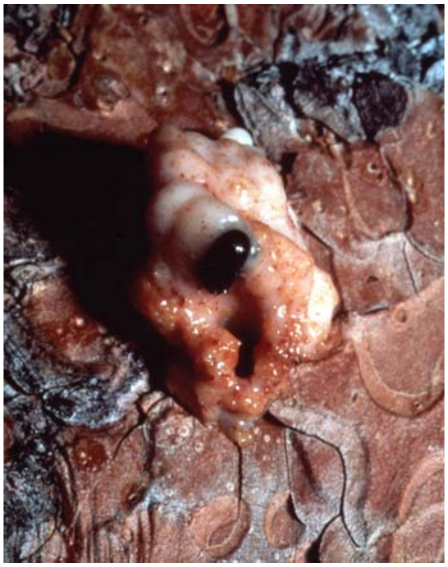
Large-scale efforts for beetle control are economically and ecologically expensive, and the uncertain benefits of control efforts should be weighed carefully against their costs (Hughes and Drever 2001). Former U.S. Forest Service Chief Jack Ward Thomas, in testimony before the U.S. Senate Subcommittee on Agricultural Research, Conservation, Forestry, and General Legislation on August 29, 1994, acknowledged that "the Forest Service logs in insect-infested stands not to protect the ecology of the area, but to remove trees before their timber commodity value is reduced by the insects."

Salvage logging after insect outbreaks can make matters worse by removing snags, parasites, and predators from the forest system. Photograph of salvage-logged area in the Siskiyou National Forest in Oregon. Photo courtesy of the Siskiyou Project.

EFFECTIVENESS OF THINNING

Thinning is often recommended to control outbreaks of bark beetles, but the evidence is mixed as to its effectiveness. Most evidence is based on tree vigor, not on directly measured insect activity in the stand. Thinning may increase tree vigor, which in turn may make the trees less susceptible to insect infestation. The premise is that if the trees are healthy and have high vigor, they may be able to "pitch out" the attacking beetles, flooding the entrance site with resin that can push out or drown the beetle. Indeed, resin flow has been found to be greater in thinned stands. Raffa and Berryman (1986) developed a computer model based on laboratory and field studies of mountain pine beetle interactions with lodgepole pine. The model, which used tree vigor as a variable, showed that stand thinning seems to provide the most effective long-term protection from beetle outbreaks. They point out that the confidence in the model would be improved if data were available to test the predictions and that unfortunately there have been few long-term studies on the dynamics of mountain pine beetle populations (Raffa and Berryman 1986).

Some direct studies of the impact of thinning on these insects have been undertaken. Mitchell et al. (1983) suggested that thinning improved the vigor of stands and reduced attacks by beetles. However, there was significant variation in the percentage of trees attacked on plots with similar vigor. The vigor of one plot failed to respond to heavy thinning and suffered the same mortality experienced in the adjacent, unthinned plot. Also, one unthinned plot had very low mortality (Mitchell et al. 1983). Larsson et al. (1983) examined the relationship between tree vigor and susceptibility to mountain pine beetle in ponderosa pine in central Oregon. Overall, low-vigor trees were more often attacked by beetles than high-vigor trees. However, variation in the



*A healthy tree may be able to "pitch out" attacking beetles by flooding the entrance site with resin, as shown here by this successful ejection of a mountain pine beetle (*Dendroctonus ponderosae*). Photograph © Dave Leatherman.*

percentage of trees attacked was considerable on plots with trees with similar vigors, especially at low and intermediate values (Larsson et al. 1983). Some thinning studies show some level of success in ameliorating mountain pine beetle infestations in lodgepole and ponderosa pine (Amman and Logan 1998).

Perhaps the work that most conclusively shows the positive impact of thinning is by Negrón (Negrón 1997, Negrón 1998, Negrón et al. 2000, Negrón et al. 2001). These studies show a positive correlation between attacked trees and poor growth. Roundheaded pine beetles (*D. adjunctus*) prefer stands and trees exhibiting poor growth, and growth rates were positively correlated to high stocking densities (i.e., dense stands) (Negrón 1997, Negrón et al. 2000). Similarly, Douglas-fir beetles attacked stands containing a high percentage of basal area represented by Douglas-fir, high tree densities, and poor growth during the five years prior to attack (Negrón 1998, Negrón et al. 2001).

Other research found no evidence that bark beetles preferentially infest trees with declining growth (Santoro et al. 2001). Sánchez-Martínez and Wagner (2002) studied the bark beetle guild in ponderosa pine forests of northern Arizona to explore if species assemblages and relative abundance differ between managed and unmanaged stands. They found no evidence to support the hypothesis that trees growing in dense stands are more colonized by bark beetles.

Some scientists have suggested caution in using thinning to control bark beetles, because geographic and climactic variables may alter the effect (Hindmarch and Reid 2001). Hindmarch and Reid (2001) found that pine engravers had longer egg galleries, more eggs per gallery, and higher egg densities in thinned stands. Warmer temperatures in thinned stands also contributed to a higher reproduction rate (Hindmarch and Reid 2001). However, pine engravers in Arizona had the opposite reaction to a similar thinning experiment (Villa-Castillo and Wagner 1996). For thinning to be effective, it must significantly reduce water stress within a stand, which is unlikely during the severe droughts when many of these outbreaks occur.

Thinning is a common recommendation for relieving stresses due to competition for limited resources (Paine and Baker 1993), but there is also evidence to suggest that thinning can exacerbate pest problems. Outbreaks of pine engravers have been shown to be initiated by stand management activities such as thinning (Goyer et al. 1998). Thinning can increase the availability and susceptibility of decaying stem and root material for some bark beetles and pathogens. In addition, the process of thinning can wound remaining trees and injure roots, providing entry points for pathogens and ultimately reducing the tree's resistance to other organisms (Paine and Baker 1993). Hagle and Schmitz (1993) suggest that thinning can be effective in maintaining adequate growing space and resources to disrupt the spread of bark beetles; but note that there is accumulating evidence to suggest that physical injury, soil compaction, and temporary stress due to changed environmental conditions caused by thinning may increase susceptibility of trees to bark beetles and pathogens.

Thinning projects are often redundant or irrelevant because forest insects—including bark beetles and defoliators—are natural thinning agents. Die-offs resulting from insect attacks may actually help restore a more natural tree species composition that had been altered by fire suppression and other human activity (Langston 1995). For instance, the mountain pine beetle is a natural thinning agent of lodgepole pine, and, in some situations, it may be advantageous to permit mountain pine beetle outbreaks to continue unhindered (Peterman 1978). Where canopy density was reduced either by thinning *or bark beetles*, surviving trees significantly increased their resistance to attack over a three-year period (Waring and Pitman 1985). Budworm-induced mortality can cause natural thinning (Hadley and Veblen 1993), and pruning and thinning by forest insects reduces competition, enhances productivity of surviving trees, and promotes non-host species (Schowalter 1994). Defoliation can lead to increased tree growth, possibly due to changes in nutrient levels in the soil or to a thinning effect (Alfaro and MacDonald 1988). Although beetles affect the standing tree biomass at a site, the losses of trees may be balanced by increased forage for a variety of animals and by natural thinning effects, which may improve not only forage quality but also timber and site quality in future years (Kovacic et al. 1985).

Reduced fire frequency has allowed large areas of forests to develop that are susceptible to forest insects. Photograph of a wildfire in Oregon by Dave Powell, USDA Forest Service (www.forestryimages.org).

FOREST INSECTS AND FIRE

Fire interacts with bark beetles in many ways. As stated earlier in this paper, reduced fire frequency has allowed large continuous areas of forests to develop that are susceptible to western spruce budworm (Anderson et al. 1987), other defoliators, and bark beetles (Ferrell 1996, Filip et al. 1996, Hessburg et al. 1994, Maloney and Rizzo 2002, McCullough et al. 1998, Mitchell 1990, Schowalter and Withgott 2001, Stephen et al. 1996, Swetnam and Lynch 1993).

There is a general impression that bark beetle epidemics increase fire severity and occurrence. This may be true in some instances, but some studies do not support this premise (Bebi et al. 2003, Pollet and Omi 2002). In Yellowstone National Park, stands that experienced high mortality from beetles (more than 50 percent of susceptible trees) in the five to seventeen years preceding the 1998 fires typically burned more intensely than uninfested stands. However, the incidence of high-intensity crown fire in stands with low to moderate beetle mortality was lower than in uninfested stands (Turner et al. 1999). This suggests that, in some stands, beetle kill may actually decrease the hazard of high-crown fire by decreasing the continuity of woody fuels in the canopy.

There is little doubt that beetle outbreaks that cause significant mortality at the stand scale increase the risk of crown fire immediately after tree mortality. However, this is often restricted to the two or three years after the foliage has died and dried but before it falls to the floor. Once the trees have defoliated, the risk of crown fire may be lower than before the outbreak. Bebi et al. (2003) quantified spatial associations of fire and spruce beetle (*Dendroctonus rufipennis*) outbreaks over more than a century and developed a multivariate logistic model. Forests that had burned in 1879 were less affected by an outbreak in the 1940s than were older stands. On the other hand, areas affected by the 1940s outbreak showed no higher susceptibility to subsequent fires (Bebi et al. 2003). Beetle-killed lodgepole pine (self-thinned to lower density) experienced significantly lower fire severity compared to adjacent burned areas in the 3,400-

hectare Robinson Fire that burned in Yellowstone National Park in 1994 (Pollet and Omi 2002).

Evidence is emerging that there may be conservation and economic benefits to using fire to control forest pests (Pollet and Omi 2002). Feeney et al. (1998) found that a thinned-and-burned treatment increased tree vigor more than in either the thinned or the control treatments and that the resulting increased resin flow may improve trees' resistance to insects in thinned-and-burned stands.

Prescribed fire has been used to try to control bark beetles, but it has not been universally successful. These fires sometimes become too hot and unintentionally scorch trees, which can invite attack by bark beetles. McHugh et al. (2003) examined the interaction between fire in ponderosa pine stands and bark beetle ecology. Mountain pine beetle showed no preference for fire-damaged trees, but trees with the most crown damage were attacked by *Ips* and other *Dendroctonus* species. Following a prescribed burn, the local abundance of *Ips pini* increased twofold, then decreased for six weeks, and finally returned to previous levels (Santoro et al. 2001). An investigation into the effects of low-intensity, late-season prescription fire on Jeffrey pine showed a highly significant correlation between burning and bark beetle presence (Bradley and Tueller 2001).

*Predators such as this red-bellied clerid beetle (*Enoclerus sphegeus*) can help control bark beetles. Photograph © Edward Ross.*

Even with these potential problems, the general conclusion is that pest problems generated by prescribed burning are mostly trivial and ephemeral and usually can be avoided by careful planning (Mitchell 1990).

THE IMPORTANCE OF NATURAL ENEMIES

There are a large number of organisms that help control populations of bark beetles and other forest pests. Over seventy natural insect enemies and associates have been recorded for the western pine beetle, and sixty for the mountain pine beetle (Dahlsten 1982). Recent evidence suggests that predators and parasites strongly influence the population dynamics of bark beetles (Cronin et al. 2000, Erbilgin 2002, Marsden et al. 1981, Raffa and Dahlsten 1995, Reeve et al. 1995, Schroeder 1996, Turchin et al. 1999). The evidence includes density-dependent mortality attributable to natural enemies in field life tables (Dahlsten and Whitmore 1989); increased brood production in predator exclusion experiments (Linit and Stephen 1983); and long-term analysis of tree mortality trends (Turchin et al. 1991). In short, forest operations that favor natural enemies in the landscape might be economically favorable compared to traditional stand management (Weslien and Schroeder 1999).

Weslien (1992) estimated that natural enemies can reduce *Ips typographus* reproduction by 83 percent. Dahlsten (1982) cited studies showing parasitism rates for southern pine beetle from as low as 4 percent to as high as 98 percent. Predation rates primarily by clerid beetles can also be high (Dahlsten 1982). Woodpeckers accounted for 28 percent of mortality of low bark beetle populations, 84 percent during outbreaks and 53 percent at epidemic densities. Broods were reduced by 98 percent by woodpeckers on heavily worked trees (Massey and Wygant 1973). Woodpeckers also cause additional mortality by removing bark, thereby drying out the bark beetles and allowing parasitoids and predators greater access. Spiders, mites, and disease also may play a role in controlling bark beetles (Dahlsten 1982).

Predation by adult beetles could be an important source of mortality in many systems but might be overlooked because of their cryptic behavior (Reeve 1997). *Thanasimus dubius* and *Platysoma cylindrica*—two of the major predators of pine engravers (*Ips pini*)—decreased the pine engraver net replacement rate by 70 percent (Aukema and Raffa 2004).

Disease and insect problems may be worse in managed stands than in natural stands. Old-growth forests have a greater diversity of insect predators, which may in turn limit pest insect populations (Franklin et al. 1989). Research has shown that tree-species complexity creates critical habitat for predators and mediates intraguild predation, thereby enhancing the effects of predators on their main prey (Finke and Denno 2002).

Populations of insects and pathogens in most forest ecosystems are kept in check by their natural predators and by other environmental factors. Removal of downed wood and snags eliminates the microhabitats needed to maintain populations of generalist insects and predators that control pest outbreaks (Filip et al. 1996).

*By feeding upon dead or dying trees, forest insects provide food to insect-gleaning species of birds such as this red-bellied woodpecker (*Melanerpes carolinus*). Photograph by James Solomon, USDA Forest Service (www.forestryimages.org).*

Species diversity and abundance for several taxa, especially predators and detritivores, were significantly lower in plantations than in older forests (Schowalter 1995). Schowalter (1995) concluded that the recent conversion of large portions of old-growth and mature forests to young plantations in the Willamette National Forest in Oregon likely has reduced regional populations of many predator and detritivore species. Reduced predator diversity increases the probability that herbivores will escape regulation by predators, which could lead to a greater likelihood of pest outbreaks (Schowalter 1995). Old-growth and roadless areas with greater diversity of composition, structure, and predators are predicted to be less vulnerable to pest outbreaks than forests simplified through management (Schowalter and Means 1989). Studies in Europe also provide evidence of the connections between stand management, overall biodiversity, and beetle control. In Sweden, species known to be common bark beetle predators were caught in significantly higher numbers in the unmanaged stands than in managed stands (Weslien and Schroeder 1999).

PHEROMONES FOR INSECT CONTROL

Mass trapping using pheromones and anti-aggregation pheromone lures are potentially useful control measures against bark beetle pests (Goyer et al. 1998).

A serious problem, however, is the inadvertent removal of predators that respond to these baits (Aukema et al. 2000). Predator populations can be significantly impacted when individuals are killed along with bark beetles in traps and logs baited with insecticide (Zhou et al. 2001). Capturing predators could negate the benefits of removing bark beetles from the environment (Ross and Daterman 1997, Zhou et al. 2001). New studies are addressing this problem (Aukema et al. 2000).

Anti-aggregation pheromones show some success at preventing infestation (Ross et al. 1996). The Douglas-fir beetle anti-aggregation pheromone MCH (3-methylcyclohex-2-en-1-one) may be effective in preventing the infestation of windthrown trees, and differences in the response of the bark beetles and predators suggest that beetles attacking trees within the MCH-treated area may be subject to higher levels of predation than would occur in the absence of MCH (Ross et al. 1996). This anti-aggregation pheromone has now been registered by the EPA (Ross et al. 2001).

GLOBAL WARMING

Global warming may have an impact on forest pests and forest pest outbreaks. Logan and Powell (2001) predict that the mountain pine beetle may expand its range to both higher elevations and higher latitudes as the climate warms. This expansion has potentially serious implications for high-elevation pines, such as whitebark pine and bristlecone pine, that did not evolve with mountain pine beetle. Models developed by Logan and Bentz (1999) predict that an increase in temperature of 2.5 degrees Celsius would be sufficient to convert an unsuitable habitat into a suitable one.

Warmer temperatures also are expected to affect forest insects directly. In particular, survival of the mountain pine beetle, the lodgepole needleminer (*Coleotechnites milleri*), and the Douglas-fir tussock moth is expected to increase, while survival of the western spruce budworm is expected to decrease (Safranyik 1990).

The extent and impact of pest expansion is hard to quantify. The effects of both human land use and changes in climatic variables other than temperature will complicate forest range shifts, and hence will complicate bark beetle range shifts (Williams and Liebhold 2002). For example, changing precipitation patterns will alter the frequency and geographical extent of fire and drought disturbances, complicating the ability to predict future forest disturbances (Williams and Liebhold 2002). In some cases, increased temperatures may shorten the lifecycles of some species of insects. On the other hand, increased temperatures may increase insect mortality because of the loss of snow cover as insulation (Ayres and Lombardero 2000).

The effects of climate change are not limited to the insect pests themselves; there may also be changes in host tree defenses and in the abundance of natural enemies, mutualists, and competitors (Ayres and Lombardero 2000). Unlike the situation with exotic species, it seems reasonable to expect that, as conditions become favorable for mountain pine beetle, conditions will simultaneously become more favorable for the beetles' biotic associates, such as predators and parasites (Logan and Powell 2001).

CONCLUSION

Over the last one hundred years, logging on public lands has been promoted for "insect control." More recently, the Healthy Forests Restoration Act of 2003 (Public Law 108-148) used forest insect outbreaks as a justification for increasing logging and limiting environmental protections.

Insects, including those that attack and sometimes kill patches of trees, are integral components of healthy forest ecosystems. Insects help decompose and recycle nutrients; build soils; maintain genetic diversity within tree species; generate snags and down logs required by wildlife and fish; and provide food to birds and small mammals. These insect species have been associated with North American coniferous forests for many thousands of years. Over this vast expanse of time, many tree species have adapted to and perhaps even depend on these insects.

There is no evidence that once an infestation has started we can log our way out of it. Even thinning, which is widely promoted as a solution, has mixed results. Caution should be used when thinning for long-term pest suppression because of the potential for increasing the simplicity of a forest and thus its susceptibility to future infestation. Logging and thinning may also create conditions that are more favorable for outbreaks of the very insects that managers are trying to control. The fact that managed landscapes tend to be less diverse with large, contiguous blocks of one or a few susceptible species and age classes makes catastrophic outbreaks of many pathogens and insects more likely. In contrast, old-growth and more mature forests have higher species diversity of both trees and animal species and are less likely to have stand-destroying insect outbreaks.

There is an urgent need for federal and state agencies and for land managers to reevaluate their current strategy for managing forest insects and to adopt a perspective that manages for forest ecosystem integrity. Although each forest will have site-specific issues, here are some general guidelines to follow when considering pest insects and forest management.

- Maintain and restore high-quality late-successional and old-growth forest conditions. Diverse, old forests contain an array of natural predators and pathogens, and are more resilient to forest insect pests.
- Ensure structural and species diversity when logging, including the retention of large trees and snags, downed wood, and canopy closure. These practices can help minimize large outbreaks of insect pests.
- Minimize soil compaction and harm to trees and tree roots when doing any thinning or logging. Soil compaction and tree damage can increase the susceptibility of forest stands to insect attack.
- Utilize prescribed fire to promote more natural forest conditions. Insect pests are less of a problem under diverse natural conditions. [Note: Fire should be used carefully, as there is some evidence that fires that damage tree cambium can potentially exacerbate insect problems.]
- Reduce current road densities, particularly in ecologically significant areas. Roads can serve as corridors for dispersal for non-native invasive insect species.

Logging is not the solution to forest insect outbreaks and in the long run could increase the likelihood of epidemics. Some amount of insect activity is inevitable, but many insects and pathogens can seriously injure only those trees and forests that are already under some form of environmental stress, and epidemics of these agents are increasingly recognized as symptoms of, not the reasons for, poor forest health (Wickman 1992). Rather than combat insects as pests, we should view their population swings as indicators of changing conditions in these forests and seek to address the underlying causes (Schowalter and Withgott 2001).

LITERATURE CITED

Aber, J., N. Christensen, I. Fernandez, J. Franklin, L. Hidinger, M. Hunter, J. MacMahon, D. Mladenoff, J. Pastor, D. Perry, R. Slangen, and H. van Miegroet. 2000. Applying ecological principles to management of the U.S. national forests. *Issues in Ecology Number 6.* Ecological Society of America, Washington, D.C.

Alfaro, R.I., and R.N. MacDonald. 1988. Effects of defoliation by western false hemlock looper on Douglas-fir tree ring chronology. *Tree-Ring Bulletin* 48: 3–11. Cited in Alfaro, R.I. and R.F. Shepherd. 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir tussock moth. *Forest Science* 37: 959–64.

Alfaro, R.I., G.A. Van Sickle, A.J. Thompson, and E. Wegurtzi. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. *Canadian Journal of Forest Resources* 12: 780–87.

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact of succession. In *The Role of Arthropods in Forest Ecosystems: Proceedings in the Life Sciences*, ed. by W.J. Mattson, pp. 3–18. Springer–Verlag, New York, NY.

Amman, G.D., and J.A. Logan. 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. *American Entomologist* 44(3): 166–77.

Anderson, L., C.E. Carlson, and R.H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management* 22: 251–60.

Aukema, B.H., D.L. Dahlsten, and K.F. Raffa. 2000. Exploiting behavioral disparities among predators and prey to selectively remove pests: Maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology* 28(3): 651–60.

Aukema, B.H., and K.F. Raffa. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonization strategy and the absence of emergent multiple predator effects. *Ecological Entomology* 29: 129–38.

Ayres, M.P., and M.J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment* 262: 263–86.

Bebi, P., D. Kulakowski, and T.T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84(2): 362–71.

Bergeron, Y., A. Leduc, H. Morin, and C. Joyal. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research* 25: 1375–84.

Berryman, A.A. 1982. Population dynamics of bark beetles. In *Bark Beetles in North American Conifers,* ed. by J.B. Mitton and K.B. Sturdgeon, pp. 264–314. University of Texas Press, Austin, TX.

Bradley, T., and P. Tueller. 2001. Effects of fire on bark beetle presence on Jeffrey pine in Lake Tahoe Basin. *Forest Ecology and Management* 142: 205–14.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114: 236–42.

Clancy, K.M. 1993. Research approaches to understanding the roles of insect defoliators in forest ecosystems. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, pp. 211–17. USDA General Technical Report RM-247.

Cronin, J.T., J.D. Reeve, R. Wilkens, and P. Turchin. 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90: 127–38.

Dahlsten, D.L. 1982. Relationships between bark beetles and their natural enemies. In *Bark Beetles in North American Conifers*, ed. by J.B. Mitton and K.B. Sturgeon, pp. 140–82. University of Texas Press, Austin, TX.

Dahlsten, D.L., and M.C. Whitmore. 1989. Potential for biological control of *Dendroctonus* and *Ips* bark beetles: The case for and against biological control of bark beetles. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 3–20.

Center for Applied Studies, School of Forestry, Stephen F. Austin State University, Nacogdoches, TX. Cited in Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

DeMars, C.J. Jr. and B.H. Roettgering. 1982. *Forest Insect and Disease Leaflet 1: Western Pine Beetle*. U.S. Forest Service Pacific Southwest Region.

Erbilgin, N., E.V. Nordheim, B.H. Aukema, and K.F. Raffa. 2002. Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: Within- and between-year associations with predators, competitors and habitat quality. *Environmental Entomology* 31(6): 1043–51.

Feeney, S.R., T.E. Kolb, W.W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson natural area. *Canadian Journal of Forest Resources* 28: 1295–1306.

Ferrel, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In *Sierra Nevada Ecosystem Project: Final Report to Congress, Vol. II.* Davis, CA. pp.1177–92.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Finke, D.L., and R.F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. *Ecology* 83(3): 643–52.

Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKee, and T.A. Spies. 1989. Importance of ecological diversity in maintaining long term site productivity. In *Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems*, ed. by D.A. Perry, pp. 82–97. Timber Press, Portland, OR.

Fuchs, M. 1999. *The Ecological Role of the Mountain Pine Beetle* (Dendroctonus ponderosae): *A Description of Research From the Literature*. Prepared by Foxtree Ecological Consulting for British Columbia Parks Service, Victoria, BC.

Goyer, R.A., M.R. Wagner, and T.D. Schowalter. 1998. Current and proposed technologies for bark beetle management. *Journal of Forestry* 96(12): 29–33.

Haack, R.A., and J.W. Byler. 1993. Insects and pathogens, regulators of forest ecosystems. *Journal of Forestry* 91(9): 32–7.

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Hagle, S., and R. Schmitz. 1993. Managing root disease and bark beetles. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 209–28. Academic Press, New York, NY.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Hindmarch, T.D., and M.L. Reid. 2001. Forest thinning affects reproduction in pine engravers (Coleoptera: Scolytidae) breeding in felled lodgepole pine trees. *Environmental Entomology* 30(5): 919–24.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Klein, W.H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 148–58. University of Idaho, Pullman, WA.

Komonen, A. 2003. Hotspots of insect diversity in boreal forests. *Conservation Biology* 17(4): 976–81.

Koplin, J.R., and P.H. Baldwin. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. *The American Midland Naturalist* 83: 510–15.

Kovacic, D.A., M.I. Dyer, and A.T. Cringan. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. *Forest Ecology and Management* 13: 53–67.

Langston, N. 1995. *Forest Dreams, Forest Nightmares: The Paradox of Old Growth in the Inland West*. University of Washington Press, Seattle, WA.

Larsson, S., R. Oren, R.H. Waring, and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science* 29: 395–402.

Linit, M.J., and F.M. Stephen. 1983. Parasite and predator components of within-tree southern pine beetle mortality. *Canadian Entomologist* 115: 679–88. Cited in Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

Logan, J.A., and B.J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28(6): 924–34.

Logan, J.A., and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47(3): 160–72.

Machmer, M.M., and C. Steeger. 1995. *The Ecological Roles of Wildlife Tree Users in Forest Ecosystems*, p. 54. Land Management Handbook 35, British Columbia Ministry of Forests, Victoria, BC. Cited in Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Maloney, P.E., and D.M. Rizzo. 2002. Pathogens and insects in a pristine forest ecosystem: The Sierra San Pedro Mártir, Baja, Mexico. *Canadian Journal of Forest Research* 32: 448–57.

Marsden, M.A., M.M. Furniss, and L.N. Kline. 1981. *Modeling Seasonal Abundance: Douglas-Fir Beetle in Relation to Entomophagous Insects and Location in Trees*. USDA Forest Service General Technical Report INT-111. Intermountain Forest and Range Experiment Station, Ogden, UT.

Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120: 257–64.

Massey, C.L., and N.D. Wygant. 1973. Woodpeckers: Most important predators of spruce beetle. *Colorado Field Ornithologist* 16: 4–8. Cited in Fuchs, M. 1999. *The Ecological Role of the Mountain Pine Beetle* (Dendroctonus ponderosae*): A Description of Research from the Literature*. Prepared by Foxtree Ecological Consulting for British Columbia Parks Service, Victoria, BC.

McCullough, D.G., R.A. Werner, and D. Neumann. 1998. Fire and insects in northern boreal forest ecosystems of North America. *Annual Review of Entomology* 43: 107–27.

McHugh, C.W., T.E. Kolb, and J.L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32(3): 510–22.

Mitchell, R.G. 1990. Effects of prescribed fire on insect pests. In *Natural and Prescribed Fire in Pacific Northwest Forests*, ed. by J.D. Walstad, S.R. Radosevich, and D.V. Sandberg, pp. 111–16. Oregon State University Press, Corvallis, OR.

Mitchell, R.G., R.H. Waring, and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* 29(1): 204–11.

Muzikai, R.M., and A.M. Liebhold. 2000. A critique of silvicultural approaches to managing defoliating insects in North America. *Agricultural and Forest Entomology* 2: 97–105.

Nebeker, T.E. 1989. Bark beetles, natural enemies, management selection interactions. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 71–80. Stephen F. Austin State University, Nacogdoches, TX.

Negrón, J.F. 1997. Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico. *Canadian Journal of Forest Research* 27: 1936–45.

Negrón, J.F. 1998. Probability of infestation and extent of mortality associated with Douglas-fir beetle in Colorado Front Range. *Forest Ecology and Management* 107: 71–85.

Negrón, J.F., J.A. Anhold, and A.S. Munson. 2001. Within-stand spatial distribution of tree mortality caused by the Douglas-fir beetle (Coleoptera: Scolytidae). *Environmental Entomology* 30(2): 215–24.

Negrón, J.F., J.L. Wilson, and J.A. Anhold. 2000. Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. *Environmental Entomology* 29(1): 20–7.

Nowak, J.T., and C.W. Berisford. 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. *Journal of Economic Entomology* 93(2): 336–41.

Paine, T.D., and F.A. Baker. 1993. Abiotic and biotic predisposition. In *Beetle Pathogen Interactions in Conifer Forests*, ed. by T.D. Scholwalter and G.M. Filip, pp. 61–73. Academic Press, Inc., San Diego, CA.

Peterman, R.M. 1978. The ecological role of mountain pine beetle in lodgepole pine forests. In *Theory and Practice of Mountain Pine Beetle Management I: Lodgepole Pine Forests. Symposium Co-Sponsored by National Science Foundation … et al., held at Washington State University, Pullman, Washington, April 25–27, 1978*, pp. 16–26. U.S. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID.

Pollet, J., and P.N. Omi. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11: 1–10.

Raffa, K.F., and A.A. Berryman. 1986. A mechanistic computer model of mountain pine beetle populations interacting with lodgepole pine stands and its implications for forest managers. *Forest Science* 32(3): 789–805.

Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

Reeve, J.D. 1997. Predation and bark beetle dynamics. *Oecologia* 112: 48–54.

Reeve, J.D., M.P. Ayres, and P.L. Lorio. 1995. Host suitability, predation and bark beetle dynamics. In *Population Dynamics: New Approaches and Synthesis*, ed. by N. Cappuccino and P.W. Price, pp. 339–57. Academic Press, Inc., San Diego, CA.

Ross, D.W., and G.E. Daterman. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. *Forest Science* 43(1): 65–70.

Ross, D.W., K.E. Gibson, and G.E. Daterman. 2001. *Using MCH to Protect Trees and Stands from Douglas-fir Beetle Infestation*. USDA Forest Service, Forest Health Technology Enterprise Team, FHTET-2001-09.

Ross, D.W., K.E. Gibson, R.W. Thier, and A.S. Munson. 1996. Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 89(5): 1204–7.

Safranyik, L. 1990.Temperature and insect interactions in western North America. In *Are Forests the Answer? Proceedings of the 1990 Society of American Foresters National Convention*. Washington, D.C. Cited in Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Sánchez-Martínez, G., and M.R. Wagner. 2002. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *Forest Ecology and Management* 170: 145–60.

Santoro, A.E., M.J. Lombardero, M.P. Ayres, and J.J. Ruel. 2001. Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management* 144: 245–54.

Schowalter, T.D. 1990. Consequences of Insects. In *Symposium Proceedings: Forests – Wild and Managed—Differences and Consequences. January 19–20, 1990*, pp. 91–106. University of British Columbia, Vancouver, BC.

Schowalter, T.D. 1994. An ecosystem-centered view of insect and disease effects on forest health. In *Sustainable Ecological Systems: Implementing and Ecological Approach to Land Management*, ed. by W.W. Covington and L.F. DeBano, pp. 189–195. USDA Forest Service General Technical Report RM-247.

Schowalter, T.D. 1995. Canopy arthropod community response to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78: 115–25.

Schowalter, T.D., and J.E. Means. 1989. Pests' link to site productivity in the landscape. In *Symposium Proceedings: Maintaining Long-Term Productivity in Pacific Northwest Forests. Corvallis, OR*, ed. by D.A. Perry, pp. 248–50. Timber Press, Portland, OR.

Schowalter, T.D., and J. Withgott. 2001. Rethinking Insects. What would an ecosystem approach look like? *Conservation Biology In Practice* 2(4): 10–16.

Schroeder, L.M. 1996. Interactions between predators *Thanasimus formicarius* (Coleoptera: Cleridae) and *Rhizophagus depressus* (Coleoptera: Rhizophaidae) and the bark beetle *Tomicus piniperda* (Coleoptera: Scolytidae). *Entomophaga* 41(1): 63–75.

Shouse, B. 2003. Old-growth forest spared for now. *Science* 299: 802.

Simard, J.R., and J.M. Fryxell. 2003. Effects of selective logging on terrestrial small mammals and arthropods. *Canadian Journal of Zoology* 81: 1318–26.

Steeger, C., M.M. Machmer, and B. Gowans. 1998. *Impact of Insectivorous Birds on Bark Beetles: A Literature Review*. Pandion Ecological Research, Ymir, BC. Cited in Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Stephen, F.M., M.P. Lih, and L.E. Browne. 1996. Biological control of southern pine beetle through enhanced nutrition of its adult parasitoids. In *Proceedings: North American Forest Insect Work Conference*, ed. by R.F. Billings and T.E. Nebeker, pp. 34–5. Texas Forest Service Publ. 160.

Stone, W.E., and M.L. Wolfe. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* 122: 1–12.

Swetnam, T.W., and A.M. Lynch. 1993. Multi-century regional scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63: 399–424.

Torgerson, T.R., R.R. Manson, and R.W. Campbell. 1990. Predation by birds and ants on two forest pests in the Pacific Northwest. *Studies in Avian Biology* 13: 14–19.

Turchin, P., P. Lorio, A.D. Taylor, and R.F. Billings. 1991. Why do populations of southern pine beetles (Coleoptera: Scolytidae) fluctuate? *Environmental Entomology* 20: 401–9. Cited in Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

Turchin, P., A.D. Taylor, and J.D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: An experimental test. *Science* 285: 1068–71.

Turner, M.G., W.H. Romme, and R.H. Gardener. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9(1): 59–77.

Villa-Castillo, J., and M.R. Wagner. 1996. Effects of overstory density on *Ips pini* performance in ponderosa pine slash. *Journal of Economic Entomology* 89: 1537–45. Cited in Hindmarch, T.D., and M.L. Reid. 2001. Forest thinning affects reproduction in pine engravers (Coleoptera: Scolytidae) breeding in felled lodgepole pine trees. *Environmental Entomology* 30(5): 919–24.

Waring, R.H., and G.B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66(3): 889–97.

Weslien, J. 1992. The arthropod complex associated with *Ips typographus*: Species composition, phenology, and impact on bark beetle productivity. *Entomologica Fennica* 3: 205–13. Cited in Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

Wickman, B.E. 1990. *The Battle Against Bark Beetles in Crater Lake National Park: 1925–34. United States Department of Agriculture*. U.S. Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-259. Portland, OR.

Wickman, B.E. 1992. *Forest Health in the Blue Mountains: The Influence of Insects and Diseases*. U.S. Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-295. Portland, OR.

Williams, D.W., and A.M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4: 87–99.

Williams, J.E., and C.D. Williams. 2004. Oversimplified habitats and oversimplified solutions in our search for sustainable freshwater fisheries. *American Fisheries Society Symposium* 43: 67–89.

Wilson, J., and B. Celaya. 1998. *Bark Beetles Biology, Prevention and Control*. USDA Forest Service, Southwestern Region. Flagstaff, AZ.

Wood, D.L., R.W. Stark, W.E. Waters, W.D. Bedard, and F.W. Cobb, Jr. 1985. Treatment tactics and strategies. In *Integrated Pest Management in Pine–Bark Beetle Ecosystems*, ed. by W.E. Waters, R.W. Stark, and D.L. Wood, pp. 121–39. John Wiley and Sons, New York, NY.

Zhou, J., D.W. Ross, and C.G. Niwa. 2001. Kairomonal response of *Thanasimus undulates, Enoclerus sphegeus* (Coleoptera: Cleridae), and *Temnochila chlorodia* (Coleoptera: Trogositidae) to bark beetle semiochemicals in eastern Oregon. *Environmental Entomology* 30(6): 993–98.

Section Two: Citations by Topic

This section is designed to allow you to find citations by topic area. The topics are organized in the same order as in the previous summary paper, with the addition of papers about major insect pests, such as mountain pine beetle and spruce bark beetle. When you find citations of interest, please go to *Section Three* to read summaries and key points of each paper.

- **Insects and Ecosystem Function**
- **Forest Simplification and Insect Outbreaks**
- **Logging to Control Forest Insects**
- **Effectiveness of Thinning**
- **Forest Insects and Fire**
- **The Importance of Natural Enemies**
- **Pheromones for Insect Control**
- **Global Warming**
- **Mountain Pine Beetle (*Dendroctonus ponderosae*)**
- **Douglas-fir Bark Beetle (*Dendroctonus pseudotsugae*)**
- **Spruce Bark Beetle (*Ips typographus*)**
- **Western Pine Beetle (*Dendroctonus brevicomis*)**
- **Southern Pine Beetle (*Dendroctonus frontalis*)**
- **Forest Defoliators including Douglas-fir Tussock Moth (*Orgyia pseudotsugata*) and Spruce Budworm (*Choristoneura* spp.)**

INSECTS AND ECOSYSTEM FUNCTION

Alfaro, R.I., and R.F. Shepherd. 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir tussock moth. *Forest Science* 37(3): 959–64.

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact of succession. In *The Role of Arthropods in Forest Ecosystems: Proceedings in the Life Sciences*, ed. by W.J. Mattson, pp. 3–18. Springer–Verlag, New York, NY.

Amman, G.D., and J.A. Logan 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. *American Entomologist* 44(3): 166–77.

Berryman, A.A. 1982. Population dynamics of bark beetles. In *Bark Beetles in North American Conifers*, ed. by J.B. Mitton and K.B. Sturgeon, pp. 264–314. University of Texas Press, Austin, TX.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114: 236–42.

Clancy, K.M. 1993. Research approaches to understanding the roles of insect defoliators in forest ecosystems. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, pp. 211–17. USDA General Technical Report RM-247.

Ferrel, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In *Sierra Nevada Ecosystem Project: Final Report to Congress, Vol. II.* Davis, CA. pp.1177–92.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Fuchs, M. 1999. *The Ecological Role of the Mountain Pine Beetle (*Dendroctonus ponderosae*): A Description of Research from the Literature*. Prepared by Foxtree Ecological Consulting for British Columbia Parks Service, Victoria, BC.

Goheen, D.J., and E.M. Hansen. 1993. Effects of pathogens and bark beetles on forests. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 175–96. Academic Press, San Diego, CA.

Haack, R.A., and J.W. Byler. 1993. Insects and pathogens, regulators of forest ecosystems. *Journal of Forestry* 91(9): 32–7.

Haack, R.A., and G. Paiz-Schwartz. 1997. Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas Biosphere Reserve, Guatemala. *Entomological News* 108(1): 67–76.

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Hagle, S., and R. Schmitz. 1993. Managing root disease and bark beetles. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 209–28. Academic Press, New York, NY.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Johnson, C.G. Jr., R.R. Clausnitzer, P.J. Mehringer, and C.D. Oliver. 1994. *Biotic and Abiotic Processes of Eastside Ecosystems: The Effects of Management on Plant and Community Ecology, and on Stand and Landscape Vegetation Dynamics*. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-322.

Komonen, A. 2003. Hotspots of insect diversity in boreal forests. *Conservation Biology* 17(4): 976–81.

Kovacic, D.A., M.I. Dyer, and A.T. Cringan. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. *Forest Ecology and Management* 13: 53–67.

Lattin, J.D. 1993. Arthropod diversity and conservation in old growth Northwest forests. *American Zoology* 33: 578–87.

Lindgren, B.S., and K.J. Lewis. 1997. The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study. In *Proceedings: Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests*, ed. by J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, pp. 122–30. USDA Forest Service General Technical Report NE-236.

Lovett, G.M., L.M. Christenson, P.M. Groffman, C.G. Jones, J.E. Hart, and M.J. Mitchell. 2002. Insect defoliation and nitrogen cycling in forests. *BioScience* 52(4): 335–41.

Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120: 257–64.

Matsuoka, S.M., C.M. Handel, and D.R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. *Canadian Journal of Zoology* 79: 1678–90.

Mattson, W.J., and N.D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515–22.

Nowak, J.T., and C.W. Berisford. 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. *Journal of Economic Entomology* 93(2): 336–41.

Økland, B., and A. Berryman. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. *Agricultural and Forest Entomology* 6: 141–46.

Økland, B., and O.N. Bjørnstad. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. *Population Ecology* 45: 213–19.

Paine, T.D., and F.A. Baker. 1993. Abiotic and biotic predisposition. In *Beetle Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 61–73. Academic Press, Inc., San Diego, CA.

Parks, C.G. 1993. The Influence of Induced Host Moisture Stress on the Growth and Development of Western Spruce Budworm and *Armillaria ostoyae* on Grand Fir Seedlings. Ph.D. dissertation. Oregon State University.

Payer, D.C., and D.J. Harrison. 2000. Structural differences between forests regenerating following spruce budworm defoliation and clear-cut harvesting: Implications for marten. *Canadian Journal of Forest Research* 30(12): 1965–72.

Peltonen, M. 1999. Windthrows and dead standing trees as bark beetle breeding material at forest-clearcut edge. *Scandinavian Journal of Forest Research* 14: 505–11.

Peterman, R.M. 1978. The ecological role of mountain pine beetle in lodgepole pine forests. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Symposium Co-Sponsored by National Science Foundation … et al., held at Washington State University, Pullman, Washington, April 25-27, 1978*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 16–26. U.S. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID.

Reeve, J.D., M.P. Ayres, and P.L. Lorio, Jr. 1995. Host suitability, predation and bark beetle population dynamics. In *Population Dynamics: New Approaches and Synthesis*, ed. by N. Cappuccino and P.W. Price, pp. 339–57. Academic Press, Inc., San Diego, CA.

Romme, W.H., D.H. Knight, and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist* 127(4): 484–94.

Schowalter, T.D. 1990. Consequences of insects. In *Symposium Proceedings. Forests – Wild and Managed: Differences and Consequences. January 19-20, 1990*, pp. 91–106. University of British Columbia, Vancouver, BC.

Schowalter, T.D. 1994. An ecosystem-centered view of insect and disease effects on forest health. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, ed. by W.W. Covington and L.F. DeBano, pp. 189–95. USDA Forest Service General Technical Report RM-247.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78: 115–25.

Schowalter, T.D., W.W. Hargrove, and D.A. Crossley, Jr. 1986. Herbivory in forested ecosystems. *Annual Review of Entomology* 31: 177–96.

Schowalter, T.D., and J. Withgott. 2001. Rethinking insects. What would an ecosystem approach look like? *Conservation Biology In Practice* 2(4): 10–16.

Schroeder, L.M., and A. Lindlow. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Coleoptera: Scolytidae) following a storm felling: A comparison between stands with and without removal of wind felled trees. *Agricultural and Forest Entomology* 4: 47–56.

Shouse, B. 2003. Old-growth forest spared for now. *Science* 299: 802.

Stone, W.E., and M.L. Wolfe. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* 122: 1–12.

Velben, T.T., K.S. Hadley, M.S. Reid, and A.J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreaks in Colorado. *Ecology* 72: 213–31.

Wickman, B.E. 1978. *A Case Study of Douglas-Fir Tussock Moth Outbreak and Stand Conditions 10 Years Later*. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Paper PNW-224, Portland, OR.

Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *Journal of Forestry* 78: 31–3.

FOREST SIMPLIFICATION AND INSECT OUTBREAKS

Aber, J., N. Christensen, I. Fernandez, J. Franklin, L. Hidinger, M. Hunter, J. MacMahon, D. Mladenoff, J. Pastor, D. Perry, R. Slangen, and H. van Miegroet. 2000. Applying ecological principles to management of the U.S. national forests. *Issues in Ecology No. 6.* Ecological Society of America, Washington, D.C.

Anderson, L., C.E. Carlson, and R.H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management* 22: 251–60.

Bergeron, Y., A. Leduc, H. Morin, and C. Joyal. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research* 25: 1375–84.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114: 236–42.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Haack, R.A., and G. Paiz-Schwartz. 1997. Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas Biosphere Reserve, Guatemala. *Entomological News* 108(1): 67–76.

Habeck, J.R. 1990. Old growth ponderosa pine-western larch forests in western Montana: Ecology and management. *Northwest Environmental Journal* 6(2): 271-92.

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Lehmkuhl, J.F., P.F. Hessburg, R.L. Everett, M.H. Huff, and R.D. Ottmar. 1994. *Historical and Current Forest Landscapes of Eastern Oregon and Washington. Part 1: Vegetation Pattern and Insect and Disease Hazards*. USDA Forest Service General Technical Report PNW-GTR-328, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Maloney, P.E., and D.M. Rizzo. 2002. Pathogens and insects in a pristine forest ecosystem: The Sierra San Pedro Mártir, Baja, Mexico. *Canadian Journal of Forest Research* 32: 448–57.

Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120: 257–64.

Martikainen, P., J. Siitonen, L. Kaila, P. Punttila, and J. Rauh. 1999. Bark beetles (Coleoptera: Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *Forest Ecology and Management* 116: 233–45.

Mattson, W.J., and N.D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515–22.

McCullough, D.G., R.A. Werner, and D. Neumann. 1998. Fire and insects in northern boreal forest ecosystems of North America. *Annual Review of Entomology* 43: 107–27.

Naeem, S., F.S. Chapin III, R. Costanza, P.R. Ehrlich, F.B. Golley, D.U. Hooper, J.H. Lawton, R.V. O'Neill, H.A. Mooney, O.E. Sala, A.J. Symstad, and D. Tilman. 1999. Biodiversity and ecosystem functioning: Maintaining natural life support processes. *Issues in Ecology No. 4*. Ecological Society of America, Washington, D.C.

Nowak, J.T., and C.W. Berisford. 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. *Journal of Economic Entomology* 93(2): 336–41.

Paine, T.D., and F.A. Baker. 1993. Abiotic and biotic predisposition. In *Beetle Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 61–73. Academic Press, Inc., San Diego, CA.

Raffa, K.F., and A.A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: A basis for reciprocal adaptations? *The American Naturalist* 129(2): 234–62.

Schowalter, T.D. 1990. Consequences of insects. In *Symposium Proceedings. Forests – Wild and Managed: Differences and Consequences. January 19-20, 1990*, pp. 91–106. University of British Columbia, Vancouver, BC.

Schowalter, T.D. 1994. An ecosystem-centered view of insect and disease effects on forest health. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, ed. by W.W. Covington and L.F. DeBano, pp. 189–95. USDA Forest Service General Technical Report RM-247.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78: 115–25.

Schowalter, T.D., and P. Turchin. 1993. Southern pine beetle infestation development: Interaction between pine and hardwood basal areas. *Forest Science* 39: 201–10.

Schowalter, T.D., and J. Withgott. 2001. Rethinking insects. What would an ecosystem approach look like? *Conservation Biology In Practice* 2(4): 10–16.

Shouse, B. 2003. Old-growth forest spared for now. *Science* 299: 802.

Similä, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: The effects of forest age and naturalness on species assemblages. *Biological Conservation* 106: 19–27.

Stephen, F.M., M.P. Lih, and L.E. Browne. 1996. Biological control of southern pine beetle through enhanced nutrition of its adult parasitoids. In *Proceedings: North American Forest Insect Work Conference*, ed. by R.F. Billings and T.E. Nebeker, pp. 34–5. Texas Forest Service Publication 160.

Swetnam, T.W., and A.M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63(4): 399–424.

Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

LOGGING TO CONTROL FOREST INSECTS

Amman, G.D., and J.A. Logan 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. *American Entomologist* 44(3): 166–77.

Bentz, B.J., G.D. Amman, and J.A. Logan. 1993. A critical assessment of risk classification systems for the mountain pine beetle. *Forest Ecology and Management* 61(3–4): 349–66.

Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *Journal of Forestry* 74: 294–97.

Cronin, J.T., P. Turchin, J.L. Hayes, and C.A. Steiner. 1999. Area-wide efficacy of a localized forest pest management practice. *Environmental Entomology* 28(3): 496–504.

DeMars, C.J. Jr., and B.H. Roettgering. 1982. *Forest Insect and Disease Leaflet 1: Western Pine Beetle*. USDA Forest Service, Pacific Southwest Region.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKee, and T.A. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. In *Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems*, ed. by D.A. Perry, pp. 82–97. Timber Press, Portland, OR.

Furniss, R.L., and V.M. Carolin. 1977. *Western Forest Insects*. USDA Forest Service Misc. Pub. 1339, Washington, D.C.

Hedgren, P.O., L.M. Schroeder, and J. Weslien. 2003. Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. *Agricultural and Forest Entomology* 5: 67–74.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Klein, W.H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 148–58. University of Idaho, Pullman, WA.

Komonen, A. 2003. Hotspots of insect diversity in boreal forests. *Conservation Biology* 17(4): 976–81.

Lindenmayer, D.B., D.R. Foster, J.F. Franklin, M.L. Hunter, R.F. Noss, F.A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. *Science* 303: 1303.

Lundquist, J.E. 1995. Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA. *Forest Ecology and Management* 74: 37–48.

Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120: 257–64.

Martikainen, P., J. Siitonen, L. Kaila, P. Punttila, and J. Rauh. 1999. Bark beetles (Coleoptera: Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *Forest Ecology and Management* 116: 233–45.

Muzika, R.M., and A.M. Liebhold. 2000. A critique of silvicultural approaches to managing defoliating insects in North America. *Agricultural and Forest Entomology* 2: 97–105.

Nebeker, T.E. 1989. Bark beetles, natural enemies, management selection interactions. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 71–80. Stephen F. Austin State University, Nacogdoches, TX.

Nowak, J.T., and C.W. Berisford. 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. *Journal of Economic Entomology* 93(2): 336–41.

Payer, D.C., and D.J. Harrison. 2000. Structural differences between forests regenerating following spruce budworm defoliation and clear-cut harvesting: Implications for marten. *Canadian Journal of Forest Research* 30(12): 1965–72.

Radeloff, V.C., D.J. Mladenoff, and M.S. Boyce. 2000. The changing relation of landscape patterns and jack pine budworm populations during an outbreak. *Oikos* 90: 417–30.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78: 115–25.

Schroeder, L.M., and A. Lindlow. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Coleoptera: Scolytidae) following a storm felling: A comparison between stands with and without removal of wind felled trees. *Agricultural and Forest Entomology* 4: 47–56.

Siira-Pietikäinen, A., J. Haima, A. Kanninen, J. Pietikäinen, and H. Fritze. 2001. Responses of decomposer community to root-isolation and addition of slash. *Soil Biology & Biochemistry* 33: 1993–2004.

Simard, J.R., and J.M. Fryxell. 2003. Effects of selective logging on terrestrial small mammals and arthropods. *Canadian Journal of Zoology* 81: 1318–26.

Similä, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: The effects of forest age and naturalness on species assemblages. *Biological Conservation* 106: 19–27.

Stephen, F.M., M.P. Lih, and L.E. Browne. 1996. Biological control of southern pine beetle through enhanced nutrition of its adult parasitoids. In *Proceedings: North American Forest Insect Work Conference*, ed. by R.F. Billings and T.E. Nebeker, pp. 34–5. Texas Forest Service Publication 160.

Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

Wickman, B.E. 1990. *The Battle Against Bark Beetles in Crater Lake National Park: 1925–34*. United States Department of Agriculture. US Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-259.

Wood, D.L., R.W. Stark, W.E. Waters, W.D. Bedard, and F.W. Cobb, Jr. 1985. Treatment tactics and strategies. In *Integrated Pest Management in Pine–Bark Beetle Ecosystems*, ed. by W.E. Waters, R.W. Stark, and D.L. Wood, pp 121–39. John Wiley and Sons, New York, NY.

EFFECTIVENESS OF THINNING

Amman, G.D., and J.A. Logan. 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. *American Entomologist* 44(3): 166–77.

Bentz, B.J., G.D. Amman, and J.A. Logan. 1993. A critical assessment of risk classification systems for the mountain pine beetle. *Forest Ecology and Management* 61(3–4): 349–66.

Christiansen, E., R.H. Waring, and A.A. Berryman. 1987. Resistance of conifers to bark beetle attack: Searching for general relationships. *Forest Ecology and Management* 22: 89–106.

Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *Journal of Forestry* 74: 294–97.

Cronin, J.T., P. Turchin, J.L. Hayes, and C.A. Steiner. 1999. Area-wide efficacy of a localized forest pest management practice. *Environmental Entomology* 28(3): 496–504.

Feeney, S.R., T.E. Kolb, W.W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson natural area. *Canadian Journal of Forest Resources* 28: 1295–1306.

Ferrel, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In *Sierra Nevada Ecosystem Project: Final Report to Congress, Vol. II.* Davis, CA. pp.1177–92.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Goyer, R.A., M.R. Wagner, and T.D. Schowalter. 1998. Current and proposed technologies for bark beetle management. *Journal of Forestry* 96 (12): 29–33.

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Hagle, S., and R. Schmitz. 1993. Managing root disease and bark beetles. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 209–28. Academic Press, New York, NY.

Hindmarch, T.D., and M.L. Reid. 2001. Forest thinning affects reproduction in pine engravers (Coleoptera: Scolytidae) breeding in felled lodgepole pine trees. *Environmental Entomology* 30(5): 919–24.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Kolb, T.E., K.M. Holmberg, M.R. Wagner, and J.E. Stone. 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiology* 18: 375–81.

Larsson, S., R. Oren, R.H. Waring, and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science* 29: 395–402.

Lindgren, B.S., and K.J. Lewis. 1997. The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study. In *Proceedings: Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests*, ed. by J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, pp. 122–30. USDA Forest Service General Technical Report NE-236.

McDowell, N., J.R. Brooks, S.A. Fitzgerald, and B.J. Bond. 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant, Cell and Environment* 26: 631–44.

Mitchell, R.G., and H.K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *Forest Science* 37(5): 1390–1408.

Mitchell, R.G., R.H. Waring, and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* 29(1): 204–11.

Muzika, R.M., and A.M. Liebhold. 2000. A critique of silvicultural approaches to managing defoliating insects in North America. *Agricultural and Forest Entomology* 2: 97–105.

Nebeker, T.E. 1989. Bark beetles, natural enemies, management selection interactions. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 71–80. Stephen F. Austin State University, Nacogdoches, TX.

Negrón, J.F. 1997. Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico. *Canadian Journal of Forest Research* 27: 1936–45.

Negrón, J.F. 1998. Probability of infestation and extent of mortality associated with Douglas-fir beetle in Colorado Front Range. *Forest Ecology and Management* 107: 71–85.

Negrón, J.F., J.A. Anhold, and A.S. Munson. 2001. Within-stand spatial distribution of tree mortality caused by the Douglas-fir beetle (Coleoptera: Scolytidae). *Environmental Entomology* 30(2): 215–24.

Negrón, J.F., J.L. Wilson, and J.A. Anhold. 2000. Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. *Environmental Entomology* 29(1): 20–7.

Olsen, W.K., J.M. Schmid, and S.A. Mata. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *Forest Science* 42(3): 310–27.

Paine, T.D., and F.A. Baker. 1993. Abiotic and biotic predisposition. In *Beetle Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 61–73. Academic Press, Inc., San Diego, CA.

Perkins, D.L., and D.W. Roberts. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* 174: 495–510.

Peterman, R.M. 1978. The ecological role of mountain pine beetle in lodgepole pine forests. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Symposium Co-Sponsored by National Science Foundation … et al., held at Washington State University, Pullman, Washington, April 25-27, 1978*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 16–26. U.S. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID.

Pollet, J., and P.N. Omi. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11: 1–10.

Raffa, K.F., and A.A. Berryman. 1986. A mechanistic computer model of mountain pine beetle populations interacting with lodgepole pine stands and its implications for forest managers. *Forest Science* 32(3): 789–805.

Reid, M.L., and T. Robb. 1999. Death of vigorous trees benefits bark beetles. *Oecologia* 120: 555–62.

Sánchez-Martínez, G., and M.R. Wagner. 2002. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *Forest Ecology and Management* 170: 145–60.

Santoro, A.E., M.J. Lombardero, M.P. Ayres, and J.J. Ruel. 2001. Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management* 144: 245–54.

Sartwell, C., and R.E. Stevens. 1975. Mountain pine beetle in ponderosa pine: Prospects for silvicultural control in second-growth stands. *Journal of Forestry* 73: 136–40.

Schowalter, T.D. 1994. An ecosystem-centered view of insect and disease effects on forest health. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, ed. by W.W. Covington and L.F. DeBano, pp. 189–95. USDA Forest Service General Technical Report RM-247.

Schowalter, T.D., and P. Turchin. 1993. Southern pine beetle infestation development: Interaction between pine and hardwood basal areas. *Forest Science* 39: 201-210.

Shouse, B. 2003. Old-growth forest spared for now. *Science* 299: 802.

Shore, T.L., L. Safranyik, W.G. Riel, M. Ferguson, and J. Castonguay. 1999. Evaluation of factors affecting tree and stand susceptibility to the Douglas-fir beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* 131: 831–39.

Siira-Pietikäinen, A., J. Haima, A. Kanninen, J. Pietikäinen, and H. Fritze. 2001. Responses of decomposer community to root-isolation and addition of slash. *Soil Biology & Biochemistry* 33: 1993–2004.

Waring, R.H., and G.B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66(3): 889–97.

Wood, D.L., R.W. Stark, W.E. Waters, W.D. Bedard, and F.W. Cobb, Jr. 1985. Treatment tactics and strategies. In *Integrated Pest Management in Pine–Bark Beetle Ecosystems*, ed. by W.E. Waters, R.W. Stark, and D.L. Wood, pp. 121–39. John Wiley and Sons, New York, NY.

FOREST INSECTS AND FIRE

Anderson, L., C.E. Carlson, and R.H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management* 22: 251–60.

Bebi, P., D. Kulakowski, and T.T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84(2): 362–71.

Bradley, T., and P. Tueller. 2001. Effects of fire on bark beetle presence on Jeffrey pine in Lake Tahoe Basin. *Forest Ecology and Management* 142: 205–14.

Brennan, L.A., and S.M. Hermann. 1994. Prescribed fire and forest pests: Solutions for today and tomorrow. *Journal of Forestry* November: 34–7.

Feeney, S.R., T.E. Kolb, W.W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson natural area. *Canadian Journal of Forest Resources* 28: 1295–1306.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Haack, R.A., and G. Paiz-Schwartz. 1997. Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas Biosphere Reserve, Guatemala. *Entomological News* 108(1): 67–76.

Holsten, E.H., R.A Werner, and R.L. DeVelice. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. *Environmental Entomology* 24(6): 1539–47.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak.* Report commissioned by The David Suzuki Foundation, Vancouver, BC.

McCullough, D.G., R.A. Werner, and D. Neumann. 1998. Fire and insects in northern boreal forest ecosystems of North America. *Annual Review of Entomology* 43: 107–27.

McHugh, C.W., T.E. Kolb, and J.L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32(3): 510–22.

Mitchell, R.G. 1990. Effects of prescribed fire on insect pests. In *Natural and Prescribed Fire in Pacific Northwest Forests*, ed. by J.D. Walstad, S.R. Radosevich, and D.V. Sandberg, pp. 111–16. Oregon State University Press, Corvallis, OR.

Pollet, J., and P.N. Omi. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11: 1–10.

Sánchez-Martínez, G., and M.R. Wagner. 2002. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *Forest Ecology and Management* 170: 145–60.

Santoro, A.E., M.J. Lombardero, M.P. Ayres, and J.J. Ruel. 2001. Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management* 144: 245–54.

THE IMPORTANCE OF NATURAL ENEMIES

Aukema, B.H., D.L. Dahlsten, and K.F. Raffa. 2000. Exploiting behavioral disparities among predators and prey to selectively remove pests: Maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology* 28(3): 651–60.

Aukema, B.H., and K.F. Raffa. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonization strategy and the absence of emergent multiple predator effects. *Ecological Entomology* 29: 129–38.

Bergeron, Y., A. Leduc, H. Morin, and C. Joyal. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research* 25: 1375–84.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114: 236–42.

Cronin, J.T., J.D. Reeve, R. Wilkens, and P. Turchin. 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90: 127–38.

Dahlsten, D.L. 1982. Relationships between bark beetles and their natural enemies. In *Bark Beetles in North American Conifers*, ed. by J.B. Mitton and K.B. Sturgeon, pp. 140–82. University of Texas Press, Austin, TX.

Dodds, K.J., C. Graber, and F.M. Stephen. 2001. Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). *Environmental Entomology* 30(1): 17–22.

Erbilgin, N., E.V. Nordheim, B.H. Aukema, and K.F. Raffa. 2002. Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: Within- and between-year associations with predators, competitors and habitat quality. *Environmental Entomology* 31(6): 1043–51.

Fielding, N.J., and H.F. Evans. 1997. Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain. *Biocontrol News and Information* 18(2): 51–60.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Finke, D.L., and R.F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. *Ecology* 83(3): 643–52.

Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKee, and T.A. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. In *Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems*, ed. by D.A. Perry, pp. 82–97. Timber Press, Portland, OR.

Furniss, R.L., and V.M. Carolin. 1977. *Western Forest Insects.* USDA Forest Service Misc. Pub. 1339, Washington, D.C.

Gilbert, M., and J. Grégoire. 2003. Site condition and predation influence a bark beetle’s success: A spatially realistic approach. *Agricultural and Forest Entomology* 5: 87–96.

Haack, R.A., and G. Paiz-Schwartz. 1997. Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas Biosphere Reserve, Guatemala. *Entomological News* 108(1): 67–76.

Joseph, G., R.G. Kelsey, R.W. Peck, and C.G. Niwa. 2001. Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. *Journal of Chemical Ecology* 27(4): 697–715.

Koplin, J.R., and P.H. Baldwin. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. *The American Midland Naturalist* 83: 510–15.

Lindgren, B.S., and D.R. Miller. 2002. Effect of verbenone on attraction of predatory and woodboring beetles (Coleoptera) to kairomones in lodgepole pine forests. *Environmental Entomology* 31(5): 766–73.

Lombardero, M.J., M.P. Ayres, R.W. Hofstetter, J.C. Moser, and K.D. Lepzig. 2003. Strong indirect interactions of *Tarsonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Oikos* 102: 243–52.

Marsden, M.A., M.M. Furniss, and L.N. Kline. 1981. *Modeling Seasonal Abundance Douglas-fir Beetle in Relation to Entomophagous Insects and Location in Trees*. USDA Forest Service General Technical Report INT-111. Intermountain Forest and Range Experiment Station, Ogden, UT.

Nebeker, T.E. 1989. Bark beetles, natural enemies, management selection interactions. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 71–80. Stephen F. Austin State University, Nacogdoches, TX.

Nowak, J.T., and C.W. Berisford. 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. *Journal of Economic Entomology* 93(2): 336–41.

Otvos, I.S. 1979. The effects of insectivorous bird activities in forest ecosystems: An evaluation. In *The Role of Insectivorous Birds in Forest Ecosystems*, ed. by J.G. Dickson, R.N. Conner, R.R. Fleet, J.A. Jackson, and J.C. Kroll, pp. 341–74. Academic Press, New York, NY.

Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

Reeve, J.D. 1997. Predation and bark beetle dynamics. *Oecologia* 112: 48–54.

Reeve, J.D., M.P. Ayres, and P.L. Lorio, Jr. 1995. Host suitability, predation and bark beetle population dynamics. In *Population Dynamics: New Approaches and Synthesis*, ed. by N. Cappuccino and P.W. Price, pp. 339–57. Academic Press, Inc., San Diego, CA.

Ross, D.W., and G.E. Daterman. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. *Forest Science* 43(1): 65–70.

Ross, D.W., K.E. Gibson, R.W. Thier, and A.S. Munson, 1996. Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 89(5): 1204–07.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78: 115–25.

Schroeder, L.M. 1996. Interactions between predators *Thanasimus formicarius* (Coleoptera: Cleridae) and *Rhizophagus depressus* (Coleoptera: Rhizophaidae) and the bark beetle *Tomicus piniperda* (Coleoptera: Scolytidae). *Entomophaga* 41(1): 63–75.

Schroeder, L.M., and J. Weslien. 1994. Reduced offspring reproduction in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and α–pinene, which attract antagonistic insects. *Journal of Chemical Ecology* 20: 1429–44.

Shook, R.S., and P.H. Baldwin. 1970. Woodpecker predation on bark beetles in Engelmann spruce logs as related to stand density. *Canadian Entomologist* 102: 1345–54.

Stephen, F.M., M.P. Lih, and L.E. Browne. 1996. Biological control of southern pine beetle through enhanced nutrition of its adult parasitoids. In *Proceedings: North American Forest Insect Work Conference*, ed. by R.F. Billings and T.E. Nebeker, pp. 34–5. Texas Forest Service Publication 160.

Stephen, F.M., M.P. Lih, and G.W. Wallis. 1989. Impact of arthropod natural enemies on *Dendroctonus frontalis* (Coleoptera: Scolytidae) mortality and their potential role in infestation growth. In

Potential for Biological Control of Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 169–85. Stephen F. Austin State University Press, Nacogdoches, TX.

Sullivan, B.T., E.M. Pettersson, K.C. Seltmann, and C.W. Berisford. 2000. Attraction of the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. *Environmental Entomology* 29(6): 1138–51.

Turchin, P., A.D. Taylor, and J.D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: An experimental test. *Science* 285: 1068–71.

Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

Zhou, J., D.W. Ross, and C.G. Niwa. 2001. Kairomonal response of *Thanasimus undatulus, Enoclerus sphegeus* (Coleoptera: Cleridae), and *Temnochila chlorodia* (Coleoptera: Trogositidae) to bark beetle semiochemicals in eastern Oregon. *Environmental Entomology* 30(6): 993–98.

PHEROMONES FOR INSECT CONTROL

Aukema, B.H., D.L. Dahlsten, and K.F. Raffa. 2000. Exploiting behavioral disparities among predators and prey to selectively remove pests: Maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology* 28(3): 651–60.

Aukema, B.H., and K.F. Raffa. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonization strategy and the absence of emergent multiple predator effects. *Ecological Entomology* 29: 129–38.

Erbilgin, N., J.S. Powell, and K.F. Raffa. 2003. Effect of varying monoterpene concentrations on the response of *Ips pini* (Coleoptera: Scolytidae) to its aggregation pheromone: Implications for pest management and ecology of bark beetles. *Agricultural and Forest Entomology* 5: 269–74.

Huber, D.P.W., and J.H. Borden. 2001. Protection of lodgepole pines from mass attack by mountain pine beetle, *Dendroctonus ponderosae*, with nonhost angiosperm volatiles and verbenone. *Entomologia Experimentalis et Applicata* 92: 131–41.

Joseph, G., R.G. Kelsey, R.W. Peck, and C.G. Niwa. 2001. Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. *Journal of Chemical Ecology* 27(4): 697–715.

Kelsey, R.G., and G. Joseph. 2001. Attraction of *Scolytus unispinosus* bark beetles to ethanol in water-stressed Douglas-fir branches. *Forest Ecology and Management* 144: 229–38.

Laidlaw, W.G., B.G. Prenzel, M.L. Reid, S. Fabris, and H. Wieser. 2003. Comparison of the efficacy of pheromone-baited traps, pheromone-baited trees, and felled trees for the control of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Environmental Entomology* 32(3): 477–83.

Lindgren, B.S., and D.R. Miller. 2002. Effect of verbenone on attraction of predatory and woodboring beetles (Coleoptera) to kairomones in lodgepole pine forests. *Environmental Entomology* 31(5): 766–73.

Raffa, K.F., and A.A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53(1): 27–49.

Raffa, K.F., and A.A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: A basis for reciprocal adaptations? *The American Naturalist* 129(2): 234–262.

Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

Ross, D.W., and G.E. Daterman. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. *Forest Science* 43(1): 65–70.

Ross, D.W., K.E. Gibson, and G.E. Daterman. 2001. *Using MCH to Protect Trees and Stands from Douglas-fir Beetle Infestation*. USDA Forest Service Forest Health Technology Enterprise Team FHTET-2001-09.

Ross, D.W., K.E. Gibson, R.W. Thier, and A.S. Munson, 1996. Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 89(5): 1204–07.

Schroeder, L.M., and J. Weslien. 1994. Reduced offspring reproduction in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and α–pinene, which attract antagonistic insects. *Journal of Chemical Ecology* 20: 1429–44.

Strom, B.L., R.A. Goyer, and P.J. Shea. 2001. Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. *Entomologia Experimentalis et Applicata* 100: 63–7.

Sullivan, B.T., E.M. Pettersson, K.C. Seltmann, and C.W. Berisford. 2000. Attraction of the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. *Environmental Entomology* 29(6): 1138–51.

Wallin, K.F., and K.F. Raffa. 2000. Influences of host chemicals and internal physiology on the multiple steps of postlanding host acceptance behavior of *Ips pini* (Coleoptera: Scolytidae). *Environmental Entomology* 29(3): 442-53.

Wallin, K.F., and K.F. Raffa. 2002. Density-mediated responses of bark beetles to host allelochemicals: A link between individual behavior and population dynamics. *Ecological Entomology* 27: 484–92.

Zhou, J., D.W. Ross, and C.G. Niwa. 2001. Kairomonal response of *Thanasimus undatulus, Enoclerus sphegeus* (Coleoptera: Cleridae), and *Temnochila chlorodia* (Coleoptera: Trogositidae) to bark beetle semiochemicals in eastern Oregon. *Environmental Entomology* 30(6): 993–98.

GLOBAL WARMING

Ayres, M.P., and M.J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment* 262: 263–86.

Kühnholtz, S., J.H. Borden, and A. Uzunovic. 2001. Secondary ambrosia beetles in apparently healthy trees: Adaptations, potential causes and suggested research. *Integrated Pest Management Reviews* 6: 209–219.

Logan, J.A., and B.J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28(6): 924–34.

Logan, J.A., and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47(3): 160–72.

Mattson, W.J., and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37(2): 110–18.

Percy, K.E., C.S. Awmack, R.L. Lindroth, M.E. Kubiske, B.J. Kopper, J.G. Isebrands, K.S. Pregitzer, G.R. Hendrey, R.E. Dickson, D.R. Zak, E. Oksanen, J. Sober, R. Harrington, and D.F. Karnosky. 2002. Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. *Nature* 420: 403–07.

Volney, W.J.A., and R.A. Fleming. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment* 82: 283–94.

Williams, D.W., and A.M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4: 87–99.

MOUNTAIN PINE BEETLE (DENDROCTONUS PONDEROSAE)

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact of succession. In *The Role of Arthropods in Forest Ecosystems: Proceedings in the Life Sciences*, ed. by W.J. Mattson, pp. 3–18. Springer–Verlag, New York, NY.

Amman, G.D., and J.A. Logan 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. *American Entomologist* 44(3): 166–77.

Bentz, B.J., G.D. Amman, and J.A. Logan. 1993. A critical assessment of risk classification systems for the mountain pine beetle. *Forest Ecology and Management* 61(3–4): 349–66.

Berryman, A.A. 1982. Population dynamics of bark beetles. In *Bark Beetles in North American Conifers*, ed. by J.B. Mitton and K.B. Sturgeon, pp. 264–314. University of Texas Press, Austin, TX.

Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *Journal of Forestry* 74: 294–97.

Fuchs, M. 1999. *The Ecological Role of the Mountain Pine Beetle (*Dendroctonus ponderosae*): A Description of Research from the Literature*. Prepared by Foxtree Ecological Consulting for British Columbia Parks Service, Victoria, BC.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak.* Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Klein, W.H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 148–58. University of Idaho, Pullman, WA.

Kovacic, D.A., M.I. Dyer, and A.T. Cringan. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. *Forest Ecology and Management* 13: 53–67.

Larsson, S., R. Oren, R.H. Waring, and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science* 29: 395–402.

Logan, J.A., and B.J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28(6): 924–34.

Logan, J.A., and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47(3): 160–72.

McHugh, C.W., T.E. Kolb, and J.L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32(3): 510–22.

Mitchell, R.G., and H.K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *Forest Science* 37(5): 1390–1408.

Olsen, W.K., J.M. Schmid, and S.A. Mata. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *Forest Science* 42(3): 310–27.

Perkins, D.L., and D.W. Roberts. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* 174: 495–510.

Peterman, R.M. 1978. The ecological role of mountain pine beetle in lodgepole pine forests. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Symposium Co-Sponsored by National Science Foundation … et al., held at Washington State University, Pullman, Washington, April 25-27, 1978*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 16–26. U.S. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID.

Raffa, K.F., and A.A. Berryman. 1986. A mechanistic computer model of mountain pine beetle populations interacting with lodgepole pine stands and its implications for forest managers. *Forest Science* 32(3): 789–805.

Raffa, K.F., and A.A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: A basis for reciprocal adaptations? *The American Naturalist* 129(2): 234–62.

Romme, W.H., D.H. Knight, and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist* 127(4): 484–94.

Sartwell, C., and R.E. Stevens. 1975. Mountain pine beetle in ponderosa pine: Prospects for silvicultural control in second-growth stands. *Journal of Forestry* 73: 136–40.

Stone, W.E., and M.L. Wolfe. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* 122: 1–12.

Waring, R.H., and G.B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66(3): 889–97.

Wickman, B.E. 1990. *The Battle Against Bark Beetles in Crater Lake National Park: 1925–34*. United States Department of Agriculture. US Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-259.

Williams, D.W., and A.M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4: 87–99.

*DOUGLAS-FIR BARK BEETLE (*DENDROCTONUS PSEUDOTSUGAE*)*

Furniss, R.L., and V.M. Carolin. 1977. *Western Forest Insects*. USDA Forest Service Misc. Pub. 1339, Washington, D.C. www.barkbeetles.org/ips/westips.html

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Laidlaw, W.G., B.G. Prenzel, M.L. Reid, S. Fabris, and H. Wieser. 2003. Comparison of the efficacy of pheromone-baited traps, pheromone-baited trees, and felled trees for the control of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Environmental Entomology* 32(3): 477–83.

Marsden, M.A., M.M. Furniss, and L.N. Kline. 1981. *Modeling Seasonal Abundance Douglas-fir Beetle in Relation to Entomophagous Insects and Location in Trees*. USDA Forest Service General Technical Report INT-111. Intermountain Forest and Range Experiment Station, Ogden, UT.

Negrón, J.F. 1998. Probability of infestation and extent of mortality associated with Douglas-fir beetle in Colorado Front Range. *Forest Ecology and Management* 107: 71–85.

Negrón, J.F., J.A. Anhold, and A.S. Munson. 2001. Within-stand spatial distribution of tree mortality caused by the Douglas-fir beetle (Coleoptera: Scolytidae). *Environmental Entomology* 30(2): 215–24.

Ross, D.W., and G.E. Daterman. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. *Forest Science* 43(1): 65–70.

Ross, D.W., K.E. Gibson, R.W. Thier, and A.S. Munson, 1996. Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 89(5): 1204–07.

Shore, T.L., L. Safranyik, W.G. Riel, M. Ferguson, and J. Castonguay. 1999. Evaluation of factors affecting tree and stand susceptibility to the Douglas-fir beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* 131: 831–39.

*SPRUCE BARK BEETLE (*IPS TYPOGRAPHUS*)*

Bentz, B.J., and A.S. Munson. 2000. Spruce beetle population suppression in northern Utah. *Western Journal of Applied Forestry* 15(3): 122–28.

Hedgren, P.O., L.M. Schroeder, and J. Weslien. 2003. Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. *Agricultural and Forest Entomology* 5: 67–74.

Økland, B., and A. Berryman. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. *Agricultural and Forest Entomology* 6: 141–46.

Økland, B., and O.N. Bjørnstad. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. *Population Ecology* 45: 213–19.

Peltonen, M. 1999. Windthrows and dead standing trees as bark beetle breeding material at forest-clearcut edge. *Scandinavian Journal of Forest Research* 14: 505–11.

Schroeder, L.M., and A. Lindlow. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Coleoptera: Scolytidae) following a storm felling: A comparison between stands with and without removal of wind felled trees. *Agricultural and Forest Entomology* 4: 47–56.

Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

*WESTERN PINE BEETLE (*DENDROCTONUS BREVICOMIS*)*

DeMars, C.J. Jr., and B.H. Roettgering. 1982. *Forest Insect and Disease Leaflet 1: Western Pine Beetle*. USDA Forest Service, Pacific Southwest Region.

Goyer, R.A., M.R. Wagner, and T.D. Schowalter. 1998. Current and proposed technologies for bark beetle management. *Journal of Forestry* 96 (12): 29–33.

McHugh, C.W., T.E. Kolb, and J.L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32(3): 510–22.

*SOUTHERN PINE BEETLE (*DENDROCTONUS FRONTALIS*)*

Cronin, J.T., J.D. Reeve, R. Wilkens, and P. Turchin. 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90: 127–38.

Reeve, J.D., M.P. Ayres, and P.L. Lorio, Jr. 1995. Host suitability, predation and bark beetle population dynamics. In *Population Dynamics: New Approaches and Synthesis*, ed. by N. Cappuccino and P.W. Price, pp. 339–57. Academic Press, Inc., San Diego, CA.

Schowalter, T.D., and P. Turchin. 1993. Southern pine beetle infestation development: Interaction between pine and hardwood basal areas. *Forest Science* 39: 201–10.

Stephen, F.M., M.P. Lih, and L.E. Browne. 1996. Biological control of southern pine beetle through enhanced nutrition of its adult parasitoids. In *Proceedings: North American Forest Insect Work Conference*, ed. by R.F. Billings and T.E. Nebeker, pp. 34–5. Texas Forest Service Publication 160.

Stephen, F.M., M.P. Lih, and G.W. Wallis. 1989. Impact of arthropod natural enemies on *Dendroctonus frontalis* (Coleoptera: Scolytidae) mortality and their potential role in infestation growth. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 169–85. Stephen F. Austin State University Press, Nacogdoches, TX.

Turchin, P., A.D. Taylor, and J.D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: An experimental test. *Science* 285: 1068–71.

Williams, D.W., and A.M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4: 87–99.

FOREST DEFOLIATORS INCLUDING DOUGLAS-FIR TUSSOCK MOTH (ORGYIA PSEUDOTSUGATA) AND SPRUCE BUDWORM (CHORISTONEURA SPP.)

Alfaro, R.I., and R.F. Shepherd. 1991. Tree-ring growth of interior Douglas-fir after one year's defoliation by Douglas-fir tussock moth. *Forest Science* 37(3): 959–64.

Anderson, L., C.E. Carlson, and R.H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management* 22: 251–60.

Bergeron, Y., A. Leduc, H. Morin, and C. Joyal. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research* 25: 1375–84.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114: 236–42.

Clancy, K.M. 1993. Research approaches to understanding the roles of insect defoliators in forest ecosystems. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, pp. 211–17. USDA General Technical Report RM-247.

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Johnson, C.G. Jr., R.R. Clausnitzer, P.J. Mehringer, and C.D. Oliver. 1994. *Biotic and Abiotic Processes of Eastside Ecosystems: The Effects of Management on Plant and Community Ecology, and on Stand and Landscape Vegetation Dynamics*. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-322.

Muzika, R.M., and A.M. Liebhold. 2000. A critique of silvicultural approaches to managing defoliating insects in North America. *Agricultural and Forest Entomology* 2: 97–105.

Parks, C.G. 1993. The Influence of Induced Host Moisture Stress on the Growth and Development of Western Spruce Budworm and *Armillaria ostoyae* on Grand Fir Seedlings. Ph.D. dissertation. Oregon State University.

Payer, D.C., and D.J. Harrison. 2000. Structural differences between forests regenerating following spruce budworm defoliation and clear-cut harvesting: Implications for marten. *Canadian Journal of Forest Research* 30(12): 1965–72.

Radeloff, V.C., D.J. Mladenoff, and M.S. Boyce. 2000. The changing relation of landscape patterns and jack pine budworm populations during an outbreak. *Oikos* 90: 417–30.

Schowalter, T.D., and J. Withgott. 2001. Rethinking insects. What would an ecosystem approach look like? *Conservation Biology In Practice* 2(4): 10–16.

Swetnam, T.W., and A.M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63(4): 399–424.

Volney, W.J.A., and R.A. Fleming. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment* 82: 283–94.

Wickman, B.E. 1978. *A Case Study of Douglas-Fir Tussock Moth Outbreak and Stand Conditions 10 Years Later*. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Paper PNW-224, Portland, OR.

Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *Journal of Forestry* 78: 31–3.

Section Three: Summaries of Relevant Research Papers

This section includes summaries and key findings of over 150 articles relating to “pest” insects and insect control in temperate forests in North America. The section is in alphabetical order by first author. To locate an article about a specific topic, refer to the topic-based lists in Section Two.

Aber, J., N. Christensen, I. Fernandez, J. Franklin, L. Hidinger, M. Hunter, J. MacMahon, D. Mladenoff, J. Pastor, D. Perry, R. Slangen, and H. van Miegroet. 2000. Applying ecological principles to management of the U.S. national forests. *Issues in Ecology No. 6.* Ecological Society of America, Washington, D.C.

Summary: The authors identify major ecological considerations that should be incorporated into sound forest management policy and their potential impacts on current practice. There is no evidence to support the view that natural forests or reserves are more vulnerable to disturbances such as wildfire, windthrow, and pests than are intensively managed forests. Indeed, there is evidence natural systems may be more resistant in many cases. The spread of native and exotic pests and pathogens in many forest systems can be linked to the simplification and fragmentation of the forest. From an ecological standpoint, the strategy with the greatest probability of long-term success in protecting forests against pests and pathogens is one that encourages the maintenance of a diverse set of controls, such as occurs in nature.

Alfaro, R.I., and R.F. Shepherd. 1991. Tree-ring growth of interior Douglas-fir after one year’s defoliation by Douglas-fir tussock moth. *Forest Science* 37(3): 959–64.

Summary: The study indicates that growth stimulation was noted in the year when tussock moth feeding took place. With Douglas-fir, the more an individual tree is defoliated by tussock moth, the more it compensates afterwards; those trees most eaten increased their growth the most later. High defoliation levels (over 50 percent) resulted in growth reduction in trees in years two and three.

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact of succession. In *The Role of Arthropods in Forest Ecosystems: Proceedings in the Life Sciences*, ed. by W.J. Mattson, pp. 3–18. Springer–Verlag, New York, NY.

Summary: Mountain pine beetle epidemics in lodgepole pine forests of the inland West are part of a natural boom-and-bust cycle that has occurred for centuries. Mountain pine beetle populations typically increase to epidemic levels when large homogenous areas of lodgepole pine mature, providing a sustainable food resource. The insect selectively kills susceptible trees from specific size classes, thereby facilitating development of a forest that is structurally, genetically, and compositionally more diverse and less prone to beetle attack, and thus starting the cycle over again.

Amman, G.D., and J.A. Logan. 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. *American Entomologist* 44(3): 166–77.

Summary: The authors summarize thinning efforts and their efficacy in affecting future outbreaks of mountain pine beetle. They point out that pine forests and mountain pine beetle have coevolved over countless millennia. In pre-European times, this relationship most likely was characterized by "normative outbreaks," a term used to describe outbreaks of a native insect that are "part and parcel of normal plant biology." They point to failed attempts to use direct-control measures, such as pesticides and cutting, after an infestation starts. They suggest that by the early 1970s it had become apparent that controlling mountain pine beetle outbreaks by directly killing beetles was not working. They point to thinning studies that show some level of success in ameliorating mountain pine beetle infestations in lodgepole and ponderosa pine. They conclude by saying that it is evident that, after over sixty years of using silviculture to try to control mountain pine beetle, we are not going to eliminate the beetle from western forests, nor should we. There is an emerging realization that we need to develop the understanding required to incorporate natural disturbance events within attainable and sustainable forest management objectives.

Anderson, L., C.E. Carlson, and R.H. Wakimoto. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. *Forest Ecology and Management* 22: 251–60.

Summary: The authors inferred the frequency, duration, and intensity of western spruce budworm outbreaks through an analysis of radial increment cores and fire history from basal-area scars on old-growth pines and firs. Data were compared between the pre-fire-suppression period (1814–1910) and the fire-suppression period (1911–1983). Outbreak frequency did not differ, but the duration and intensity of feeding activity were greater since fire suppression began. They conclude that reduced fire frequency has allowed extensive, continuous areas of forests susceptible to western spruce budworm to develop. Harvesting practices that remove the seral ponderosa pine and western larch aggravated the problem.

Aukema, B.H., D.L. Dahlsten, and K.F. Raffa. 2000. Exploiting behavioral disparities among predators and prey to selectively remove pests: Maximizing the ratio of bark beetles to predators removed during semiochemically based trap-out. *Environmental Entomology* 28(3): 651–60.

Summary: Mass trapping using semiochemical lures is a potentially useful control measure against bark beetle pests. A serious problem, however, is the inadvertent removal of predators that respond to these baits as kairomones. Lures that contain enantiomers of ipsdienol most preferred by *Ips pini* in combination with lanierone can selectively remove three to six times more pests than predators during the spring. Delaying deployment until summer can result in thirty-nine times more pests than predators. In contrast, lures that contain enantiomers of ipsdienol most preferred by predators can inadvertently remove two or more predators for each bark beetle trapped.

Aukema, B.H., and K.F. Raffa. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonization strategy and the absence of emergent multiple predator effects. *Ecological Entomology* 29: 129–38.

Summary: The hypothesis that decreased risk of predation is a potential benefit to aggregations of bark beetles was tested using pine engravers (*Ips pini*) and its two major predators, *Thanasimus dubius* and *Platysoma cylindrica*. The proportional impacts of predators decreased with increased herbivore colonization density, but were still large. Each predator species decreased the net replacement rate of *I. pini* by approximately 42 percent, and their combined effect was approximately 70 percent.

Ayres, M.P., and M.J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. ***The Science of the Total Environment*** **262: 263–86.**

Summary: The effects of climate change and disturbance on forest herbivores and pathogens were theorized. A number of outcomes were predicted for these two groups in light of changing climate: 1) direct effects on the development and survival of herbivores, 2) changes in host tree defenses, and 3) changes in the abundance of natural enemies, mutualists, and competitors. In some cases, increased temperatures may shorten lifecycles of some species of insects. This may also lead to increased mortality because of the loss of snow cover as insulation.

Bebi, P., D. Kulakowski, and T.T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. ***Ecology*** **84(2): 362–71.**

Summary: The authors quantified spatial associations of fire and spruce beetle (*Dendroctonus rufipennis*) outbreaks over more than a century in a subalpine forest landscape in northwestern Colorado, and developed a multivariate logistic model of probability of the occurrence of outbreaks. Forests that had burned in 1879 were less affected by the outbreak in the 1940s than older stands. On the other hand, areas affected by the spruce beetle outbreak in the 1940s showed no higher susceptibility to subsequent fires. The results of this study do not support the increase in fire occurrence that is often expected to follow spruce beetle outbreaks.

Bentz, B.J., G.D. Amman, and J.A. Logan. 1993. A critical assessment of risk classification systems for the mountain pine beetle. ***Forest Ecology and Management*** **61(3–4): 349–66.**

Summary: In this study, four hazard/risk rating systems were evaluated using data from 105 stands in northern Montana. The authors found that none of the systems evaluated was found to predict adequately mountain pine beetle mortality that occurred in the stands. The reasons why hazard rating systems fail to accurately predict bark beetle outbreaks are: 1) the lack of consideration of bark beetle population levels at the time of system development, 2) the minimal information on bark beetle dynamics, and 3) the minimal information on the spatial dynamics of insects and stands.

Bentz, B.J., and A.S. Munson. 2000. Spruce beetle population suppression in northern Utah. ***Western Journal of Applied Forestry*** **15(3): 122–28.**

Summary: This paper describes a project to suppress an endemic spruce beetle population in an isolated spruce stand in northwestern Utah. The authors used baited pheromone traps, selective harvesting, and burning of infested trees and trap trees as control efforts. The number of standing, currently infested spruce trees was reduced by 91 percent over three years. They contend that the suppression effort was successful because of the isolated nature of the stand, early detection efforts, and easy accessibility of the stands. They note that although these types of treatments may help reduce beetle levels, an increase in windthrow could result in another population expansion.

Bergeron, Y., A. Leduc, H. Morin, and C. Joyal. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. ***Canadian Journal of Forest Research*** **25: 1375–84.**

Summary: The authors looked at mortality caused by a spruce budworm (*Choristoneura fumiferana*) outbreak at 624 sites in northwestern Quebec. Abiotic factors—such as moisture regime, stoniness, and thickness of the organic layer—did not have a significant correlation to tree mortality, but the study suggests that forest composition plays an important role in tree mortality.

Coniferous stands intermixed with deciduous stands appear to be less vulnerable than large stands dominated by conifers. This may be related to a higher abundance of natural enemies in these intermixed stands. The study also found that isolated forest patches are less likely to be infested by the western spruce budworm.

Berryman, A.A. 1982. Population dynamics of bark beetles. In *Bark Beetles in North American Conifers*, ed. by J.B. Mitton and K.B. Sturgeon, pp. 264–314. University of Texas Press, Austin, TX.

Summary: A detailed account of bark beetle population dynamics. The presence of large numbers of dead trees immediately following outbreaks may lead to fires, which in turn create favorable conditions for the lodgepole pines to regenerate. Beetles attack the stands when the trees are at an age in which the accumulation of seeds is optimal for regeneration of the new stand. These pine trees have serotinous cones, pinecones that require heat from a fire in order to open and release the seed. By indirectly increasing the likelihood of beneficial fires, the bark beetles interact with the lodgepole pines in such a way that optimizes the fitness of both species. Such infestations, which may seem devastating from one person's point of view, play a critical role in the ecosystem.

Bradley, T., and P. Tueller. 2001. Effects of fire on bark beetle presence on Jeffrey pine in Lake Tahoe Basin. *Forest Ecology and Management* 142: 205–14.

Summary: An investigation into the effects of low-intensity, late-season prescription fire on Jeffery pine and the associated short-term presence of various bark beetles was completed on forests along the north edge of Lake Tahoe, Nevada. The results showed a highly significant correlation between burning and bark beetle presence. The study also showed a positive relationship between burn-severity measures and bark beetle presence in fire-injured Jeffery pine. The authors conclude that while the study shows an undesirable beetle response to prescription burning, a long-term study is needed to provide additional information. They point out that prescription fire is still an important tool for sustainable ecosystem management.

Brennan, L.A., and S.M. Hermann. 1994. Prescribed fire and forest pests: Solutions for today and tomorrow. *Journal of Forestry* 92(11): 34–7.

Summary: This paper summarizes some studies on the effect of prescribed fire on insect and disease populations. The authors suggest that there is emerging evidence that there may be conservation and economic benefits to using fire to control forest pests.

Cappuccino, N., D. Lavertu, Y. Bergeron, and J. Régnière. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia* 114: 236–42.

Summary: The authors investigated the effect of forest diversity on the impact of the spruce budworm (*Choristoneura fumiferana*). Mortality of balsam fir caused by budworm was greater in extensive conifer stands than in habitat islands of fir surrounded by deciduous forest.

Christiansen, E., R.H. Waring, and A.A. Berryman. 1987. Resistance of conifers to bark beetle attack: Searching for general relationships. *Forest Ecology and Management* 22: 89–106.

Summary: This paper reviews work on the relationship between conifer resistance to bark beetles and tree vigor. The authors cite experimental studies to show a link between tree resistance to bark beetles and the amount of current and stored photosynthate that is available for defense. They conclude by hypothesizing that the ability of trees to withstand attacks by bark beetles is linked to the amount of carbohydrates that can be utilized directly for defensive wound reactions. Therefore, any factor that restricts the size of the canopy or its photosynthetic efficiency can weaken a tree's resistance.

Clancy, K.M. 1993. Research approaches to understanding the roles of insect defoliators in forest ecosystems. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, pp. 211–17. USDA General Technical Report RM-247.

Summary: The author reviewed empirical approaches used to investigate the roles of insect defoliators as recyclers of nutrients and regulators of primary production. The author points out that these are native insects that have evolved with their host trees over thousands of years. They are undoubtedly important components of the forest ecosystem, functioning as nutrient recyclers, agents of disturbance, members of food chains, and regulators of productivity, diversity, and density.

Cole, W.E., and D.B. Cahill. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *Journal of Forestry* 74: 294–97.

Summary: The authors looked at three stands of lodgepole pine and correlated tree diameter and phloem production with bark beetle infestation. They concluded that stands with trees that do not reach ten inches diameter at breast height (dbh) could have lowered probabilities for epidemics, although, out of the three stands they looked at, one stand would still have a fairly high chance of infestation even with cutting to ten inches dbh.

Cronin, J.T., J.D. Reeve, R. Wilkens, and P. Turchin. 2000. The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90: 127–38.

Summary: This paper established and modified the distribution equations for the southern pine beetle (*Dendroctonus frontalis*) and the bark beetle predator, the checkered beetle (*Thanasimus dubius*). The model shows a high dispersal rate for predators, with a lower rate for the bark beetles. The fact that the checkered beetles have a dispersal ability greater than their pine beetle prey lends further support to the prediction that this species is an important predator of southern pine beetle. Research such as this can assist in making natural/biological control much more effective by using specific timing of semiochemical manipulation, sex-ratio selection, and precision in predator release.

Cronin, J.T., P. Turchin, J.L. Hayes, and C.A. Steiner. 1999. Area-wide efficacy of a localized forest pest management practice. *Environmental Entomology* 28(3): 496–504.

Summary: This is one of only a few studies that have examined the movement of forest pest populations. This study used mark-and-recapture techniques to determine the dispersal patterns of areas treated with a cut-and-leave technique (infested trees are felled and left in the forest) as well as untreated areas. Overall, colonization success for treated infestations was almost four times that of untreated infestations. This suggests the cut-and-leave tactic may favor increased densities of flying beetles, possibly infesting additional stands of timber. The authors state: "*Even more striking is the paucity of studies that have examined the consequences of human intervention on pest movement patterns. In fact, we know of no studies that have experimentally evaluated the effects of management strategies on the dispersal of insect pests in forest systems.*"

Dahlsten, D.L. 1982. Relationships between bark beetles and their natural enemies. In *Bark Beetles in North American Conifers*, ed. by J.B. Mitton and K.B. Sturgeon, pp. 140–82. University of Texas Press, Austin, TX.

Summary: The author looked at the complex of organisms that coevolved with the beetles and that affect their mortality and natality through parasitoidism, predation, and competition. A salient feature of bark beetle communities is the staggering number of organisms associated with them. Over seventy natural insect enemies and associates have been recorded for the western pine beetle and sixty species for the mountain pine beetle. Natural enemies inflict significant mortality of bark beetles. The author cited studies showing parasitism rates from as low as 4 percent to as high as 98 percent. Predation rates primarily by clerid beetles was also high in some instances, and western pine beetles were three times as abundant in logs from which clerids were excluded. Woodpeckers can consume 20 to 30 percent of beetles, and in a beetle epidemic these predators may consume up to 98 percent. They also cause additional mortality by removing bark, thereby drying out the bark beetles and allowing parasitoids and predators greater access. Spiders, mites, and disease also may play a role in bark beetle control.

DeMars, C.J. Jr., and B.H. Roettgering. 1982. *Forest Insect and Disease Leaflet 1: Western Pine Beetle*. USDA Forest Service, Pacific Southwest Region.

Summary: This publication focuses on *Dendroctonus brevicomis* identification, attack behavior, preferred hosts and range, natural controls, and treatment. Western pine beetle suppression projects often fail because the basic underlying cause for the population outbreak has not changed. Typically, if a habitat favorable to high levels of western pine beetle populations persists, suppression—by whatever means—will probably fail.

Dodds, K.J., C. Graber, and F.M. Stephen. 2001. Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). *Environmental Entomology* 30(1): 17–22.

Summary: Laboratory bioassays demonstrated that all sizes of larvae of the bark beetle competitor, the Carolina sawyer (*Monochamus carolinensis*), readily attack and feed on bark beetle larvae (*Ips calligraphus*). Density-dependent factors, such as predation, can impact bark beetle dynamics, particularly during outbreaks, and the consequences of this behavior may have important implications for bark beetle population dynamics.

Erbilgin, N., E.V. Nordheim, B.H. Aukema, and K.F. Raffa. 2002. Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: Within- and between-year associations with predators, competitors and habitat quality. *Environmental Entomology* 31(6): 1043–51.

Summary: Population levels of two *Ips* species and three predator populations (*Thanasimus dubius*, *Platysoma cylindrica*, and *P. parallelum*) were monitored. The number of *Ips* captured later in the season was lower in stands with higher numbers of predators early in the season. Likewise, higher predator numbers reduced *Ips* numbers in subsequent years.

Erbilgin, N., J.S. Powell, and K.F. Raffa. 2003. Effect of varying monoterpene concentrations on the response of *Ips pini* (Coleoptera: Scolytidae) to its aggregation pheromone: Implications for pest management and ecology of bark beetles. *Agricultural and Forest Entomology* 5: 269–74.

Summary: This paper describes research into the optimal chemical blend for attracting bark beetles while preventing the capture of natural enemies. The authors looked at varying levels of α-pinene and lanierone and the attraction to *Ips pini* and its predator *Thanasimus dubius*. The prey showed a parabolic attraction to increasing levels of α-pinene, with attraction low when the concentrations of α-pinene were at their lowest and highest levels. This is thought to indicate an overall preference for a middle stage of attack, when tree defenses are lowered (from preliminary attack) but before other predators arrive and before resources become scarce. The study indicates that separate lures are needed to effectively sample both predators and bark beetles.

Feeney, S.R., T.E. Kolb, W.W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson natural area. *Canadian Journal of Forest Resources* 28: 1295–306.

Summary: The study assessed the effects of restoration treatments on growth and leaf physiology in three treatments of pre-settlement-age ponderosa pines in northern Arizona: (1) thinned from below, (2) thinned and prescribed burned, and (3) control. Compared with the control, trees in both thinned stands had greater leaf nitrogen content, leaf toughness, and basal area increment. Resin flow was greater in the thinned and burned treatment than in either the thinned or control treatments. Increased resin flow may improve insect resistance in thinned-and-burned stands.

Ferrel, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. In *Sierra Nevada Ecosystem Project: Final Report to Congress, Vol. II.* Davis, CA. pp.1177–92.

Summary: The author reports on current conditions, key pests, biotic and other environmental factors affecting outbreaks, the effects on forest composition and structure, and mitigation methods. Sierra forests have high levels of mortality caused by bark beetles infesting trees stressed by drought, fire, overly dense stands, and pathogens. Past logging and fire exclusion are partially responsible for this situation. Mortality has been greatest in overly dense stands, especially those where past logging and/or fire exclusion practices have promoted tree species susceptible to insects, pathogens, fire, and drought. In California, drought is probably the most important predisposing factor. But overly dense stands, fire, logging, urbanization, air pollution, snow breakage, windthrow, and flooding can also weaken trees and cause them to become susceptible to pathogens and insects.

Fielding, N.J., and H.F. Evans. 1997. Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain. *Biocontrol News and Information* 18(2): 51–60.

Summary: The paper describes an integrated pest management strategy carried out by the UK Forestry Commission and the particular role of the predator *Rhizophagus grandis* in the biological control program. The authors contend that in continental Europe, *R. grandis* appears to exert significant population regulation to maintain populations of *D. micans* below economically damaging thresholds (with occasional exceptions, such as during consecutive drought years). Evidence from Britain shows a strong link between reduced pest populations and increased predator levels.

Filip, G.M., T.R. Torgersen, C.A. Parks, R.R. Mason, and B.E. Wickman. 1996. Insects and disease factors in the Blue Mountains. In *Search for a Solution: Sustaining the Land, People and Economy of the Blue Mountains*, ed. by R.G. Jaindl and T.M. Quigley, pp. 169–202. American Forests, Washington, D.C.

Summary: Many forest stands in the Blue Mountains of Oregon are experiencing poor health. Some of these stands are more susceptible to insect and disease outbreaks. There are many forest stands in the interior mountain West that have similar no-fire and overstocking issues and yet appear to be in relatively good health. Why? The answer may involve the population dynamics of the forest insects, disease pathogens, and their natural enemies. Populations of insects and pathogens in most forest ecosystems are kept in check by their natural predators and by environmental factors such as wildfire and climate. Removal of downed wood and snags eliminates the habitats needed to maintain populations of generalist insects and pathogen predators that control pest outbreaks.

Finke, D.L., and R.F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. *Ecology* 83(3): 643–52.

Summary: The authors conducted research into habitat complexity, which they found creates critical habitat for predators and mediates intraguild predation, thereby enhancing the effects of predators on their main prey.

Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKee, and T.A. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. In *Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems*, ed. by D.A. Perry, pp. 82–97. Timber Press, Portland, OR.

Summary: Disease and insect problems may be worse in managed stands than in natural stands. The authors suggest that old-growth forests have greater diversity of insect predators, which may in turn limit pest insect populations. They also suggest that damage by herbivorous insects could increase as the area of old-growth forests diminishes.

Fuchs, M. 1999. *The Ecological Role of the Mountain Pine Beetle (*Dendroctonus ponderosae*): A Description of Research from the Literature*. Prepared by Foxtree Ecological Consulting for British Columbia Parks Service, Victoria, BC.

Summary: A summary of research reported in the literature investigating the ecological role of the mountain pine beetle, as well as ideas about the beetle's ecological role from descriptive literature. Numerous authors have reiterated the assertion that the mountain pine beetle has probably been an integral part of lodgepole pine ecosystems almost as long as the ecosystems have existed, and it is universally accepted that mountain pine beetle epidemics play an integral role in the structure and dynamics of lodgepole pine ecosystems. Outbreaks accelerate forest succession to other tree species in some areas, as well as create the conditions for stand-replacing fires that maintain the dominance of lodgepole pines. In the absence of fire, the effect of mountain pine beetles on forest succession depends on the degree of mortality, the successional role of pine at a given location, and the presence and size of later successional species.

Furniss, R.L., and V.M. Carolin. 1977. *Western Forest Insects.* USDA Forest Service Misc. Pub. 1339, Washington, D.C.

Summary: A comprehensive list of the *Ips* species of the western U.S. with morphological characteristics, general distribution, and gallery identification aids. Since outbreaks in standing, healthy trees are sporadic and of short duration, the application of direct control measures seldom contributes much to reducing damage. Control efforts should be directed toward reducing any slash through piling and burning or spreading in the sun to dry. The authors suggest that the removal of windthrown or storm-damaged trees will lessen *Ips* outbreaks, but do not cite any studies to support this. They considered both tree resistance and natural enemies to be important factors in the subsidence of Douglas-fir beetle outbreaks.

Gilbert, M., and J. Grégoire. 2003. Site condition and predation influence a bark beetle's success: A spatially realistic approach. *Agricultural and Forest Entomology* 5: 87–96.

Summary: Field surveys of a spruce stand in France were carried out for several abundant populations of a bark beetle (*Dendroctonus micans*) and a major predator (*Rhizophagus grandis*). The predator populations persisted in the same locations where they were released, and their effects on bark beetles reached a climax six to ten years after they were released. Three strong trends were exhibited in the predator vs. prey association between these two species: 1) there was a strong correlation in spatial structure between predator and prey at the stand level, 2) distribution of prey (and eventually predators) was strongly correlated with landscape and spatial structure, particularly steep slopes and southern-facing slopes (presumably because of variable water stress), and 3) bark beetle attack density was significantly reduced in areas were predators had been released six to eight years earlier.

Goheen, D.J., and E.M. Hansen. 1993. Effects of pathogens and bark beetles on forests. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 175–96. Academic Press, San Diego, CA.

Summary: Pathogenic fungi and bark beetles are important components of most coniferous forest ecosystems. The authors address the varied roles that root pathogens and bark beetles play in western coniferous forests. Although these organisms may lead to tree death, they may also improve soil fertility and growing conditions for surrounding trees, as well as increase the non-economic diversity value of the forest by promoting non-host vegetation and creating new habitat for cavity-nesting birds and mammals.

Goyer, R.A., M.R. Wagner, and T.D. Schowalter. 1998. Current and proposed technologies for bark beetle management. *Journal of Forestry* 96 (12): 29–33.

Summary: This paper provides an overview of existing bark beetle management in forests in the Pacific Northwest, the South, and the Southwest. The authors propose thinning; removing dense understories; promoting predators and parasites; and using pheromones as tools for bark beetle management. They conclude that although bark beetles are destructive to timber management, from an ecological perspective their roles are to open the canopy, thin dense stands of stressed trees, and initiate decomposition. These roles likely enhance the health of surviving trees by reducing competition for water and nutrients; the beetles are in effect acting as nature's loggers. The authors point out that the window of opportunity for bark beetles to colonize fire-killed trees is relatively short. Trees killed by fire may not have sufficient bark to support the insects, and dead or injured trees that do not have enough bark are suitable for colonization for only a single year, after which the phloem is too dry for successful reproduction. They also point out that the historical records indicate that the western pine beetle, which prefers mature trees, was the major pest in Southwest forests, but because most of the mature forest have been replaced by high-density young forests, the troublesome bark beetles today are the pine engravers, *Ips* sp. Outbreaks of *Ips* pine engravers are initiated by stand-management activities, such as thinning (because they inhabit the slash), and environmental stress, such as drought.

Haack, R.A., and J.W. Byler. 1993. Insects and pathogens, regulators of forest ecosystems. *Journal of Forestry* 91(9): 32–7.

Summary: The authors contend that epidemics of forest insects and pathogens have always occurred. However, past management practices have probably increased the frequency, intensity, and extent of outbreaks. They also suggest that selective killing of susceptible trees tends to increase overall stand fitness. Through the process of natural selection, most native insects and pathogens reach a dynamic state of equilibrium with their hosts and natural enemies. Insects and other invertebrates contribute significantly to biomass decomposition, carbon cycling, nutrient cycling, and energy flow in forest ecosystems and are thus pivotal to maintaining soil fertility and long-term health. They are the primary regulators of nutrient and energy flow in critical ecosystem processes. The authors conclude that effective ecosystem management must integrate the functional roles of insect and microbial communities.

Haack, R.A., and G. Paiz-Schwartz. 1997. Bark beetle (Coleoptera: Scolytidae) outbreak in pine forests of the Sierra de las Minas Biosphere Reserve, Guatemala. *Entomological News* 108(1): 67–76.

Summary: A bark beetle outbreak in Guatemala led researchers to investigate the conditions that caused the phenomenon. They determined that the stands that were attacked were typically unmanaged, overstocked, water-stressed, over-grazed, and on steep slopes. Another factor that likely favored the current bark beetle outbreak was severe drought conditions. The authors suggest that natural enemies likely aided in the collapse of the outbreak.

Habeck, J.R. 1990. Old growth ponderosa pine-western larch forests in western Montana: Ecology and management. *Northwest Environmental Journal* 6(2): 271–92.

Summary: The author suggests that high-grading in these forests increases the relative abundance of shade-tolerant trees, which are more susceptible to insects.

Hadley, K.S., and T.T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Resources* 23: 479–91.

Summary: The authors examined the effects of historically documented outbreaks of western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) on succession, stand structure, and radial growth of host (Douglas-fir) and non-host species in Rocky Mountain National Park. They found that dense stands exhibit higher budworm-induced mortality, which hastens the natural thinning process and shifts dominance toward the non-host species. The insect outbreaks appear to result in short-term adjustments in stand structure and in competitive status of host and non-host trees, rather than in major, long-term shifts in relative dominance.

Hagle, S., and R. Schmitz. 1993. Managing root disease and bark beetles. In *Beetle-Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 209–28. Academic Press, New York, NY.

Summary: Root pathogens and bark beetles are natural components of conifer forest ecosystems. Soil damage resulting from logging with heavy equipment can increase the susceptibility of future forests to insects and disease. Repeated partial harvest—such as selection cutting, sanitation/salvage cutting, or even-aged management—increases both the frequency and severity of root disease in stands. These stands are in turn more susceptible to bark beetle outbreaks. Thinning can be effective in maintaining adequate growing space and resources to disrupt bark beetle spread, but the total volume removed by thinning can exceed the volume killed by beetles. Furthermore, accumulating evidence suggests that physical injury, soil compaction, and temporary stress due to changed environmental conditions may increase resources available for bark beetles and pathogens. Even under ideal growing conditions, vigorous stands are still beset with root pathogens and bark beetle epidemics. Changes are required to make forest management consistent with the ecological principles that govern forest health. This does not mean we should necessarily return stands to the conditions that existed prior to Euro-American settlement, although a management emphasis on maintaining healthy forests would result in a significant shift toward those conditions.

Hedgren, P.O., L.M. Schroeder, and J. Weslien. 2003. Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. *Agricultural and Forest Entomology* 5: 67–74.

Summary: A study in Sweden on edges of stands of clearcut spruce tested whether wind-felled trees at the sites would act as breeding locations for spruce bark beetles (*Ips typographus*). Zero, one, and five cut trees colonized by *I. typographus* were left at clear-cut edges. Edges with naturally wind-felled trees were also included. During the following two summers, the number of killed trees did not differ between edges with and without felled trees. The authors found that felled trees act as “focal points” for beetle attacks; however, several wind-felled trees can remain without significantly increasing the threat of an outbreak. The number of killed trees per kilometer of edge increased with edge length. One possible mechanism behind such a pattern is that, on a landscape-scale, long edges collect and arrest more flying individuals than shorter ones. Therefore, longer edges will increase the probability of recruiting the number of beetles required to overcome the defenses of living trees.

Hessburg, P.F., R.G. Mitchell, and G.M. Filip. 1994. *Historical and Current Roles of Insects and Pathogens in Eastern Oregon and Washington Forested Landscapes*. USDA Forest Service General Technical Report PNW-GTR-327.

Summary: The paper examines, by climax conifer series, the historic and current roles of insects and pathogens. The authors conclude that all forests have been altered to some degree by a century of resource management (especially selective harvest) and fire protection. The greatest changes in vegetation, insect, and pathogen response have occurred in the low- and middle-elevation grand fir/Douglas-fir, lodgepole pine, and ponderosa pine climax forests. They conclude that the difference between historic and current conditions is the scale of the interaction between insects, pathogens, and their hosts in both time and space. Although large insect outbreaks occurred before European settlement, the landscape patterns of vegetation ensured that most disturbances were brief and spatially confined. Some insects now appear to operate nearly continuously over entire landscapes. The paper specifically discusses western spruce budworm, Douglas-fir tussock moth, Douglas-fir beetle, pine bark beetles, fir engraver, and spruce beetle.

Hindmarch, T.D., and M.L. Reid. 2001. Forest thinning affects reproduction in pine engravers (Coleoptera: Scolytidae) breeding in felled lodgepole pine trees. *Environmental Entomology* 30(5): 919–24.

Summary: A trial was carried out in mature lodgepole pine (*Pinus contorta*) stands in Alberta. Half of the treatments were in stands that were thinned. Pine engraver beetles (*Ips pini*) in the thinned stands exhibited a higher attraction rate of mates by males, while females had longer egg galleries, more eggs per gallery, and higher egg densities. Warmer temperatures in thinned stands also contributed to a higher reproduction rate. The number of males and females setting on logs was also higher in thinned stands. Ultimately, the authors suggest caution in using thinning to control bark beetles, as geographic and climactic variables may alter the effect.

Holsten, E.H., R.A Werner, and R.L. DeVelice. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. *Environmental Entomology* 24(6): 1539–47.

Summary: The authors looked at the impact of a spruce beetle outbreak on Lutz spruce in Alaska. They noted that forest structure changed with decreased tree density, but tree composition remained essentially the same. They noted a decrease in understory plant diversity in beetle-killed but unburned sites. Sites that were beetle-killed, followed by those with controlled burns, had higher overall understory plant diversity. They also noted that the surviving trees showed increased radial growth as a result of increased growing space and implied that these fast-growing trees may reduce stand susceptibility to future infestations by spruce beetles, at least in the short term.

Huber, D.P.W., and J.H. Borden. 2001. Protection of lodgepole pines from mass attack by mountain pine beetle, *Dendroctonus ponderosae*, with nonhost angiosperm volatiles and verbenone. *Entomologia Experimentalis et Applicata* 92: 131–41.

Summary: A number of angiosperm nonhost volatiles and green leaf volatiles were tested alone and as supplements to the anti-aggregation pheromone verbenone for their ability to disrupt attack by mountain pine beetle on lodgepole pine. Placing devices emitting nonhost volatiles and green leaf volatiles often caused bark beetles to avoid marked trees. Several blends showed promise in mediating bark beetle communication. The results show that it is possible to protect single, susceptible lodgepole pine trees from attack by mountain pine beetle by utilizing various combinations of nonhost- and beetle-derived semiochemicals.

Hughes, J., and R. Drever. 2001. *Salvaging Solutions: Science-Based Management of British Columbia's Pine Beetle Outbreak*. Report commissioned by The David Suzuki Foundation, Vancouver, BC.

Summary: This report—funded by The David Suzuki Foundation, The Sierra Legal Defense Fund, and Canadian Parks and Wilderness Society (BC Chapter)—focuses on statistically supported control measures (or lack thereof) for pine beetles in British Columbia. The report concludes that bark beetles are the second-biggest source of natural disturbance after fire and that protected areas must remained unlogged, even in light of an outbreak. Additionally, 1) bark beetles are native species and natural and important agents of renewal and succession in forests, 2) management interventions have never before controlled a large outbreak, 3) sanitation and salvage clearcutting differ from natural disturbance in their effects and tend to decrease habitat complexity and diversity, 4) logging and sanitation harvest can increase future susceptibility, 5) logging after a natural disturbance can cause disturbance outside the natural range of variability, 6) the legacy value of the snags and coarse woody debris may outweigh the economic value of any timber recovered, and 7) basic questions about bark beetle ecology still need to be answered, despite nearly one hundred years of management experience.

Citing several sources, the authors assert that the weight of opinion seems to be that most control efforts to date have had little effect on the final size of outbreaks, although they may have slowed beetle progress and prolonged outbreaks in some cases. They also assert, based on models of the population dynamics of mountain pine beetles and other insects, that control of outbreaks is theoretically possible but would require treatment of almost all infected trees.

Large-scale efforts for beetle control are economically and ecologically expensive, and the uncertain benefits of control efforts should be weighed carefully against their costs. Since future outbreaks are inevitable, forest managers should include realistic estimates of beetle damage on projected long-term timber supply.

Johnson, C.G., Jr., R.R. Clausnitzer, P.J. Mehringer, and C.D. Oliver. 1994. *Biotic and Abiotic Processes of Eastside Ecosystems: The Effects of Management on Plant and Community Ecology, and on Stand and Landscape Vegetation Dynamics*. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-322.

Summary: The authors point out that even in areas where insect outbreaks occur, natural recovery is often relatively rapid. Many forests of the Blue Mountains that were hard hit in the early 1990s by large outbreaks of western spruce budworm and Douglas-fir tussock moth have largely recovered.

Joseph, G., R.G. Kelsey, R.W. Peck, and C.G. Niwa. 2001. Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. *Journal of Chemical Ecology* 27(4): 697–715.

Summary: The authors reported results of an experiment with traps baited with pheromone, 4-allylanisole (4AA), and ethanol and their effectiveness at capturing various scolytids and predators. If ethanol accumulates and 4AA declines in severely stressed pine trees, the trees are likely to be more susceptible to attack by secondary bark beetles than are healthy trees. 4-allylanisole may have some utility for managing the behavior of secondary bark beetles sensitive to this compound.

Kelsey, R.G., and G. Joseph. 2001. Attraction of *Scolytus unispinosus* bark beetles to ethanol in water-stressed Douglas-fir branches. *Forest Ecology and Management* 144: 229–38.

Summary: The authors reported that needles and woody tissue from water-stressed Douglas-fir branches exhibited a higher concentration of ethanol, which functioned as a primary host attractant for *Scolytus unispinosus*. The authors hypothesize that ethanol functions as a primary attractant for *S. ventralis* as well, since no aggregation pheromone has been discovered for either species. Water stress increases ethanol concentration, which may act as a primary attractant for this bark beetle. Components of atmospheric pollutants also appear to increase ethanol levels in trees that take them up, leading to a higher number of attacks on unstressed trees.

Klein, W.H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 148–58. University of Idaho, Pullman, WA.

Summary: The author traces mountain pine beetle epidemics from beginning to end and details control efforts that employed a variety of methods. More than 30,000 infested ponderosa pines and 20,000 infested lodgepole pines were treated in 1910 and 1911 on the Wallowa-Whitman National Forest in Oregon. The treatments included felling and peeling, felling and scoring the top, and felling and burning. Chemical methods were employed in the 1940s and 1950s. Thousands of acres of DDT, and other toxic chemicals such as lindane were used in control attempts across the inter-mountain West. The author points to one drastic approach called Operation Pushover. More than 1,800 acres of lodgepole pine on the Wasatch National Forest were literally mowed down by heavy tractors linked together, and the surrounding stands were sprayed with chemicals. In spite of these myriad control attempts, mountain pine beetle outbreaks occurred with increasing frequency and even more damaging results. The author suggests that doing nothing and letting infestations run their course may be a viable option.

Kolb, T.E., K.M. Holmberg, M.R. Wagner, and J.E. Stone. 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiology* 18: 375–81.

Summary: The authors compared foliar physiology and two measurements of tree resistance to insect attack among ponderosa pines growing in thinned stands in northern Arizona. The two mechanisms of tree resistance that were assessed were resin production in response to wounding (a measure to determine success of bark beetles) and foliar toughness (a measure of success of foliar-feeding insects). They found that trees in stands that were heavily thinned (low stand basal area) had thicker phloem and higher resin production than stands with high stand basal area but foliar toughness differed significantly on only three of the seven days sampled. They conclude that trees in the high-basal-area stands are more stressed and therefore have lower defensive capabilities against insect attack than trees in low-basal-area stands.

Komonen, A. 2003. Hotspots of insect diversity in boreal forests. *Conservation Biology* 17(4): 976–81.

Summary: A research article on insect biodiversity and the detrimental effects of logging. The author determines that mass annihilation of wood-decaying macrofungi and insect microhabitats from logging has a hugely detrimental effect on arthropod diversity.

Koplin, J.R., and P.H. Baldwin. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. *The American Midland Naturalist* 83: 510–15.

Summary: This study looked at predation by northern three-toed and hairy woodpeckers on the spruce beetle in northern Colorado. They found that the woodpeckers consumed up to 26 percent of the brood of the endemic population of beetles. Citing other studies, the authors contend that densities of broods of epidemic populations of spruce beetle are reduced by between 45 and 98 percent by woodpecker predation. They attribute greater mortality during epidemics to an influx of woodpeckers and to more beetles in standing trees that woodpeckers can feed on in winter.

Kovacic, D.A., M.I. Dyer, and A.T. Cringan. 1985. Understory biomass in ponderosa pine following mountain pine beetle infestation. *Forest Ecology and Management* 13: 53–67.

Summary: Understory herbaceous biomass was estimated in ponderosa pine stands with recovery ages ranging from zero to ten years after attack by mountain pine beetle. Total biomass peaked around five years after pine beetle infestation. Herbaceous biomass was fifty to one hundred times as great in ponderosa stands five years after mountain pine beetle infestation than in uninfested stands. Biomass gradually declined through ten years after infestation; however, understory biomass remained considerably higher than those in non-infested stands. The authors estimated that it is possible that levels of wildlife habitat will remain elevated above pre-infestation levels for ten to fifteen years following beetle infestation. Although the standing-tree biomass may be reduced at a site, the losses may be balanced by increased forage and natural thinning effects, which may improve not only forage quality but also timber and site quality in the stands.

Kühnholz, S., J.H. Borden, and A. Uzunovic. 2001. Secondary ambrosia beetles in apparently healthy trees: Adaptations, potential causes and suggested research. *Integrated Pest Management Reviews* 6: 209–19.

Summary: Several species of ambrosia beetles (Platypodidae and Scolytinae) that normally inhabit only dying or weakened trees—or after other, more aggressive species of beetles have inhabited a host—are beginning to attack apparently healthy trees. The most likely causes include: 1) early flight (before trees have recovered fully), possibly associated with climate change, 2) possibility of crossover to another fungal strain on dead tissue of living trees, 3) potentially pathogenic fungi that have hybridized with exotic strains, 4) completely new strains of fungi establishing, and 5) a complex chemical ecology that allows secondary ambrosia beetles to detect and colonize trees that may temporarily appear to be stressed and suitable. Further research is suggested.

Larsson, S., R. Oren, R.H. Waring, and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science* 29: 395–402.

Summary: The authors examined the relationship between tree vigor and susceptibility to mountain pine beetles in ponderosa pines in central Oregon. Overall, low-vigor trees were more often attacked by beetles than high-vigor trees. However, variation in the percentage of trees attacked was considerable on plots with similar vigors, especially at low and intermediate values. The variation could not be correlated with vigor, basal area, leaf area, or number of trees. Considerable variation in attacks was also found among control plots, seemingly without any correlation to stand characteristics.

Lattin, J.D. 1993. Arthropod diversity and conservation in old growth Northwest forests. *American Zoology* 33: 578–87.

Summary: A single old-growth forest in Oregon contains at least 3,400 species of arthropods, which collectively contribute to ecosystem function in ways that are just now being elucidated.

Laidlaw, W.G., B.G. Prenzel, M.L. Reid, S. Fabris, and H. Wieser. 2003. Comparison of the efficacy of pheromone-baited traps, pheromone-baited trees, and felled trees for the control of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Environmental Entomology* 32(3): 477–83.

Summary: This study tested the efficacy of several treatments for capturing dispersing/mating adults of the Douglas-fir beetle. The most effective method was the use of a synthetic attractant pheromone (frontalin) in conjunction with funnel traps located around the dispersing population. Using the trap-tree method resulted in spill-over into adjacent stands, as trees became saturated after a certain beetle density was reached. Traps, however, were able to capture over twice as many beetles. A single trap was determined to be as effective as three to four felled/removed trees, and much more cost effective. Trapping a larger proportion of males limited the mating success of the females of this monogamous species.

Lehmkuhl, J.F., P.F. Hessburg, R.L. Everett, M.H. Huff, and R.D. Ottmar. 1994. *Historical and Current Forest Landscapes of Eastern Oregon and Washington. Part 1: Vegetation Pattern and Insect and Disease Hazards*. USDA Forest Service General Technical Report PNW-GTR-328, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Summary: The authors used a series of historic and current photographs to analyze historic and current vegetation composition and structure in forty-nine sample watersheds within six basins in eastern Oregon and Washington. They concluded that the forests became more dense in vertical and horizontal canopy structures as understory cover increased with the regeneration of mostly shade-tolerant species. The distribution of age classes and structure has changed, with smaller areas of early-seral and old-forest stages present today.

Lindenmayer, D.B., D.R. Foster, J.F. Franklin, M.L. Hunter, R.F. Noss, F.A. Schmiegelow, and D. Perry. 2004. Salvage harvesting policies after natural disturbance. *Science* 303: 1303.

Summary: This study focused on the effects of "fixing" ecosystems and salvaging tree value after large disturbances. The main focus was on wildfires; however, bark beetles are also natural disturbance agents. The authors concluded that "disturbances are key ecosystem processes, rather than ecological disasters that require human repair." Salvage harvesting undermines many of the ecological benefits of disturbances. It also leads to a greater threat of future fire, the removal of critical habitat for many forest-dwelling species, and the impairment of ecosystem recovery. In addition, two major disturbances in rapid succession (such as fire, then harvesting) can be devastating to many species.

Lindgren, B.S., and K.J. Lewis. 1997. The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study. In *Proceedings: Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests*, ed. by J.C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, and S.M. Salom, pp. 122–30. USDA Forest Service General Technical Report NE-236.

Summary: The authors assessed the historical natural impact of spruce beetle and other forest-health agents on stands and landscape-level ecological processes. This paper presents some preliminary findings from the study. Spruce beetle outbreaks act as species-specific "high grading" agents, removing mostly large trees. Affected stands remain dominated by spruce, apparently due to this species' lower susceptibility or higher tolerance to stem and root decay than subalpine fir's.

Lindgren, B.S., and D.R. Miller. 2002. Effect of verbenone on attraction of predatory and woodboring beetles (Coleoptera) to kairomones in lodgepole pine forests. *Environmental Entomology* 31(5): 766–73.

Summary: Experiments tested the effect of the synthetic anti-aggregant verbenone on predators. The research was carried out in mature lodgepole pine in British Columbia. Traps were baited with various synthetic kairomones/pheromone blends known to attract members of the bark beetle guild and their beetle predators (primarily Cleridae, Colydiidae, and Tenebrionidae). Catches of several species of bark beetle predators shifted downward at a rate inversely proportional to the release rates of verbenone. In light of the greater capture rates for a few predators and parasitoids of mature bark beetles with higher concentrations of verbenone, the authors hypothesize that verbenone keeps away those predators that specialize on larval and pupal bark beetles, probably because it is indicative of a late-stage attack.

Logan, J.A., and B.J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28(6): 924–34.

Summary: Using a model approach, the authors demonstrated the potential for the movement of mountain pine beetle populations to higher elevations and latitudes under warming climate. In one case, they found that warming by just 2.5 degrees Celsius was sufficient to convert an unsuitable habitat into a suitable one. Similarly, increasing temperature by the same amount resulted in the phenological disruption of a previously favorable habitat.

Logan, J.A., and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47(3): 160–72.

Summary: Using a modeling approach at a specific site in Idaho, the authors project that the mountain pine beetle may expand its range both to higher elevations and to higher latitudes as the climate warms. This expansion has potentially serious implications for high-elevation five-needle pines, such as whitebark pine and bristlecone pine, which have not evolved with mountain pine beetle. The authors point out that, unlike the situation with exotic species, it seems reasonable to expect that conditions that become favorable for the mountain pine beetle will simultaneously become more favorable to the beetle's biotic associates, such as predators and parasites.

Lombardero, M.J., M.P. Ayres, R.W. Hofstetter, J.C. Moser, and K.D. Lepzig. 2003. Strong indirect interactions of *Tarsonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Oikos* 102: 243–52.

Summary: This research investigated the tetratrophic interaction between host trees, bark beetles, fungal symbionts, and phoretic mites. The experiments found an interesting dynamic in the population structure and number of bark beetles in response to the addition of a fungal competitor (*Ophistoma minus*) to mutualistic bark beetle fungi. Also, *O. minus* is an antagonist to bark beetle larvae and can cause 100 percent mortality in some bark beetle broods. This may have very serious effects on bark beetle species that have mutualistic fungi populations.

Lovett, G.M., L.M. Christenson, P.M. Groffman, C.G. Jones, J.E. Hart, and M.J. Mitchell. 2002. Insect defoliation and nitrogen cycling in forests. *BioScience* 52(4): 335–41.

Summary: Researchers studied the fate of nitrogen consumed by gypsy moth caterpillars (*Lymantria dispar*) eating foliage and depositing frass on the forest floor. Contrary to conventional wisdom, the researchers found that the nitrogen in the frass did not wash away or leach into the groundwater. Nitrogen from frass was more likely to stay in the forest substrate as available nitrogen.

Lundquist, J.E. 1995. Pest interactions and canopy gaps in ponderosa pine stands in the Black Hills, South Dakota, USA. *Forest Ecology and Management* 74: 37–48.

Summary: Coarse-woody-debris composition and gap frequency, size, and cause were assessed in three stands with different management histories. A qualitative model was developed that suggests that management activity 1) diminishes pest-caused structural diversity in the forest ecosystem, 2) decreases functional diversity associated with interacting diseases, insects, and other disturbance agents, and 3) alters the abundance and decomposition of dead wood.

Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences and control. *Issues In Ecology No. 5*. Ecological Society of America, Washington, D.C.

Summary: In the current era of trans-continental travel and commerce, humans are constantly introducing biota to locations outside their native range. While many immigrant species fail to establish, a certain number do. Some of those can, or already have had, severe effects on the integrity of the communities and ecosystems they invade. While it is next to impossible to identify likely new invaders before the fact, identifiable factors that facilitate the successful founding of invasive species include: escape from predators, parasites, or diseases; vacant niches; and human-caused disturbance.

Maloney, P.E., and D.M. Rizzo. 2002. Pathogens and insects in a pristine forest ecosystem: The Sierra San Pedro Mártir, Baja, Mexico. *Canadian Journal of Forest Research* 32: 448–57.

Summary: A large area of "healthy" forest dominated by pines and white fir was surveyed for mortality and cause of mortality. Percent cumulative mortality ranged from 2 percent to 24 percent, of which 78 percent of observed mortality was attributable to bark beetles and pathogens, although percent mortality varied by tree species. Insects and disease, along with fire, exhibited a strong influence over stand composition and regeneration. The authors concluded that the relative importance of fire and pest organisms appears to be different between this forest and similar mixed-conifer forests of the Sierra Nevada. While fire is mainly responsible for subcanopy mortality in the Sierra San Pedro Mártir, insects and pathogens are important for overstory mortality. They conclude that in fire-suppressed forests, insects and diseases, in association with periodic drought events, have largely replaced fire as the main stand-thinning agents in the Sierra Nevada. Insects, diseases, and fire maintain tree diversity and evenness in the Sierra San Pedro Mártir.

Marsden, M.A., M.M. Furniss, and L.N. Kline. 1981. *Modeling Seasonal Abundance Douglas-fir Beetle in Relation to Entomophagous Insects and Location in Trees*. USDA Forest Service General Technical Report INT-111. Intermountain Forest and Range Experiment Station, Ogden, UT.

Summary: The authors use regression analysis and the logistic function to relate quantitatively the mortality of Douglas-fir beetle population density to the number of predators and parasites. The model may be useful in demonstrating the importance of natural enemies. For example, the average mortality of Douglas-fir beetle progeny after egg-hatch in successfully attacked trees was 58 percent.

Martikainen, P., J. Siitonen, L. Kaila, and P. Punttila. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. *Journal of Applied Entomology* 120: 257–64.

Summary: The authors compared population levels of bark beetles in non-epidemic conditions between intensively managed forests in Finland and in less-intensively managed forests across the border in Russia. There was little difference in the overall numbers of bark beetle species and individuals at the two sites, despite clear differences in forest structure. They conclude that foresters are often concerned that areas of natural forest may harbor large numbers of pests and act as dispersal centers to other areas; however, the available information does not support this hypothesis.

Martikainen, P., J. Siitonen, L. Kaila, P. Punttila, and J. Rauh. 1999. Bark beetles (Coleoptera: Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *Forest Ecology and Management* 116: 233–45.

Summary: The authors compared bark beetles and associated beetle species among Norway spruce that was mature managed (age between ninety-five and 120 years, cut stumps abundant), overmature managed (over 120 years, cut stumps abundant), and old growth (over 160 years, no or few stumps present). The study showed that the assemblages of both bark beetles and their associates are richer in old-growth than in mature-managed stands. They conclude that the richer complex of secondary bark beetles and the natural enemies in old-growth forests could mean that competition, predation, and parasitism control populations of primary bark beetles more efficiently in old-growth forests, and that primary bark beetles may stay at non-epidemic levels.

Matsuoka, S.M., C.M. Handel, and D.R. Ruthrauff. 2001. Densities of breeding birds and changes in vegetation in an Alaskan boreal forest following a massive disturbance by spruce beetles. *Canadian Journal of Zoology* 79: 1678–90.

Summary: Researchers studied ecological changes following an outbreak of spruce beetles (*Dendroctonus rufipennis*) in spruce stands. The beetles tended to ignore black spruce in favor of white spruce, thereby changing the stand characteristics. Spruce beetle selectively killed the larger white spruce, resulting in mortality of 71 percent (± 9 percent) for large trees, 42 percent (± 11 percent) of medium-sized trees, 7 percent (± 3 percent) for small trees, compared with 1.1 percent (± 0.7 percent) for black spruce of all sizes. By differentially altering the forest patches, this widespread outbreak of spruce beetles served to maintain a mosaic-like structure of the forest types and successional stages in the region. High densities of understory plants (most notably alders and crowberry) accompanied a high mortality level of mature spruce. Contrary to predictions, forest stands that suffered a high level of spruce mortality did not support lower densities of tree-nesting birds (with the exception of the ruby-crowned kinglet) compared to stands that had suffered low mortalities; nor were densities of woodpeckers higher in areas with high densities of beetle-killed spruce. Even species strongly associated with mature white spruce, such as boreal chickadees and varied thrushes, did not decline with increases in spruce mortality.

Mattson, W.J., and N.D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515–22.

Summary: The authors review evidence on primary production in forests. They contend that insects act as regulators of primary production and nutrient cycling, and thus they perform a vital function in ecosystem dynamics. The authors show that low to moderate levels of herbivory do not harm plants and contend that herbivory by insects can benefit both individual plants and plant communities. They point to studies that demonstrate that caterpillars that defoliate trees in periodic outbreaks can harm trees in some years and help them in others. Outbreaks usually begin in stands that are in poor condition, and thus herbivory can lead to healthier systems.

Mattson, W.J., and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37(2): 110–18.

Summary: The authors maintain that water stress alters trees and their thermal environment so that stressed trees become progressively more susceptible (through erosion of their defenses) and suitable (through enhancement of certain constitutive traits) to their adapted consumers, allowing the plant-eating insects to achieve faster growth, higher rates of survival, and more successful reproduction. But the authors note that experimental tests of this subject are lacking.

McCullough, D.G., R.A. Werner, and D. Neumann. 1998. Fire and insects in northern boreal forest ecosystems of North America. *Annual Review of Entomology* 43: 107–27.

Summary: This paper reviews the literature on the effects of fire-insect interactions on ecological succession; the use of prescribed fire for insect control; and the effects of fire on insect diversity in northern and boreal forests in North America. Fire and insects are critical, intrinsic natural disturbance agents that have been shown to interact synergistically to affect forest succession, nutrient cycling, floral composition, and species diversity. They contend that fire suppression, sometimes in combination with logging practices, has resulted in profound changes in forest species composition and structure. Associated with these changes is an increased vulnerability of forest stands to damage during insect outbreaks.

McDowell, N., J.R. Brooks, S.A. Fitzgerald, and B.J. Bond. 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant, Cell and Environment* 26: 631–44.

Summary: This study showed that the growth and physiology of old ponderosa pine trees are responsive to stand-density reductions. The authors infer that this may be a mechanism that can be used to provide some resistance to colonization by mountain pine beetle.

McHugh, C.W., T.E. Kolb, and J.L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology* 32(3): 510–22.

Summary: This study examined the interaction between fire in ponderosa pine (*Pinus ponderosa*) stands and bark beetle ecology. Several species of *Ips* and *Dendroctonus* were surveyed for, as well as wood borers (Buprestidae and Cerambycidae). Overall, the colonizers of the fire-damaged trees were (from most populous to the least): wood borers (*Ips* spp.), red turpentine beetle (*D. valens*), western pine beetle (*D. brevicomis*), roundhead pine beetle (*D. adjunctus*), and mountain pine beetle (*D. ponderosae*). Three types of fire were examined (fall prescribed burn, spring wildfire, and summer wildfire), each which resulted in slightly different total crown death (TCD) rates. The fall burn had the lowest TCD, while the spring burn had the highest. The authors point out that the experiment was carried out during drought conditions, so tree host defenses were possibly at low levels. Mountain pine beetle showed no preference for fire-damaged trees. Western pine beetle is known to attack fire-damaged trees, and a nominal amount were found in the stands; however, the authors hypothesize that the population was not in an outbreak because there were no source populations near enough to the fire-damaged stands to take advantage of the potential new hosts. The roundheaded pine beetle showed little proclivity for entering fire-damaged trees. Red turpentine beetles attacked fire-damaged trees, but are not considered a serious cause of mortality (except in conjunction with other beetle attacks). Woodborers were the most common colonizers of fire-damaged trees but are not considered likely sources of tree mortality. Overall, the trees with the most crown damage were attacked by *Ips* and *Dendroctonus* species. This resulted in higher mortality for trees with greater TCD.

Mitchell, R.G. 1990. Effects of prescribed fire on insect pests. In *Natural and Prescribed Fire in Pacific Northwest Forests*, ed. by J.D. Walstad, S.R. Radosevich, and D.V. Sandberg, pp. 111–16. Oregon State University Press, Corvallis, OR.

Summary: A summary of the impact of prescribed fire on insect pests. The author states that fire has long been a significant ecological force in most forest ecosystems, and there is strong evidence that wildfire control policies (and in some cases logging) have greatly increased the problems presented by some well-known forest insect pests. No matter how carefully they are managed, prescribed fires sometimes become too hot and unintentionally scorch trees. In ponderosa pine, crown scorch can invite attack by bark beetles. The general conclusion of the article is that pest problems generated by prescribed burning are mostly trivial and ephemeral and usually can be avoided by careful planning.

Mitchell, R.G., and H.K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *Forest Science* 37(5): 1390–1408.

Summary: Five years of mountain pine beetle infestation on lodgepole pine in an early-outbreak situation were analyzed using generalized linear models. The analysis shows that large trees seem to be preferentially selected. Tree vigor proved to be only marginally significant in the colonization model and contributed very little to the probability of a tree being colonized.

Mitchell, R.G., R.H. Waring, and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* 29(1): 204–11.

Summary: Thinned and unthinned stands of lodgepole pine in eastern Oregon were evaluated to determine their vigor and susceptibility to attack by outbreak populations of the mountain pine beetle. Overall, thinning from below seemed to improve vigor of stands and reduced beetle attack. However, there was some variation in the percentage of trees attacked on plots with similar vigors. The vigor of one plot failed to respond to heavy thinning and suffered the same mortality experienced in the adjacent, unthinned plot. Also, one unthinned plot had very low mortality.

Muzika, R.M., and A.M. Liebhold. 2000. A critique of silvicultural approaches to managing defoliating insects in North America. *Agricultural and Forest Entomology* 2: 97–105.

Summary: A variety of silvicultural techniques have been suggested for managing forest-defoliating insects. The silvicultural objectives that the authors critiqued included minimizing defoliation or minimizing damage from defoliation. The authors suggest that the theoretical foundations of many approaches have been built upon observation and correlation, and very little reliable empirical evidence exists to support the objectives of silvicultural manipulations. They go on to state that the existing experimental data have yielded inconsistent results. They conclude that well-designed, long-term studies are needed to clarify the effect of silviculture on defoliators and their effect on forests.

Naeem, S., F.S. Chapin III, R. Costanza, P.R. Ehrlich, F.B. Golley, D.U. Hooper, J.H. Lawton, R.V. O'Neill, H.A. Mooney, O.E. Sala, A.J. Symstad, and D. Tilman. 1999. Biodiversity and ecosystem functioning: Maintaining natural life support processes. *Issues in Ecology No. 4*. Ecological Society of America, Washington, D.C.

Summary: Human modification to the living community in an ecosystem can alter ecological functions and life-support services that are vital to the well-being of human societies. Biodiversity in managed ecosystems is poor. Less biodiverse communities and ecosystems are more susceptible to adverse weather (such as drought) and exotic invaders, and have greatly reduced rates of biomass production and nutrient cycling.

Nebeker, T.E. 1989. Bark beetles, natural enemies, management selection interactions. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 71–80. Stephen F. Austin State University, Nacogdoches, TX.

Summary: Management tactics, such as salvage operations, remove many parasites and predators from the forest system. There is very little information, and no dedicated studies, on how thinning affects these natural enemies of bark beetles. The author points out that one major concern is that many options for bark beetle control have not been evaluated for their impact on natural enemies. Therefore, outbreaks could be prolonged because of a reduction in the effectiveness of natural enemies.

Negrón, J.F. 1997. Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico. *Canadian Journal of Forest Research* 27: 1936–45.

Summary: The author used classification trees and linear regression to build a model to predict probabilities of infestation and amount of mortality resulting from the roundheaded pine beetle, *Dendroctonus adjunctus*. The data suggest that stands infested by the roundheaded beetle exhibited poor growth during the five years before the onset of an outbreak. The presence of abundant host types and smaller-diameter trees were also important determinants of potential infestation.

Negrón, J.F. 1998. Probability of infestation and extent of mortality associated with Douglas-fir beetle in Colorado Front Range. *Forest Ecology and Management* 107: 71–85.

Summary: The author sampled infested and uninfested areas within Douglas-fir stands in the Colorado Front Range. The author suggests that Douglas-fir beetles attacked stands that contained a high percentage of basal area represented by Douglas-fir, high tree densities, and poor growth during the last five years prior to attack. Trees prone to attack within infested stands also exhibited reduced growth rates.

Negrón, J.F., J.A. Anhold, and A.S. Munson. 2001. Within-stand spatial distribution of tree mortality caused by the Douglas-fir beetle (Coleoptera: Scolytidae). *Environmental Entomology* 30(2): 215–24.

Summary: This research was undertaken in order to determine if predictions can be made as to which stands of Douglas-fir are susceptible to Douglas-fir beetle. Researchers found a correlation between basal area/growth rate and likelihood of attack. Their models indicate that increased stocking levels are correlated to increased mortality after bark beetle infestation.

Negrón, J.F., J.L. Wilson, and J.A. Anhold. 2000. Stand conditions associated with roundheaded pine beetle (Coleoptera: Scolytidae) infestations in Arizona and Utah. *Environmental Entomology* 29(1): 20–7.

Summary: The study correlated the occurrence of and mortality levels caused by roundheaded pine beetle (*Dendroctonus adjunctus*) with reduced growth rates in ponderosa pine (*Pinus ponderosa*) at both the stand and tree scale in Arizona and Utah. The results of the study suggest that the roundheaded pine beetles prefer stands and trees that exhibit poor growth. The growth rates were tied to high stocking densities.

Nowak, J.T., and C.W. Berisford. 2000. Effects of intensive forest management practices on insect infestation levels and loblolly pine growth. *Journal of Economic Entomology* 93(2): 336–41.

Summary: The study monitored the differences in growth and insect infestation levels related to management activities in loblolly pine. They report higher insect pests in plantation-style timber stands, particularly after intense management activities. Tip moth infestation levels fluctuated more in areas without competing vegetation. One possible reason is that the natural enemies of tip moths exert more consistent influence in areas with herbaceous weeds. They concluded that intensive management may disrupt the balance between common insect pests, such as the tip moth, and their natural enemies. Also, new pests such as coneworms may become more prevalent as standard management practices intensify.

Økland, B., and A. Berryman. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. *Agricultural and Forest Entomology* 6: 141–46.

Summary: The authors analyzed a time series of spruce bark beetles caught in pheromone traps from 1979 to 2000 in approximately one hundred localities throughout southeast Norway. They conclude that windfelling is probably an important driver for the dynamic of spruce bark beetle. They also conclude that drought may be a trigger for outbreaks of spruce bark beetles.

Økland, B., and O.N. Bjørnstad. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. *Population Ecology* 45: 213–19.

Summary: The article presents a spatio-temporal analysis of the population dynamics of *Ips typographus* based on pheromone trap data from southeast and mid-Norway in the post-epidemic period 1979–2002. The mean abundance of beetles declined linearly with latitude. In addition, the time-series means were higher in areas with high forest productivity and rocky soils predisposed to drought. Windfall was the external variable showing the most parallel pattern of correlation to the beetle dynamics. The authors suggest that large windfall events may be major instigators and synchronizers of beetle outbreaks.

Olsen, W.K., J.M. Schmid, and S.A. Mata. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *Forest Science* 42(3): 310–27.

Summary: The authors analyzed stand characteristics associated with mountain pine beetle within a 2.15-acre plot to determine characteristics most strongly correlated with beetle success. Mountain pine beetle-attacked trees generally occurred in groups or clusters. Maximum diameter was not different between infested and non-infested groups. This lack of association of beetle-infested groups with maximum diameter-at-breast-height in ponderosa pine clearly differs from previous studies that observed such an association in lodgepole pine. The groups of mountain pine beetle-attacked trees did not coincide with the highest basal areas, but did occur where basal areas were relatively high (150 to 250 square feet per acre).

Otvos, I.S. 1979. The effects of insectivorous bird activities in forest ecosystems: An evaluation. In *The Role of Insectivorous Birds in Forest Ecosystems*, ed. by J.G. Dickson, R.N. Conner, R.R. Fleet, J.A. Jackson, and J.C. Kroll, pp. 341–74. Academic Press, New York, NY.

Summary: A summary of studies that evaluate the impact of insectivorous birds on pest insects. Insectivorous birds play an important role in the population dynamics of many forest insects. Birds act as mortality agents and positively influence bark beetle parasites and predators by disturbing the bark, which creates increased access to the beetles.

Paine, T.D., and F.A. Baker. 1993. Abiotic and biotic predisposition. In *Beetle Pathogen Interactions in Conifer Forests*, ed. by T.D. Schowalter and G.M. Filip, pp. 61–73. Academic Press, San Diego, CA.

Summary: Healthy trees typically limit insect and pathogen activity through physical and chemical defenses. Storm damage, pollution, fungal diseases, soil compaction, and soil aeration can all lead to a greater susceptibility to bark beetles. Thinning is a common recommendation for relieving stresses due to competition for limited resources, and selectively reducing the number of trees in a stand can increase growth and resistance in remaining trees. However, thinning can increase the availability and susceptibility of decaying stem and root material for some bark beetles and pathogens. The process of thinning can wound remaining trees and injure roots, providing entry points for pathogens and ultimately reducing resistance to other organisms.

Parks, C.G. 1993. *The Influence of Induced Host Moisture Stress on the Growth and Development of Western Spruce Budworm and* Armillaria ostoyae *on Grand Fir Seedlings*. Ph.D. dissertation. Oregon State University.

Summary: The author evaluated the impact of water stress on western spruce budworm defoliation and *Armillaria* root-rot (the fungus *Armillaria ostoyae*). Western spruce budworm larvae that fed on water-stressed seedlings had higher survival rates, grew faster, and produced larger pupae than those that fed on well-watered seedlings. Foliage nutrient patterns and phenolic chemistry are implicated as the reason for this trend. The study also found that one and/or two years of defoliation did not appear to weaken the physiological condition of the seedlings. Conversely, water-stressed plants that were also defoliated produced more buds, had earlier bud phenology, contained reserves of carbohydrates, and had little *Armillaria*-caused mortality. The author suggests that, during drought, short-term defoliation may be beneficial to grand fir and its associated forest community by reducing the uptake of nutrients and water by budworm hosts, thereby liberating it to be used by non-hosts (e.g., ponderosa pine or larch) that are perhaps better adapted to periodic drought conditions. Also, the additive effects of simultaneously occurring *A. ostoyae* and western spruce budworm may not be as severe as conventionally believed.

Payer, D.C., and D.J. Harrison. 2000. Structural differences between forests regenerating following spruce budworm defoliation and clear-cut harvesting: Implications for marten. *Canadian Journal of Forest Research* 30(12): 1965–72.

Summary: The authors looked at the use of clearcuts and areas where spruce budworm has caused mortality in relation to the American marten. When establishing new territories, martens avoid clearcuts but do not avoid stands with a history of extensive tree mortality caused by eastern spruce budworm. Although live tree basal area was similar between stand types, the results showed that the vertical structure provided by large snags can offset the limited availability of live trees for the marten, particularly where coarse woody debris and understory vegetation are plentiful.

Peltonen, M. 1999. Windthrows and dead standing trees as bark beetle breeding material at forest-clearcut edge. *Scandinavian Journal of Forest Research* 14: 505–11.

Summary: The spatial distribution of windthrows and dead, standing trees, and the occurrence of two bark beetle species (*Ips typographus* and *Tomicus piniperda*), were studied at forest clearcut edges in Finland. There was no correlation between an increase in the number of killed trees per kilometer of forest edge and increased numbers of colonized, wind-felled trees. The results indicate the windthrows do not necessarily increase bark beetle-induced tree mortality under endemic conditions.

Percy, K.E., C.S. Awmack, R.L. Lindroth, M.E. Kubiske, B.J. Kopper, J.G. Isebrands, K.S. Pregitzer, G.R. Hendrey, R.E. Dickson, D.R. Zak, E. Oksanen, J. Sober, R. Harrington, and D.F. Karnosky. 2002. Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. *Nature* 420: 403–07.

Summary: Experimental manipulations using CO_2 and O_3 emitters of a stand consisting of trembling aspen, sugar maple, and paper birch in northern Wisconsin attempted to discern the effects of the compounds on herbivores and natural enemies. CO_2 and O_3, singly and in combination, affected productivity and physical and chemical defenses, which in turn affected insects and disease populations. The researchers conclude that the herbivores would proliferate in response to increased plant production/decreased plant health, and natural enemies would have difficulty tracking herbivore populations.

Perkins, D.L., and D.W. Roberts. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* 174: 495–510.

Summary: The authors developed a logistic regression model from reconstructed pre-epidemic and post-epidemic stand conditions from the widespread mountain pine beetle epidemic that occurred from 1909 to 1940. High basal area and high stand densities were positively correlated with attacked stands. The authors caution this model is limited to whitebark pine in central Idaho and requires verification with independent data from outside the region.

Peterman, R.M. 1978. The ecological role of mountain pine beetle in lodgepole pine forests. In *Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Symposium Co-Sponsored by National Science Foundation … et al., held at Washington State University, Pullman, Washington, April 25-27, 1978*, ed. by A.A. Berryman, G.D. Amman, and R.W. Stark, pp. 16–26. U.S. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID.

Summary: The author points out that the mountain pine beetle is a natural thinning agent of lodgepole pine. In this capacity, the bark beetle creates fuel for the fires that are so important for the reproduction of its host tree. Furthermore, the actions of the insect decreases the likelihood that dense lodgepole pine stands will be produced in the next generation. The author suggests that we change our view of the mountain pine beetle as a pest to thinking of it as a management tool. In some situations, it may be advantageous to permit outbreaks of mountain pine beetles to continue unhindered.

Pollet, J., and P.N. Omi. 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *International Journal of Wildland Fire* 11: 1–10.

Summary: Beetle-killed lodgepole pine (self-thinned to lower density) experienced significantly lower fire severity compared to adjacent, burned areas in the 3,400-hectare Robinson Fire that burned in Yellowstone National Park in 1994.

Radeloff, V.C., D.J. Mladenoff, and M.S. Boyce. 2000. The changing relation of landscape patterns and jack pine budworm populations during an outbreak. *Oikos* 90: 417–30.

Summary: Researchers studied the outbreak of jack pine budworm (*Choristoneura pinus pinus*) in northwest Wisconsin. They found statistically significant relationships between landscape pattern—namely the abundance of jack pine and jack pine stand edge in the landscape—and jack pine budworm populations. The most important finding suggests that the relationship between landscape patterns and jack pine changes over time during an outbreak. Stand edges contributed to budworm fitness early in the season by offering a large number of male pollen cones. However, the edges became a sink for budworms late in the season as predation increased.

Raffa, K.F., and A.A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53(1): 27–49.

Summary: The authors demonstrate the ability of healthy host trees to mask the effectiveness of pheromonal communication between beetles. Trees that are apparently healthy can mask pheromones in the abdomens and frass of colonizing beetles by using compounds in the resin flows. However, this relationship is inversely proportional to the number of beetles attacking a given tree.

Raffa, K.F., and A.A. Berryman. 1986. A mechanistic computer model of mountain pine beetle populations interacting with lodgepole pine stands and its implications for forest managers. *Forest Science* 32(3): 789–805.

Summary: The authors developed a computer model based on laboratory and field studies of mountain pine beetle interactions with lodgepole pine. The model, which used tree vigor as an important biological condition, shows that stand thinning seems to provide the most effective long-term protection from beetle outbreaks. Confidence in the model would be improved if data were available to test the predictions; unfortunately, there have been few long-term studies on the dynamics of mountain pine beetle populations.

Raffa, K.F., and A.A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: A basis for reciprocal adaptations? *The American Naturalist* 129(2): 234–62.

Summary: The authors examined the mountain pine beetle/lodgepole pine and the fir engraver/grand fir systems. They looked at the physiological, behavioral, and ecological aspects of conifer-bark beetle interactions and generalized the relationship between host properties and survival under natural conditions. Monoterpene concentration, monoterpene composition, oleoresin flow, and chance all play a role. The mountain pine beetle can overwhelm healthy lodgepole pine under certain circumstances, but the fir engraver is restricted to unhealthy trees. As even-aged stands mature, food supply increases and populations of bark beetles may become large enough to overwhelm the defenses of most trees. In the case of mixed-age stands, individual trees decline, producing a small but steady supply of susceptible hosts.

Raffa, K.F., and D.L. Dahlsten. 1995. Differential responses among natural enemies and prey to bark beetle pheromones. *Oecologia* 102: 17–23.

Summary: Recent evidence suggests that predators and parasites strongly influence the population dynamics of bark beetles. The authors conducted experiments with a transcontinentally distributed bark beetle, *Ips pini,* and demonstrated that the most abundant predators in California and Wisconsin were more attracted to prey from distant sources than to those of local sources. Conversely, local *I. pini* populations were most attractive to local conspecifics. Understanding the differences and similarities among predator, parasite, and prey responses to bark beetle pheromones could improve estimates of relative pest and natural enemy abundance, and reduce natural enemy mortality during semiochemical-based trap-outs.

Reeve, J.D. 1997. Predation and bark beetle dynamics. *Oecologia* 112: 48–54.

Summary: This study looked at the impact of predation in influencing bark beetle dynamics and population trends. The results indicate that adult clerid beetles (*Thanasimus dubius*) appear to be major natural predators of bark beetles. The author suggests that, under field conditions, *T. dubius* would slow the attack process. Because it diminishes the overall pool of adult beetles, the clerid beetle would also reduce the total number of infested trees. Predation by adult clerids could be an important source of mortality in systems, but these beetles might be overlooked because of their cryptic behavior. Combined with the effects of clerid larvae on the brood, predation may be a top-down force that is an important general component of bark beetle dynamics, along with the role of host-tree resistance.

Reeve, J.D., M.P. Ayres, and P.L. Lorio, Jr. 1995. Host suitability, predation and bark beetle population dynamics. In *Population Dynamics: New Approaches and Synthesis*, ed. by N. Cappuccino and P.W. Price, pp. 339–57. Academic Press, Inc., San Diego, CA.

Summary: The authors examined the hypothesis that outbreaks of the southern pine beetle are generated by factors that affect host tree suitability, especially water availability. They suggest that drought may increase or decrease suitability for bark beetles, depending on the initial water status of the trees and the severity of the drought. A surfeit of water may also render pines more suitable for bark beetles. They also reported preliminary results from research designed to quantify the potential effects of the clerid beetle, *Thanasimus dubius*, a predator. Their research showed that *T. dubius* adults at natural densities can kill up to 53 percent of the southern pine beetle adults attempting to colonize a tree. They believe that this is an underestimate of overall mortality, as *T. dubius* larvae feed on southern pine beetle larvae beneath the bark and it is hard to estimate their predation effect.

Reid, M.L., and T. Robb. 1999. Death of vigorous trees benefits bark beetles. *Oecologia* 120: 555–62.

Summary: The authors considered tree size and phloem thickness (indices of tree vigor) and recent growth rate (last year's growth increment, mean annual increment, basal area increment in the last five and ten years, and periodic growth ratio). They examined the relationship between these indices in three stands aged 60, 77, and 126 years. They found that phloem thickness, which was previously shown to have a strong positive effect on bark beetle reproduction, was only weakly associated with tree growth rate and inconsistently related to tree size. They also found that indices associated with tree vigor in recently felled trees best explained beetle reproductive performance and were positively related to parental male and female establishment on logs, female reproductive success, length of egg galleries, and proportion of eggs resulting in emerged offspring. The strong effect of tree vigor suggests that mortality of vigorous trees can contribute to increases in bark beetle populations, which could lead to outbreaks in living trees.

Romme, W.H., D.H. Knight, and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist* 127(4): 484–94.

Summary: This study examined the effects of beetle outbreaks on primary productivity in forests dominated by lodgepole pine in northeastern Wyoming. In ten stands affected by a major beetle outbreak, the authors measured the annual ring width from trees in the canopy, subcanopy, and understory from five years immediately preceding the outbreak and following the outbreak. Surviving trees in all strata grew more rapidly after the beetle outbreaks. Wood production was redistributed among canopy, subcanopy, and understory trees, and annual wood production per hectare usually returned to pre-attack levels or exceeded them within ten to fifteen years. They conclude that the beetle-pine system shows great resilience and the effects of beetles on primary productivity do not appear to be as severe as conventional wisdom maintains. Annual wood production returned quickly to previous levels in the stands, and associated ecological changes can be considered generally benign or even beneficial.

Ross, D.W., and G.E. Daterman. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. *Forest Science* 43(1): 65–70.

Summary: The authors placed multiple funnel traps baited with strong aggregation pheromone through three 259-hectare plots in northeastern Oregon during an outbreak of Douglas-fir beetle (*Dendroctonus pseudotsugae*). The study demonstrated that large numbers of dispersing beetles could be removed from the forest and that distribution of tree mortality might be controlled by using pheromone traps. However, they also trapped large numbers of the clerid predator *Thanasimus undatulus* and smaller numbers of two other bark beetle predators. Capturing these predators could negate the benefits of removing *D. pseudotsugae* from the environment.

Ross, D.W., K.E. Gibson, and G.E. Daterman. 2001. *Using MCH to Protect Trees and Stands from Douglas-fir Beetle Infestation*. USDA Forest Service Forest Health Technology Enterprise Team FHTET-2001-09.

Summary: The paper promotes a method of controlling bark beetles using Douglas-fir beetle anti-aggregation pheromone 3-methylcyclohex-2-en-1-one (MCH). MCH has now been registered by the EPA.

Ross, D.W., K.E. Gibson, R.W. Thier, and A.S. Munson. 1996. Optimal dose of an antiaggregation pheromone (3-methylcyclohex-2-en-1-one) for protecting live Douglas-fir from attack by *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 89(5): 1204–7.

Summary: The Douglas-fir beetle anti-aggregation pheromone 3-methylcyclohex-2-en-1-one (MCH) was previously shown to be effective in preventing the infestation of windthrown trees. The objective of this study was to identify the lowest effective dose of MCH for protecting live Douglas-fir from infestation by Douglas-fir beetle. Three doses of MCH were assessed, and all three doses resulted in similar and significant reductions in the number of Douglas-fir beetles collected in pheromone-baited funnel traps. The numbers of predators caught in the traps were unaffected by any of MCH doses. The differences in response of the bark beetles and predators suggest that beetles attacking trees within the MCH-treated area may be subject to higher levels of predation than would occur in the absence of MCH. The results demonstrate that MCH can effectively protect Douglas-fir from infestation by the Douglas-fir beetle.

Sánchez-Martínez, G., and M.R. Wagner. 2002. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *Forest Ecology and Management* 170: 145–60.

Summary: The authors studied the bark beetle guild in ponderosa pine forests of northern Arizona to explore whether species assemblages and relative abundance differ between managed and unmanaged stands. Four stand conditions were assessed: (1) unmanaged stands with high tree density, (2) thinned stands, (3) thinned and burned (with prescribed fire) stands, and (4) stands that had been burned by stand-replacing wildfires. Similar species assemblages occurred across all stand conditions independent of thinning and independent of the occurrence of fire. The study found no evidence to support the hypothesis that trees growing in dense stands are more colonized by bark beetles.

Santoro, A.E., M.J. Lombardero, M.P. Ayres, and J.J. Ruel. 2001. Interactions between fire and bark beetles in an old growth pine forest. *Forest Ecology and Management* 144: 245–54.

Summary: Researchers examined what effects fire (including prescribed burns) had on the functional and numeric responses of bark beetle populations in mature red pines (*Pinus resinosa*) in Minnesota. Following a prescribed burn, the local abundance of *Ips pini* increased twofold, then decreased for six weeks, and finally returned to previous levels. Many trees that sustained no visible crown damage from the fire were attacked by *Ips* within the scorched region of the bole. Oleoresin flow increased substantially in trees with scorched boles, which may limit the probability that the trees will be ultimately killed by the bark beetles. Contrary to other research, this study also found no evidence that *Ips* were preferentially infesting trees with declining growth. Other *Ips* species showed no population fluctuations. A known *Ips* predator (*Thanasimus dubius* (Coleoptera: Cleridae)) increased 30 to 90 percent.

Sartwell, C., and R.E. Stevens. 1975. Mountain pine beetle in ponderosa pine: Prospects for silvicultural control in second-growth stands. *Journal of Forestry* 73: 136–40.

Summary: Citing several historical thinning studies, the authors contend that thinning dense stands of second-growth ponderosa pine can lessen bark beetle outbreaks in these stands.

Schowalter, T.D. 1990. Consequences of insects. In *Symposium Proceedings. Forests – Wild and Managed: Differences and Consequences. January 19-20, 1990*, pp. 91–106. University of British Columbia, Vancouver, BC.

Summary: Forest insects and pathogens do not threaten forest resources unless changes in forest conditions facilitate population growth. Healthy trees in diverse forests are protected from potential pests by defensive compounds that kill or deter plant-feeding pests, and by the abundance of non-hosts that increase the distance between hosts and chemically hide host trees. Contrary to numerous assertions, old-growth forests are highly productive and remarkably resistant to potential pests.

Schowalter, T.D. 1994. An ecosystem-centered view of insect and disease effects on forest health. In *Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management*, ed. by W.W. Covington and L.F. DeBano, pp. 189–95. USDA Forest Service General Technical Report RM-247.

Summary: The paper describes an ecosystem-centered view of forest insects and pathogens, viewing them not as "pests" but as indicators of forest conditions. Although some insect and pathogen effects may interfere with some forest management goals, consideration of their potential role in maintaining forest health is essential to balanced assessments of impact and of the need for suppression of these organisms. The paper proposes that pruning and thinning by these organisms reduces competition, enhances productivity of survivors, and promotes non-host species. Turnover of plant parts through herbivory, mortality, and decomposition maintains nutrient-cycling processes that are essential to soil fertility and permits reallocation of resources. Because tree species are adapted to different conditions following disturbances, increased diversity promotes functional stability and recovery of the forest ecosystem.

Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78: 115–25.

Summary: The author compared arthropod community structure in replicate Douglas-fir and western hemlock canopies in intact old-growth stands; partially harvested old-growth stands; natural, mature stands; and regenerating plantations in western Oregon. Species diversity and abundance for several taxa, especially predators and detritivores, were significantly lower in plantations than older forests. Old-growth stands had less variable (tighter clustered) arthropod diversity and abundance than partially harvested stands. The data suggest that Douglas-fir canopies may largely recover old-growth structure by 150 years. The author concludes that the recent conversion of large portions of old-growth and mature forests to young plantations (in Oregon's Willamette National Forest) likely has reduced regional populations of many predator and detritivore species. Reduced predator diversity increases the probability that herbivores will escape regulation by predators, which could lead to a greater likelihood of pest outbreaks.

Schowalter, T.D., W.W. Hargrove, and D.A. Crossley, Jr. 1986. Herbivory in forested ecosystems. *Annual Review of Entomology* 31: 177–96.

Summary: This literature review considers the activities of foliage-eating and sap-sucking insects in forest ecosystems. The authors suggest that differential herbivory is the driving force behind ecosystem succession and nutrient cycling. Large-scale outbreaks of insects that defoliate trees are known to dramatically accelerate cycling rates of important nutrients, which subsequently results in increased tree growth for decades. They propose that the traditional short-term view of herbivore impact on timber production overestimates this impact, because it fails to recognize long-term recovery through compensatory growth.

Schowalter, T.D., and J.E. Means. 1989. Pests' link to site productivity in the landscape. In *Symposium Proceedings: Maintaining Long Term Productivity in Pacific Northwest Forests. Corvallis, OR*, ed. by D.A. Perry, pp. 248–50. Timber Press, Portland, OR.

Summary: The authors discuss landscape patterns and their influence on pest insects. Three components have important impacts on pests: patch size, diversity of age classes, and roads. Pest success increases with forest simplification. Decrease in habitat diversity results in declines of important pest predators, such as spiders and birds. Reduced stand size and age-class diversity; planting of monocultures; and intersections of roads increase the likelihood of pests finding suitable hosts. They maintain that old-growth forests should be less vulnerable to pest outbreaks than the simplified forests created through management. Removal of downed wood and snags eliminates the habitats needed to maintain populations of insects that control pest outbreaks.

Schowalter, T.D., and P. Turchin. 1993. Southern pine beetle infestation development: Interaction between pine and hardwood basal areas. *Forest Science* 39: 201–10.

Summary: The authors introduced initial populations of southern pine beetles into replicate experimental plots that had been thinned and/or had hardwood removed. They concluded that landscapes with a high proportion of stands composed largely of a single tree species will be susceptible to pest outbreaks, whereas landscapes composed of more diverse stands and stand types will tend to restrict incipient outbreaks. They also found that stand susceptibility to southern pine beetle increases with pine basal area. They caution that trees that are physiologically capable of defending against small populations often succumb to the pressures of large populations. Thus, even the stands shown in the study to be relatively unfavorable for beginning infestation could suffer severe pine mortality during a southern pine beetle outbreak.

Schowalter, T.D., and J. Withgott. 2001. Rethinking insects. What would an ecosystem approach look like? *Conservation Biology In Practice* 2(4): 10–16.

Summary: The authors ask that land managers rethink the role of insects in forests. When using pest control, managers should ask whether they are treating a cause or just a symptom, because destructive outbreaks often result, directly and indirectly, from human actions, such as establishment of monocultures, fragmentation of habitat, introduction of exotic species, and suppression of fire. At the community level, outbreaks of plant-eating insects can help keep a system healthy. Where risks of fire are acceptable, insect outbreaks can be corrective over the long term. Defoliators and other insects reduce the density of trees and cull weak individuals. This can relieve the stress on the survivors and improve the overall condition of the forest. In many cases, the prime beneficiaries are the non-eaten species that dominated the forest prior to the human-aided rise of fire-tolerant species.

Schroeder, L.M. 1996. Interactions between predators *Thanasimus formicarius* (Coleoptera: Cleridae) and *Rhizophagus depressus* (Coleoptera: Rhizophaidae) and the bark beetle *Tomicus piniperda* (Coleoptera: Scolytidae). *Entomophaga* 41(1): 63–75.

Summary: The occurrences of *Thanasimus formicarius*, *Rhizophagus depressus*, and *Epuraea marseuli* in cut Scots pines attacked by *Tomicus piniperda*, the pine shoot beetle, were recorded in the field. Interactions between the species were studied in caged bolts attacked by *T. piniperda*. Production of *T. piniperda* offspring per unit area of bark was reduced by 41 percent when reared with *R. depressus*, by 81 percent when reared with *T. formicarius*, and by 89 percent when all three species were reared together.

Schroeder, L.M., and A. Lindlow. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Coleoptera: Scolytidae) following a storm felling: A comparison between stands with and without removal of wind felled trees. *Agricultural and Forest Entomology* 4: 47–56.

Summary: For the four years following a major storm disturbance, the number of standing spruce trees killed by *Ips typographus* was determined in fifty-three stands. In five of the stands all of the wind-thrown trees were left, and in the other forty-eight stands all of the trees were removed. The study demonstrated a clear difference in the number of killed trees between stands with and without retention of wind-felled trees. However, the difference was relatively small, considering the large number of wind-felled spruce trees remaining in the unmanaged stands. In the four-year period, only twice as many trees were killed in the unmanaged stands compared to the managed stands. Tree mortality caused by *Ips typographus* was almost nil in the first year, peaked in the second and third year, and decreased markedly to low levels by the fourth year. The study also showed that much higher numbers of trees were killed per hectare in stand edges than in the interiors of either managed or unmanaged stands. The removal of all wind-felled spruce trees—the usual practice in managed forests—will not necessarily prevent trees from being killed by *I. typographus* in stands in following years. However, tree mortality may be reduced.

Schroeder, L.M., and J. Weslien. 1994. Reduced offspring reproduction in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and α–pinene, which attract antagonistic insects. *Journal of Chemical Ecology* 20: 1429–44.

Summary: Bolts of Scots pine attacked by the bark beetle (*Tomicus piniperda*) were baited with ethanol and α-pinene to attract antagonistic insects and thereby enhance the detrimental effects on the production of the bark beetle progeny. The number of offspring and productivity of *T. piniperda* were four to seven times higher in un-baited bolts than in baited bolts. The study suggests that bark beetle progeny production can be strongly reduced by increasing the activity of natural enemies by means of attractants.

Shook, R.S., and P.H. Baldwin. 1970. Woodpecker predation on bark beetles in Engelmann spruce logs as related to stand density. *Canadian Entomologist* 102: 1345–54.

Summary: The authors found that northern three-toed and hairy woodpeckers fed most heavily on logs in semi-open forest where the greatest brood was found. There was a 50 percent reduction in beetle brood over the winter. By fall there was a 71 percent, 83 percent, and 52 percent reduction in open, semi-open, and dense forest, respectively.

Shouse, B. 2003. Old-growth forest spared for now. *Science* 299: 802.

Summary: A drought, along with threat of fire and beetle outbreaks, caused the Mexican Ministry of the Environment to order Mexican landowners in the San Pedro Martír Mountains of Baja California to clear their land of dead trees and brush within 120 days or risk fines. An ecologist in a nearby town contacted his colleagues in the USFS and University of California, who came to Baja and presented evidence that the natural fire-adapted matrix of the national forest could resist the drought and the beetle threats without management.

Shore, T.L., L. Safranyik, W.G. Riel, M. Ferguson, and J. Castonguay. 1999. Evaluation of factors affecting tree and stand susceptibility to the Douglas-fir beetle (Coleoptera: Scolytidae). *Canadian Entomologist* 131: 831–39.

Summary: Tree and site characteristics were compared between nineteen groups of Douglas-fir infested by Douglas-fir beetle and nineteen uninfested groups to identify individual or combinations of characteristics associated with Douglas-fir beetle attack. Diameter, height, age, phloem thickness, and bark thickness showed significant differences.

Siira-Pietikäinen, A., J. Haimi, A. Kanninen, J. Pietikäinen, and H. Fritze. 2001. Responses of decomposer community to root-isolation and addition of slash. *Soil Biology & Biochemistry* 33: 1993–2004.

Summary: The relationship between forest harvesting and the impact on the forest decomposer community was studied in a stand of mature spruce (*Picea abies*). A two-factor experiment was carried out: 1) isolation of tree roots from the surrounding soil, and 2) addition of slash. Isolation increased the NH_4 content of the soil and promoted herbaceous growth. While isolation had no effect on overall microbial biomass, the community structure of the plots changed dramatically and the fungal component decreased by 40 percent. Fungivorous arthropods (collembolans and oribatid mites) decreased in number, while bacterivorous nematodes slightly increased. The addition of slash to the plots had no apparent effect on the decomposer community. The authors concluded that elimination of the root-mycorrhizal connections is one of the most important factors affecting the soil biota after timber harvest.

Simard, J.R., and J.M. Fryxell. 2003. Effects of selective logging on terrestrial small mammals and arthropods. *Canadian Journal of Zoology* 81: 1318–26.

Summary: Research in the hardwood forests of Ontario demonstrates that disturbed (logged) stands have less structural diversity, fewer mast producing tree species, and overall lower seed production than untouched stands. Consequently, logged stands have lower arthropod and small mammal diversity than undisturbed stands.

Similä, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: The effects of forest age and naturalness on species assemblages. *Biological Conservation* 106: 19–27.

Summary: The authors studied the beetle species assemblage in multiple forest succession stages (from clearcut to old growth). They advocate management strategies that more closely mimic natural disturbances, particularly to protect endangered and sensitive species as well as species with specific habitat requirements. They found that the volume of dead wood is remarkably larger after even intensive forest fire than in clear-cut stands. Although the beetle species assemblages were superficially similar in clear-cut and on burned sites, there were clear differences in saproxylic species assemblages. Also, threatened species were found exclusively, and near-threatened species mainly, in the burned sites.

Stephen, F.M., M.P. Lih, and L.E. Browne. 1996. Biological control of southern pine beetle through enhanced nutrition of its adult parasitoids. In *Proceedings: North American Forest Insect Work Conference*, ed. by R.F. Billings and T.E. Nebeker, pp. 34–5. Texas Forest Service Publication 160.

Summary: The authors contend that forest stand structure, coupled with current forest management strategies, are the primary reasons why natural enemies, and especially parasitoids, are not effective in regulating southern pine beetle populations. Their data suggest that parasitoid adults are limited by the lack of flowering plants in the pure, even-aged pine plantations. Historically—before wide-scale harvesting, fire control, and single-species even-aged stands became the standard—southern pine forests were diverse, open forests with an understory approaching two to three hundred plant species per hundred hectares. These more open forests, with their abundance of flowering annuals and perennials, would have favored survival and greater fecundity of bark beetle parasitoids.

Stephen, F.M., M.P. Lih, and G.W. Wallis. 1989. Impact of arthropod natural enemies on *Dendroctonus frontalis* (Coleoptera: Scolytidae) mortality and their potential role in infestation growth. In *Potential for Biological Control of* Dendroctonus *and* Ips *Bark Beetles*, ed. by D.L. Kulhavy and M.C. Miller, pp. 169–85. Stephen F. Austin State University Press, Nacogdoches, TX.

Summary: Using a model of southern pine beetle population dynamics, the authors simulated growth for three southern pine beetle infestations and showed a close correlation between observed and predicted numbers of infested trees through time. When the model was modified and mortality caused by natural enemies was removed, predicted infestation growth was much more rapid. Tree loss over a ninety-day period was up to forty times greater than when natural enemies were present.

Stone, W.E., and M.L. Wolfe. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* 122: 1–12.

Summary: The authors studied the impacts of a mountain pine beetle outbreak on the understory floral community in ten lodgepole pine stands in Utah. Understory biomass increased with decreasing canopy cover, but plant species diversity reached its maximum at intermediate levels of tree mortality. Their results indicate that epidemics of bark beetles in coniferous forests increase the availability of forage and browse for wildlife. In the absence of intense grazing pressure by herbivores, these stands offer nesting and foraging cover to small mammals and birds. They observed that severely disturbed stands often resemble wet meadows with dense stands of grasses and sedges (except on steep slopes). Stands with moderate mortality may give a competitive advantage to aspen.

Strom, B.L., R.A. Goyer, and P.J. Shea. 2001. Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. *Entomologia Experimentalis et Applicata* 100: 63–7.

Summary: The deterrent effect of two visual cues and olfactory disruptants was tested on the western pine beetle (*Dendroctonus brevicomis*). Multiple funnel traps placed on poles adjacent to trees were used in conjunction with black-and-white visual targets and volatile-releasing devices. The traps were baited with three commonly used attractants for bark beetles (exo-brevicomin, frontalin, and Myrcene). Two disruptants that have been shown to successfully repel bark beetles from potential host trees (verbenone and ipsdienol) were tested to deduce their effect at overriding the draw of the visual and olfactory attractants. The results showed that *D. brevicomis* was more effectively deterred by olfactory than visual cues. In addition, olfactory disruptants showed a more significant effect than any synergistic interaction between visual and olfactory cues. The authors concluded that the western pine beetle utilized olfaction more than visualization in finding hosts when compared to the southern pine beetle (*D. frontalis*).

Sullivan, B.T., E.M. Pettersson, K.C. Seltmann, and C.W. Berisford. 2000. Attraction of the bark beetle parasitoid *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) to host-associated olfactory cues. *Environmental Entomology* 29(6): 1138–51.

Summary: Bioassays and gas chromatography were carried out on bark beetles and bark beetle frass to understand their attractiveness to a bark beetle parasitoid, *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae). *R. xylophagorum* is among the most abundant parasitoid species found in association with bark beetle infestations. The results demonstrate that *R. xylophagorum* responds to a combination of attractants. This implies that improved manipulation of parasitoids to direct them toward active outbreaks/populations of bark beetles can help control them.

Swetnam, T.W., and A.M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63(4): 399–424.

Summary: Tree-ring chronologies from twenty-four mixed-conifer stands were used to reconstruct the long-term history of western spruce budworm (*Choristoneura occindetalis*) in northern New Mexico. Authors found that outbreaks of spruce budworm varied from twenty to thirty-three years. They also found that outbreaks were associated with wet/dry periods and that the extent and severity of outbreaks in the 20th century was partly a response to changes in land use. Logging and fire suppression created a dense, continuous, mixed-conifer forest with an elevated proportion of suitable budworm hosts. In contrast, pre-settlement outbreaks in the spatially and temporally heterogeneous forest sustained less severe outbreaks. One ancient stand of Douglas-fir trees over 700 years old revealed that budworms and overstory trees can coexist for extraordinary lengths of time.

Turchin, P., A.D. Taylor, and J.D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: An experimental test. *Science* 285: 1068–71.

Summary: Southern pine beetle (*Dendroctonus frontalis*) and its predators were monitored over a five-year period. The results suggest that the effects of predation influencing bark beetle populations are of a delayed, density-dependent nature. While the impacts of predators were negligible during the early increase phase of the outbreak, they grew during the year of peak population and reached a maximum during the period of population decline. The delayed nature of the impact of predation suggests that predation is an important process that contributes significantly to southern pine beetle oscillations.

Velben, T.T., K.S. Hadley, M.S. Reid, and A.J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreaks in Colorado. *Ecology* 72: 213–31.

Summary: The authors used age-structure analysis and dendrochronological techniques to investigate the effect of a major spruce beetle outbreak on stand composition, dominance, tree age and size structures, radial growth, and succession in subalpine forests in Colorado. The outbreak in the 1940s caused a shift in dominance from spruce to fir, and a reduction in average and maximum tree diameters, heights, and ages. Following the outbreak, growth rates of released trees remained high for more than forty years. Both spruce and fir will continue to dominate the stands. The predominance of accelerated growth following the spruce beetle outbreak, instead of new seedling establishment, contrasts strongly with the pattern of stand development following fire. The authors found that over the past three hundred years, spruce beetle outbreaks have occurred more frequently and have had a more rapid turnover period than stand-replacing fires. Thus, in the spruce fir forests, spruce beetle outbreaks have been the dominant disturbance.

Volney, W.J.A., and R.A. Fleming. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment* 82: 283–94.

Summary: This paper details the life history and population dynamics of the spruce budworm, jack pine budworm, and the forest tent caterpillar, and how these insects may impact boreal forests in relation to climate change. The authors conclude that the interaction of fire and insects must be accounted for in developing realistic carbon sequestration forecasts.

Wallin, K.F., and K.F. Raffa. 2000. Influences of host chemicals and internal physiology on the multiple steps of postlanding host acceptance behavior of *Ips pini* (Coleoptera: Scolytidae). *Environmental Entomology* 29(3): 442–53.

Summary: The authors discuss post-landing host acceptance behavior of pine engravers (*Ips pini*). Variations in concentrations of α-pinene had a moderate effect on post-landing host acceptance. However, the overriding factors in host acceptance appear to be attributable to (1) environmental conditions (e.g. drought), and (2) the physiological state of the beetle (e.g. lipid content).

Wallin, K.F., and K.F. Raffa. 2002. Prior encounters modulate subsequent choices in host acceptance behavior by the bark beetle *Ips pini*. *Entomologia Experimentalis et Applicata* 103: 205–18.

Summary: Laboratory bioassays indicate that *Ips pini* is rather flexible in its host-acceptance behavior. At moderate levels (i.e., with a perceived selection of stressed trees) beetles generally are more selective and may reject several vigorous trees in favor of only stressed hosts, as a healthy tree's host defenses can kill a low level of beetle entries. However, when there is a shortage, or perceived shortage, of stressed trees, individuals may alter their normal behavior and may loiter on a vigorous tree; or the individual may begin entering the potential host while releasing an aggregating cue. In this case, if the vigorous tree is attacked by a number of beetles, the host defenses may be overcome. The positive feedback exhibited by this altered behavior adds to the instability of populations exhibited in outbreaks.

Wallin, K.F., and K.F. Raffa. 2002. Density-mediated responses of bark beetles to host allelochemicals: A link between individual behavior and population dynamics. *Ecological Entomology* 27: 484–92.

Summary: The authors used a series of entry and gallery construction assays to determine whether the response by individual beetles to phloem monoterpenes is altered by pheromones and/or the presence of other beetles. They found the presence of beetles on suitable substrate, or boring into suitable substrate, elicits a behavior response in other beetles. Gallery lengths increased with an increase in aggregation pheromones, and the density of beetles on the surface affects the likelihood of and speed of entry of other beetles. The results do not support the assumption that aggregation pheromones cause a beetle to enter a tree it would otherwise reject. The study does support the view that the overall process of host selection by bark beetles involves a sequence of behavioral events that are influenced by multiple factors.

Waring, R.H., and G.B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66(3): 889–97.

Summary: The authors looked at how particular treatments impact infection by mountain pine beetle in lodgepole pine forests. The treatments included (1) fertilization with urea, (2) additions of sugar and lodgepole pine sawdust, (3) fertilization of urea and removal of most small-diameter trees, leaving approximately 20 percent of the original canopy, and (4) untreated controls. Where canopy density was reduced either by logging or *insects themselves*, surviving trees significantly increased their resistance to attack over a three-year period. Even in the control plots, initial mortality stimulated surviving trees, so that after approximately three years these areas were predicted to be relatively safe from attack.

Weslien, J., and L.M. Schroeder. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267–75.

Summary: Twelve spruce stands in central Sweden were surveyed for the spruce bark beetle (*Ips typographus*) and associated insects, including bark beetle predators. Six stands were unmanaged and had an accumulation of dead spruce trees. These stands were compared pairwise with six managed stands with similar forest composition and structure. Four species, all known to be common bark beetle predators, were caught in significantly higher numbers in the unmanaged stands. In contrast, the number of spruce beetles was close to identical for both treatments. The results demonstrate that spruce bark beetle predators may be more sensitive to certain forestry management strategies and require greater habitat complexity. Comparative studies on how populations of bark beetles and their associates are affected by forestry at the landscape scale are lacking. Until such studies have been carried out, it cannot be excluded that forest operations that favor natural enemies in the landscape might be economically favorable, compared to traditional stand management.

Wickman, B.E. 1978. *A Case Study of Douglas-Fir Tussock Moth Outbreak and Stand Conditions 10 Years Later*. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Paper PNW-224, Portland, OR.

Summary: The paper describes stand conditions before, immediately after, and ten years after a Douglas-fir tussock moth outbreak on the Modoc National Forest in northern California. The author noted that mortality tended to be concentrated in patches ranging in size from several to several hundred acres. The total percentage of the patches was relatively small, around 10 to 14 percent of the outbreak area. The reduction in stand density had positive values by lessening tree competition and enhancing growth of survivors. Over a ten-year period, the effects of tree mortality, reducing competition, and possibly nutrient cycling of insect frass during the outbreak resulted in significantly greater growth of both host and nonhost trees during the post-outbreak period. Die-offs resulting from insect attacks may actually help restore the tree-species composition altered by fire suppression and other human activity. For example, where open ponderosa pine forest has been invaded by true fir or Douglas-fir, insects often selectively attack and kill these commercially less-valuable trees, thus increasing the growth and reproduction of better-adapted pines. The author concludes that “maybe the tussock moth is doing us a favor by pointing out the fallacy of some of our forest management practices and acting as a regulator of an unstable system that we have created over vast acreages.”

Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *Journal of Forestry* 78: 31–3.

Summary: The author looked at growth rates of Douglas-fir in stands that were affected by a tussock moth outbreak in the Inyo National Forest in the Sierra Nevada. He found that defoliated white fir grew significantly faster than undefoliated white fir for thirty-six years following the Douglas-fir tussock moth outbreak, despite similar radial growth rates prior to defoliation. He concluded that the possibility of increased growth after tussock moth attack should be recognized by those assessing tree damage and stand growth for forest management planning and environmental impact statements.

Wickman, B.E. 1990. *The Battle Against Bark Beetles in Crater Lake National Park: 1925–34*. United States Department of Agriculture. USDA Forest Service Pacific Northwest Research Station General Technical Report PNW-GTR-259.

Summary: The author detailed the effort to control the mountain pine beetle (*Dendroctonus ponderosae*) at Crater Lake National Park from 1925 to 1934. Over 48,000 trees were "treated" (cut down and then burned) in the last three years of that period. The main lesson learned was that once a mountain pine beetle population erupts over a large area of susceptible forest type, and as long as environmental conditions remain favorable, there really is no way to stop the beetles until almost all the susceptible trees are either killed or removed by logging. Treating trees perhaps slows the progress of the outbreak, but the outcome is inevitable. The report states: "Perhaps the cold winter in 1932-33 helped, but most importantly, the depletion of susceptible trees ended the outbreak rather than the annual control efforts for ten years." In 1984, lodgepole pine stands in central Oregon were once again infested with mountain pine beetle. By 1985, a severe outbreak covered thousands of acres and extended south nearly to the park boundary. In 1986, beetle-killed trees were found in the northern end of the park.

Williams, D.W., and A.M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4: 87–99.

Summary: The authors use mathematical modeling to predict the dynamics of two different species of bark beetles—southern pine beetle (*Dendroctonus frontalis*) and mountain pine beetle (*D. ponderosae*)—in response to climate change. Relatively small changes in climate may shift the ranges of these species and the forests they inhabit to higher elevations and latitudes over time. For *D. ponderosae*, shifts in elevation are predicted to occur more rapidly than latitudinal shifts. For *D. frontalis*, the scientists predict a general expansion with a net movement northward. Both species will shift over the long term as host forests shift northward. The effects of both human land use and change in climatic variables other than temperature will complicate forest-range shifts, and hence will complicate bark beetle-range shifts. For example, changing precipitation patterns will alter the frequency and geographical extent of fire and drought disturbances, complicating the ability to predict future forest disturbances.

Wood, D.L., R.W. Stark, W.E. Waters, W.D. Bedard, and F.W. Cobb, Jr. 1985. Treatment tactics and strategies. In *Integrated Pest Management in Pine–Bark Beetle Ecosystems*, ed. by W.E. Waters, R.W. Stark, and D.L. Wood, pp. 121–39. John Wiley and Sons, New York, NY.

Summary: The authors contend that thinning may help increase resistance to bark beetle infestations because infestations are correlated with high stand density. On the other hand, thinning may result in physical damage to trees, soil compaction, root breakage, and periods of temporary stress resulting from a drastically changed environment, all of which can increase the risk of infestation by bark beetles and inoculation by pathogens. They also point out that despite nearly a hundred years of active management of the mountain pine beetle, evidence for the efficacy of control is scant and contradictory.

Zhou, J., D.W. Ross, and C.G. Niwa. 2001. Kairomonal response of *Thanasimus undatulus, Enoclerus sphegeus* (Coleoptera: Cleridae), and *Temnochila chlorodia* (Coleoptera: Trogositidae) to bark beetle semiochemicals in eastern Oregon. *Environmental Entomology* 30(6): 993–98.

Summary: This research tested the attractiveness of various synthetic semiochemical blends used by predators of bark beetle to identify and locate prey populations. Predator populations can be significantly impacted when individuals are killed along with bark beetles in traps and logs baited with insecticide. The conclusion is that the negative impact on non-target predators may negate any advantages won in trapping any bark beetles.

"Scott Hoffman Black's masterful synthesis of the state-of-the art science in *Logging to Control Insects* is a must for those who care about forests and forest management. It explodes many of the myths about logging to control insects and demonstrates the need for forest managers to work with and not against nature. This easy-to-use reference summarizes the latest authoritative research about the natural interactions between forests and forest insect pests, including what has worked to control insects and what has not. It is the most useful publication on the topic of forests and forest pests that I have seen and has my highest recommendation."

Mike Dombeck, Chief Emeritus, U.S. Forest Service

Front cover photo credits:

Left: *Pine tree killed by a scolytine beetle. Photograph © Edward Ross*
Upper right: *Red turpentine beetle (*Dendroctonus valens*). Photograph © Edward Ross*
Lower right: *Red-bellied clerid beetle (*Enoclerus sphegeus*). Photograph © Edward Ross*

Back photo credit:

Above: *Old-growth cedar, spruce, and hemlock in Quinault National Forest. Photograph © 1984 Gary Braasch*

ISBN 0-9744475-4-4