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Ecology and Management of Bark Beetles 【Review article】

小蠹蟲的生態和管理【綜合論述】

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Abstract

Bark beetles (Coleoptera: Curculionidae: Scolytinae) have been considered a primary threat to forests throughout the northern hemisphere. Although tree mortality to bark beetles often detracts from forest management goals, the natural role of bark beetles is canopy opening, thinning, and diversification of stand structure and composition, effects that contribute to some ecosystem services in forests managed for multiple uses. Strategies to prevent bark beetle outbreaks exploit their sensitivity to host tree condition and spacing and their reliance on pheromones to attract sufficient numbers to overwhelm tree defenses. Tree species selection at planting or through selective thinning can favor tree species that are more tolerant of site conditions and resistant to bark beetles. Pre-commercial or commercial thinning improves tree condition and creates barriers to beetle population growth and spread. Remedial options include salvage harvest, pheromones for trap-out or disruption of host location, and white paint to disrupt the dark silhouette of the tree bole. Given the labor costs and trade-offs among tactics and the marginal profitability of fiber and timber production, harvest in advance of, or salvage harvest after, bark beetle attack often is the favored management strategy. However, this strategy is not as appropriate in public forests managed for values provided by older, more vulnerable trees. High-value sites for cultural values or endangered species protection may require use of more expensive management options.

摘要

小蠹蟲 (bark beetle) (鞘翅目：象鼻蟲科：小蠹亞科) 被認為是威脅整個北半球森林的主要害蟲。儘管小蠹蟲造成的樹木死亡率往往會減損森林管理的目標，但是小蠹蟲具有一些天然的作用，它們能夠使林冠疏開、疏伐及林分結構和組成多樣化，這些作用能夠為多目標利用的森林管理提供一些生態系統服務。預防小蠹蟲大發生的策略乃利用其對寄主樹木的條件和間距的敏感性，及其依賴費洛蒙誘引足夠數目的小蠹蟲來壓制樹木的防衛。種植時樹種的選擇或選擇性疏伐都有助於樹種更能容忍生育地條件及抵抗小蠹蟲。早期商業性疏伐或商業性疏伐可以增強樹木的條件，並創建甲蟲族群增長和擴散的障礙。補救措施包括殘材伐採、費洛蒙誘殺，或破壞其對寄主的定位，及樹幹塗白漆以消除樹幹較暗的輪廓。基於人力成本以及採用的方法與纖維和木材生產的邊際利潤之間的權衡，在小蠹蟲攻擊前伐採，或在攻擊後殘材伐採，都是可行的管理策略。然而，此策略不適用管理公有林中價值高但樹齡大及較脆弱的樹木。具文化或瀕危物種保護的高價值生育地，可能需要使用更昂貴的管理措施。

Key words: Scolytinae, disturbance, population dynamics, ecosystem services, host density

關鍵詞: 小蠹亞科、擾亂、族群動態、生態系統服務、寄主密度。

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Ecology and Management of Bark Beetles

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ABSTRACT

Bark beetles (Coleoptera: Curculionidae: Scolytinae) have been considered a primary threat to forests throughout the northern hemisphere. Although tree mortality to bark beetles often detracts from forest management goals, the natural role of bark beetles is canopy opening, thinning, and diversification of stand structure and composition, effects that contribute to some ecosystem services in forests managed for multiple uses. Strategies to prevent bark beetle outbreaks exploit their sensitivity to host tree condition and spacing and their reliance on pheromones to attract sufficient numbers to overwhelm tree defenses. Tree species selection at planting or through selective thinning can favor tree species that are more tolerant of site conditions and resistant to bark beetles. Pre-commercial or commercial thinning improves tree condition and creates barriers to beetle population growth and spread. Remedial options include salvage harvest, pheromones for trap-out or disruption of host location, and white paint to disrupt the dark silhouette of the tree bole. Given the labor costs and trade-offs among tactics and the marginal profitability of fiber and timber production, harvest in advance of, or salvage harvest after, bark beetle attack often is the favored management strategy. However, this strategy is not as appropriate in public forests managed for values provided by older, more vulnerable trees. High-value sites for cultural values or endangered species protection may require use of more expensive management options.

Key words: Scolytinae, disturbance, population dynamics, ecosystem services, host density

Introduction

Historically, bark beetles (Coleoptera: Curculionidae: Scolytinae) that attack tree boles have been considered a primary threat to forests throughout the northern

hemisphere (Furniss and Carolin, 1977; Drooz, 1985; Fettig *et al.*, 2007; Lin and Wu, 2010). Periodic outbreaks of bark beetles cause annual losses of millions of dollars and pose serious challenges for forest managers (Price *et al.*, 1998),

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largely because these beetles spend most of their life cycle protected under the bark, and because many suppression options are impractical in forest ecosystems. Suppression of outbreaks is particularly difficult and expensive.

However, as a group, bark beetles are largely dependent on availability of stressed, dying or recently dead host trees, and populations typically decline as the supply of such trees is exhausted (Cairns *et al.*, 2008; Schowalter, 2012). Outbreaks generally are associated with dense forests managed for maximum timber production. Such forests provide abundant (often stressed) hosts and few barriers to spread. Bark beetles thin and diversify such forests (Schowalter and Turchin, 1993; Cairns *et al.*, 2008) and may function as regulatory agents, maintaining host populations near carrying capacity, as does predation, a role that may be useful in areas where forest management is difficult (Schowalter, 2013). Furthermore, bark beetles affect other ecosystem services valued by humans in both positive and negative ways. For these reasons, all aspects of bark beetle ecology and their effects on ecosystem services should be addressed in deciding when it may be necessary to manage outbreaks and what options to select.

This paper describes aspects of bark beetle ecology that are particularly important to their population dynamics and effects on ecosystem services. In particular, their sensitivity to host condition and density, as well as other environmental factors, can be manipulated through management practices to prevent outbreaks in healthy, diverse forests. Although less effective, several remedial options can help to suppress outbreaks when necessary.

Bark beetle diversity

Bark beetles represent a diverse group of insects that feed on phloem tissues, between the bark and sapwood, of trees. A related group, the ambrosia

beetles, mine into sapwood tissues and feed primarily on mutualistic fungi cultivated by the beetles in their galleries. Bark beetles reach their greatest diversity and economic importance in coniferous forests (Furniss and Carolin, 1977; Drooz, 1985; Lin and Wu, 2010). For example, Lin and Wu (2010) recorded 72 species of bark and ambrosia beetles from China-fir (*Cunninghamia lanceolata*) stands in central Taiwan.

This paper focuses on the phloem-feeding bark beetles. Most species are restricted to dead and dying trees and are instrumental in initiating decomposition of this coarse woody debris (Edmonds and Eglitis, 1989; Zhong and Schowalter, 1989). However, several species feed on living trees as adults and can spread tree-killing pathogens that facilitate future reproduction in dead and dying trees. A relatively small number of species can attain sufficient population sizes in weakened trees to spread and kill living trees over large areas, and these species can cause enormous losses of forest resources (Furniss and Carolin, 1977; Coulson, 1979; Chen and Tang, 2007; Ciesla, 2011; Edburg *et al.* 2012). For example, the southern pine beetle, *Dendroctonus frontalis* Zimmerman caused timber losses worth \$1.2 billion in the southern U.S. over a 28-year period (Pye *et al.*, 2011).

Species of greatest management concern globally include *D. frontalis*, sixspined ips, *Ips calligraphus* (Germar), eastern fivespined ips, *I. grandicollis* (Eichhoff) and small southern pine engraver, *I. avulsus* (Eichhoff) in the southern U.S.; mountain pine beetle, *D. ponderosae* Hopkins, western pine beetle, *D. brevicomis* LeConte, Douglas-fir beetle, *D. pseudotsugae* Hopkins, spruce beetle, *D. rufipennis* (Kirby), pine engraver beetle, *I. pini* (Say) and fir engraver beetle, *Scolytus ventralis* LeConte in western North America; great spruce bark beetle, *D. micans* (Kugelann), European spruce bark beetle, *I. typographus* (L.), and a pine engraver, *I. acuminatus*

Gyllenhal, in Eurasia and Japan; and Chinese white pine beetle, *D. armandi* Tsai and Li, in China. In addition, several species, including the native elm bark beetle, *Hylurgopinus rufipes* (Eichoff), smaller European elm bark beetle, *S. multistriatus* (Marsham) and Douglas-fir root bark beetle, *Hylastes nigrinus* (Mannerheim), vector pathogenic fungi (e.g., Dutch elm disease, caused by *Ophiostoma ulmi*, (Buisman) Melin & Nannf. and *O. novo-ulmi* Brasier, and Douglas-fir root disease, caused by *Leptographium (Ophiostoma) wagneri* var. *pseudotsugae* Harrington and Cobb), that subsequently spread via root contact among host trees in advance of colonization by the beetles.

Bark beetle ecology

Several aspects of bark beetle ecology contribute to their ability to cause significant tree mortality. First, though small, these beetles can aggregate in large numbers on individual trees, in response to a combination of beetle pheromones and host volatiles (Raffa *et al.*, 1993; Xie and Lv, 2012). The particular pheromone blends used to attract conspecifics differ among species, but all species common to particular host tree species can be attracted to trees being attacked by other beetle species. Second, these beetles are members of a complex assemblage of fungal, bacterial and mite associates that influence the success of tree colonization and beetle reproduction (Stephen *et al.*, 1993; Schowalter, 2011; Hoffstetter and Moser, 2014). In particular, blue stain fungi, *Ophiostoma* spp., carried by phoretic tarsonemid mites, contribute to tree death, a necessary condition for successful beetle colonization and reproduction (Lin *et al.*, 2003). However, sufficient numbers of beetles can girdle and kill trees in the absence of the fungus, and the fungus causes brood mortality that explains life stage adaptations to avoid infected areas (Bridges *et al.*, 1985).

Although bark beetles are often blamed for forest health problems, healthy trees are capable of defending themselves against bark beetles, which typically are restricted to recently dead, dying, diseased or stressed trees (Tisdale *et al.*, 2003; Schowalter, 2011, 2012). Healthy pine trees defend themselves through a combination of a) resin (pitch) flow, which prevents attacking beetles from penetrating the bark barrier (Hodges *et al.*, 1979; Waring and Pitman, 1983; Tisdale *et al.*, 2003; Schowalter, 2011), and b) an induced phenolic defense that isolates and encapsulates beetles and their associated pathogens in a necrotic lesion (Nebeker *et al.*, 1993). Both defenses depend on availability of water. Trees weakened by injury (especially lightning strike or storm damage), disease or stress (including drought, flooding or prior defoliation) have impaired defensive ability and become vulnerable to bark beetle colonization (Wright *et al.*, 1986; Mattson and Haack, 1987; Flamm *et al.*, 1993; Lorio, 1993; Nebeker *et al.*, 1993; Koricheva *et al.*, 1998; Gilbert and Grégoire, 2003; Lombardero *et al.*, 2006; Aukema *et al.*, 2010). Fewer beetles are necessary to overwhelm the defensive capability of weakened trees, compared to healthy trees. For example, at least 100 beetles per m² bole surface are necessary to overcome the defenses of a healthy lodgepole pine (*Pinus contorta*), whereas fewer than 50 beetles per m² are capable of killing stressed trees (Fig. 1) (Waring and Pitman, 1983). Ironically, the most rapidly-growing loblolly pines (*P. taeda*) also are highly vulnerable to *D. frontalis* because resin ducts form only in late wood produced during the summer (Lorio, 1993). Consequently, trees that produce a thicker layer of spring wood on top of the resin ducts in spring, when beetle populations are growing, tend to be more vulnerable than are slower-growing trees.

Furthermore, bark beetles are highly sensitive to host density or spacing

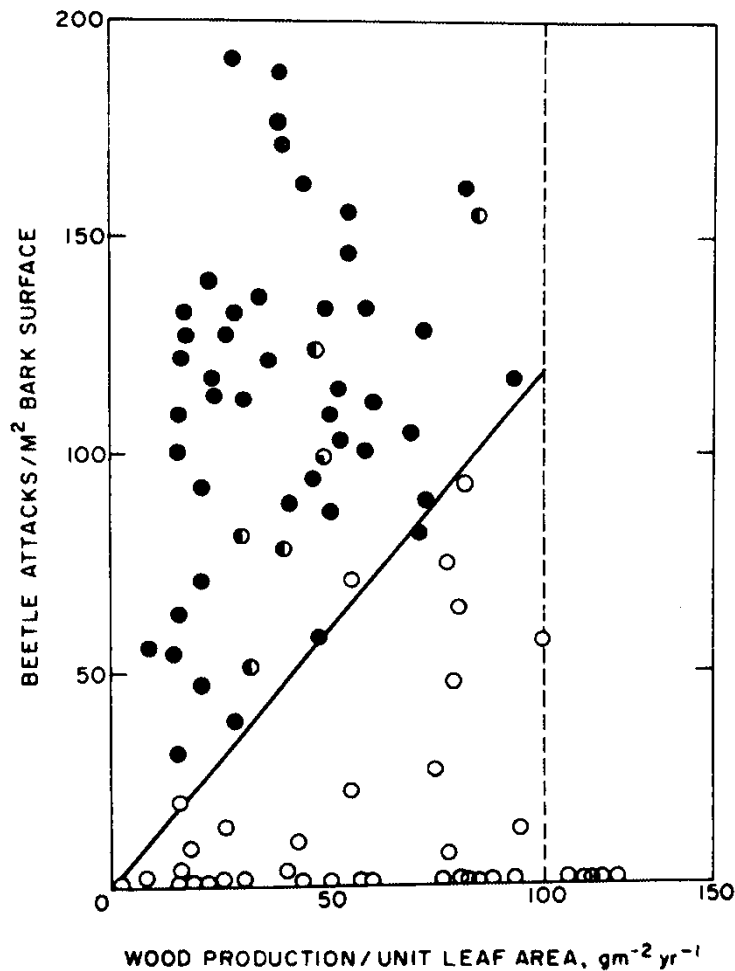


Fig. 1. The density of *Dendroctonus ponderosae* attacks necessary to kill *Pinus contorta* increases with increasing host vigor, measured as growth efficiency. The blackened portion of circles represents the degree of tree mortality. The solid line indicates the attack level predicted to kill trees of a specified growth efficiency (index of radial growth); the dotted line indicates the threshold above which beetle attacks are unlikely to cause mortality. From Waring and Pitman (1983) with permission from John Wiley & Sons.

(Schowalter *et al.*, 1981b; Schowalter and Turchin, 1993; Gilbert and Grégoire, 2003). The likelihood of mortality to nearby hosts declines exponentially with distance from source trees (Schowalter *et al.*, 1981b; Birt, 2011). Trees beyond 6 m from source trees are unlikely to be colonized, except at very high beetle population sizes (Fig. 2) (Sartwell and Stevens, 1975; Schowalter *et al.*, 1981b; Amman *et al.*, 1988). Therefore, outbreaks of bark beetles are less a threat

to forest health than a symptom of abundant trees in poor health.

As a result of tree defensive ability, endemic bark beetle populations are restricted to isolated injured or stressed trees, especially those that are lightning-struck or diseased (Flamm *et al.*, 1993; Paine and Baker, 1993; Koricheva *et al.*, 1998). Disturbances are especially important as triggers for bark beetle outbreaks. Widespread tree injury or stress as a

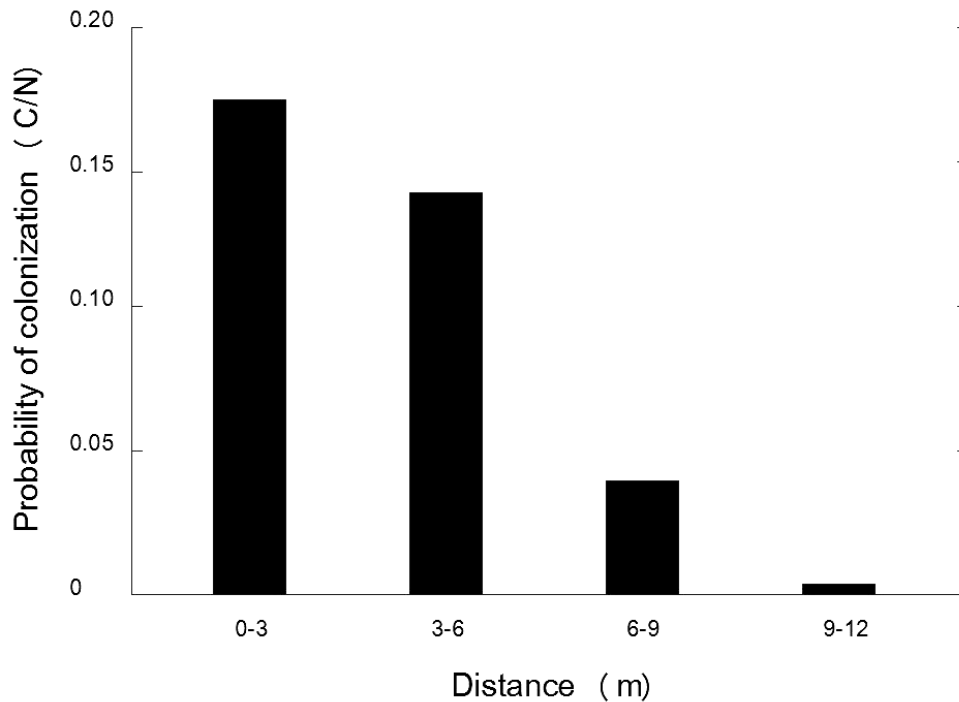


Fig. 2. Probability of colonization of pine hosts by *Dendroctonus frontalis* with distance from population sources. N = number of trees available at a given distance; C = number of trees at a given distance that were colonized within the next five days. Data from Schowalter *et al.* (1981b).

result of storm damage (Nebeker *et al.*, 1993), fire (Lombardero *et al.*, 2006) or drought (Mattson and Haack, 1987; Gilbert and Grégoire, 2003; Raffa *et al.*, 2008) increases the availability of susceptible trees near bark beetle refuge trees, allowing small populations to grow rapidly and spread to surrounding live trees, typically within 6 m, but the large number of dispersing beetles also increases the probability that many will colonize trees at greater distances (Schowalter and Turchin, 1993; Schowalter, 2011). Under favorable conditions, especially in large areas of dense, stressed pines, spot growth can continue, and multiple spots coalesce into widespread areas of tree mortality.

Populations of bark beetles, like those of other species, are regulated to some extent by a variety of predators, parasitoids and parasites, including woodpeckers,

clerid, histerid, trogossitid and monotomid beetles and fly and wasp parasitoids, as well by competing xylophages (Stephen *et al.*, 1993; Gilbert and Grégoire, 2003; Berisford, 2011; Reeve, 2011; Stephen and Clarke, 2011). Although predation and parasitism cause substantial mortality that may contribute to collapse of outbreaks, they appear to operate with long time lags (delayed density-dependence) and often fail to prevent outbreaks when host conditions are favorable to the bark beetles (Turchin *et al.*, 1999b; Gilbert and Grégoire, 2003; Berisford, 2011; Reeve, 2011). For example, Turchin *et al.* (1999b) reported that experimental exclusion of predators during a *D. frontalis* population cycle indicated negligible predation while the bark beetle population was increasing, increased predation during the year of peak bark beetle abundance, and 2-fold

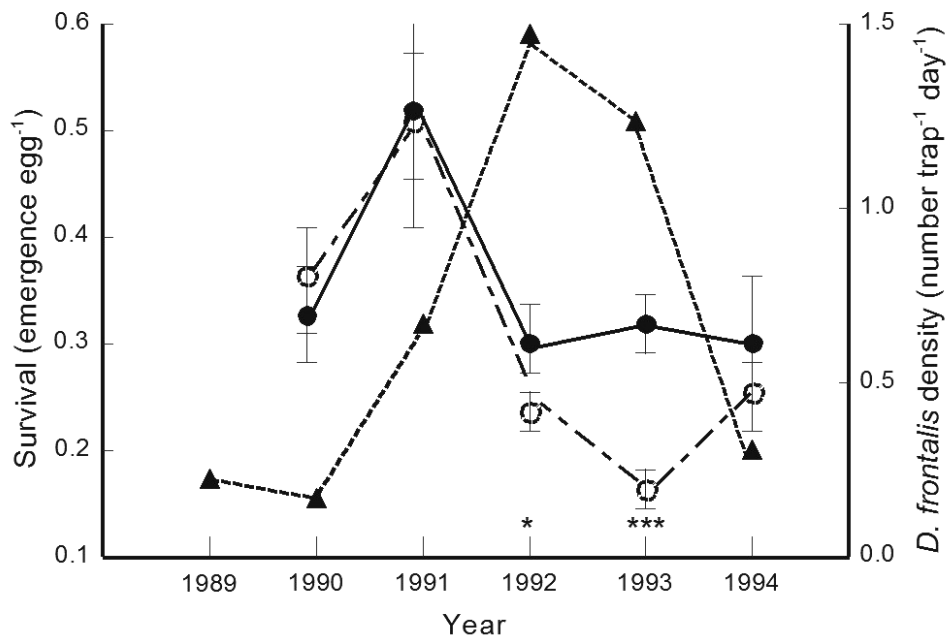


Fig. 3. Survival of *Dendroctonus frontalis*, measured as the proportion of eggs surviving to become emerging adults, when protected from predation (closed circles, solid line) and exposed to predation (open circles, broken line). Triangles and dotted line indicate the corresponding *D. frontalis* population size. * $P < 0.05$; *** $P < 0.001$. Redrawn from Turchin *et al.* (1999b).

higher predation (compared to controls) during outbreak decline (Fig. 3).

Outbreaks tend to be self-limiting as an expanding bark beetle population exhausts available resources, i.e., dense and/or stressed hosts (Coleman *et al.*, 2008). Host mortality to bark beetles promotes non-host species (Schowalter *et al.*, 1981a; Brose and Waldrop, 2010), thereby diversifying the landscape and reducing the likelihood of future outbreaks (Cairns *et al.*, 2008; Coleman *et al.*, 2008; Kayes and Tinker, 2012). Even when 75-80% of the overstory trees are killed, stem density and basal area can recover to pre-outbreak levels within 10-15 years (Romme *et al.*, 1986), but may take 60-100 years (Collins *et al.*, 2011). In fact, the lower stem density and higher diversity of the post-outbreak forest is the more sustainable, historic forest structure that is now the recommended management

goal for coniferous forests in western North America (North *et al.*, 2007).

Climate change is likely to increase the frequency and extent of bark beetle outbreaks in some areas (Williams and Liebhold, 2002; Raffa *et al.*, 2008). Altered precipitation and evapotranspiration patterns are expected to produce widespread drought and increased availability of water-stressed trees, whereas increased frequency and intensity of major storms (Gutschick and BassiriRad, 2010; Lubchenko and Karl, 2012) would increase the availability of injured trees. Greater severity and extent of bark beetle outbreaks in increasingly vulnerable forests pose a significant challenge to forest managers.

Effects on forest ecosystem services

Forests provide a number of important

ecosystem services (Schowalter, 2013) that are affected by bark beetles (see below). Bark beetles affect ecosystem services directly by killing trees and altering forest structure and composition. In addition, dead trees may increase the likelihood of subsequent fire or windthrow of isolated, surviving trees (Schowalter *et al.*, 1981a; McCullough *et al.*, 1998; Jenkins *et al.*, 2008).

Fiber and timber production have the best defined market values, making tree mortality to bark beetles appear largely destructive, especially in private commercial pine forests (Pye *et al.*, 2011). Pye *et al.* (2011) estimated that timber producers lost about \$1.2 billion to southern pine beetle, or \$43 million per year, over a 28-year period. Accelerated harvest reduces wood prices, gaining wood users about \$837 million, or \$30 million per year, over that period. Some non-host species that replace beetle-killed trees have lower commercial value. Therefore, in addition to lost timber production, tree mortality to bark beetles in some commercial forests may require unscheduled salvage harvest and replanting, which increase costs relative to revenue.

On the other hand, surviving host and non-host trees typically show increased growth following stand thinning by bark beetles. For example, Heath and Alfaro (1990) reported that growth rates of *P. contorta* and Douglas-fir (*Pseudotsuga menziesii*) had stagnated prior to an outbreak of *D. ponderosae*, but surviving trees showed significantly increased growth rates relative to rates prior to the outbreak or for non-infested stands. Romme *et al.* (1986) also reported that annual wood production by some ponderosa pine (*P. ponderosa*) stands thinned by *D. ponderosae* equaled or exceeded pre-outbreak levels within ten years. Therefore, if forests affected by bark beetles are not scheduled for harvest within this period, or if harvest can be delayed, lost timber resources may be largely replaced through

stimulated growth following an outbreak.

Public forests in North America and other regions are managed for multiple uses, including fiber and timber production, watersheds, fish and wildlife, recreation and, more recently, carbon sequestration and climate moderation (Müller and Job, 2009; Schowalter, 2013). Bark beetles can affect these services in a variety of ways, making assessment of net benefit or loss more complicated than reduced supply of fiber or timber resources (Tchakerian and Coulson, 2011).

Forest ecosystems are valued sources of fresh water, and this often is the primary management goal for forested watersheds (Schowalter, 2013). Tree mortality during bark beetle outbreaks increases water yields initially as a result of reduced foliage area and evapotranspiration and affects water quality through changes in nutrient fluxes and erosion (Leuschner, 1980; Tchakerian and Coulson, 2011; Edburg *et al.*, 2012). As coarse woody debris (from killed trees) decomposes, water storage capacity increases, and water yield would decline. The extent to which changes in water yield and quality are positive or negative depends on the area affected, needs of downstream communities and the duration of altered conditions. For example, increased water yield during a drought, a typical trigger for outbreaks (Mattson and Haack, 1987; Koricheva *et al.*, 1988; Schowalter, 2011), could be perceived as a benefit to the extent that it maintains a more constant water supply to municipalities compared to greatly reduced yield in the absence of tree mortality. By contrast, excess yield in some cases could flood downstream communities.

Wildlife and fish represent important food and recreational values provided by forests, and maintenance of their populations also is a primary forest management goal (Schowalter, 2013). For example, many woodpecker species, including the red-cockaded woodpecker,

Picooides borealis, and pileated woodpecker, *Dryocopus pileatus*, feed directly on bark beetles in the southern U.S. and may select bark beetle-killed trees for cavity nest sites (Tchakerian and Coulson, 2011). Hardwoods and other plant species replacing beetle-killed pines host a greater diversity and abundance of associated insects, fruits and nuts that provide food for a wider diversity of fish and wildlife species (Frady *et al.*, 2007; Tchakerian and Coulson, 2011).

Forest ecosystems provide various spiritual, recreational and other cultural services, including hiking, backpacking, hunting, fishing and educational and scientific activities (Coulson and Meeker, 2011; Schowalter, 2013). Extensive tree mortality resulting from bark beetle outbreaks may be viewed as unattractive or hazardous (Michalson, 1975). Sheppard and Picard (2006) compiled a number of studies in which subjects were shown pairs of photos, one with insect damage, the other without. In general, visual preference declined more steeply with increasing tree mortality below a threshold of about 10% of visual landscape affected than it did above this threshold. In some cases, visual preference was affected by a subject's awareness of the cause. Müller and Job (2009) reported that tourist attitudes toward bark beetle outbreaks in a national park in Germany were largely neutral and against control efforts but were more positive toward non-control among tourists who were more knowledgeable about bark beetles and the process of forest recovery following such natural disturbances. These results suggest that visual impact of an outbreak on viewers' perception peaks relatively early and that educational efforts may instill more positive public perception of outbreaks.

Bark beetles are instrumental in initiating decomposition of coarse woody debris, both by penetrating the bark barrier and by inoculating wood with

saprophytic microorganisms. Decomposition of coarse woody debris is significantly slower when bark beetles are excluded (Ausmus, 1977; Swift, 1977; Dowding, 1984; Edmonds and Eglitis, 1989; Zhong and Schowalter, 1989). Decomposition of coarse woody debris can increase the availability of nutrients, previously bound in wood, for plant uptake and incorporation in new foliage production (Wood *et al.*, 2009). However, pulses of woody debris deposition also can retard decomposition in some forests (Zimmerman *et al.*, 1995), and decomposition releases stored carbon to the atmosphere (Kurz *et al.*, 2008; Schowalter, 2011).

Large-scale pine mortality during outbreaks of bark beetles can reduce carbon uptake, as well as increasing carbon emission from decaying trees, resulting in a net flux of CO₂ from forests to the atmosphere, at least in the short term (Kurz *et al.*, 2008). However, Brown *et al.* (2010) noted that forests recovering from mortality to *D. ponderosae* remained growing-season carbon sinks as a result of increased photosynthesis by remaining healthy trees and understory vegetation. By contrast, nearby clear-cut harvested stands remained carbon sources ten years after harvest. They suggested that deferred harvest of insect-attacked stands with substantial secondary structure would prevent such stands from becoming carbon sources over extended periods. Furthermore, Brown *et al.* (2012) and Pfeifer *et al.* (2011) found that carbon stocks recovered to pre-outbreak levels within 25 years and as quickly as five years.

Clearly, bark beetles influence forest values and services in complex, potentially complementary, ways. Therefore, understanding the complex effects of bark beetles on long-term forest structure and biogeochemical cycling is necessary to evaluate all the benefits and costs of outbreaks in order to optimize management decisions (Edburg *et al.*, 2012; Schowalter, 2013).

Management options

The sensitivity of bark beetles to host condition and spacing make prevention of outbreaks through silvicultural practices relatively easy, whereas protection of beetles under bark for much of their life cycle makes control within trees extremely difficult and expensive. Obviously, applying preventative practices over large areas may be difficult or impossible, especially in mountainous terrain or during large-scale droughts or cyclonic storms (e.g., typhoons or hurricanes). When outbreaks do occur, or high value trees or stands are threatened, several remedial options should be considered.

Preventative options

The key to preventing bark beetle outbreaks is maintaining healthy, well-spaced trees. Appropriate tree species selection and regular thinning minimize the probability of environmental stress over the course of forest development and interfere with bark beetle population growth and spread.

Tree species selection, either at planting or through vegetation management, influences future bark beetle population growth. Tree species planted on sites where they did not occur historically become exposed to environmental conditions to which they are not adapted. Such trees may become stressed and susceptible to bark beetles. For example, loblolly pine planted on dry upland sites is likely to be stressed by water limitation (Schowalter, 2012), whereas longleaf pine (*P. palustris*), native to such sites, is more tolerant of drought and more resistant to bark beetles. Replacing commercial loblolly pine plantations with longleaf pine on drier sites in public forests in the southern U.S. has restored historic forest structure to these sites and mitigated bark beetle activity.

The diversity of site-adapted tree species

also reduces the likelihood of beetle outbreaks. A mixture of tree species creates a more complex environment within which beetles must detect and reach suitable hosts (Belanger and Malac, 1980). Hicks (1980) suggested that competition from lowland hardwood species predisposed pines to bark beetle attack. However, Schowalter and Turchin (1993) demonstrated that high density of loblolly pines increased the growth and spread of experimental *D. frontalis* populations, regardless of non-host density. Tree mortality was significantly higher in dense, pure pine stands, compared to low density pine stands, regardless of hardwood density (Fig. 4). In addition, diverse vegetation provides a diversity of habitat and prey resources that promotes predator, parasitoid and parasite populations (Berisford, 2011).

Host density can be maintained at levels that prevent bark beetle population growth in several ways. Planting density can be manipulated where conditions permit. Pine stands typically are harvested by clearcutting (all trees cut), although shelterwood, or selective, cutting (scattered trees left to provide natural seed source) also is practiced. Clearcutting requires replanting of pine seedlings, whereas shelterwood cutting relies on natural seedling recruitment. These two harvest practices have somewhat different consequences for bark beetles. Clearcutting followed by replanting produces even-aged pine forests with relatively little genetic variation, resulting in uniform stand structure and future susceptibility to bark beetles. Shelterwood cutting and natural seeding produce an uneven-aged forest with greater variation in future susceptibility to bark beetles.

Selective thinning to reduce pine density has been used widely to reduce the risk of outbreaks and their spread across forest landscapes (Brown *et al.*, 1987; Schowalter and Turchin, 1993; Turchin *et al.*, 1999a; Fettig *et al.*, 2007). Thinning

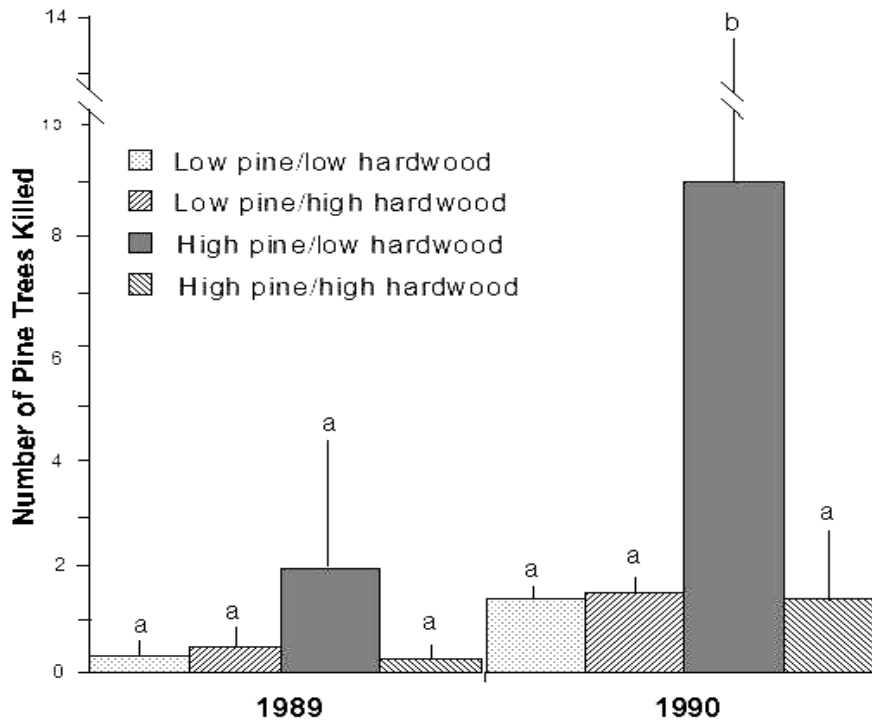


Fig. 4. Effect of host (pine) and non-host (hardwood) densities on population growth of *Dendroctonus frontalis*, measured as pine mortality, in 1989 (Mississippi) and 1990 (Louisiana). Low pine basal area is 11-14 m²/ha; high pine basal area is 23-29 m²/ha; low hardwood basal area is 0-4 m²/ha; high hardwood basal area is 9-14 m²/ha. Vertical lines indicate standard error of the mean. Bars under same letter did not differ at an experiment-wise error rate of $P < 0.05$ for data combined for the two years. From Schowalter and Turchin (1993).

reduces susceptibility to bark beetles in several ways (Fettig *et al.*, 2007). First, reduced host density directly reduces resource availability for beetles. Second, increased tree spacing reduces competition between trees for water and nutrients, minimizing and delaying effects of drought (Brown *et al.*, 1987). Third, a more open canopy reduces the effectiveness of pheromone communication between host-seeking beetles and colonized trees, thereby preventing mass attack, and raises stand temperatures to levels that can reduce beetle survival (Fares *et al.*, 1980; Amman *et al.*, 1988). Studies of bark beetle responses to host tree density indicate that tree mortality declines as

host density declines, with population spread and tree mortality virtually eliminated at an average host spacing of 6 m (Sartwell and Stevens, 1975; Schowalter *et al.*, 1981b; Amman *et al.*, 1988; Schowalter and Turchin, 1993).

Periodic natural or prescribed fires can reduce host density and growth of competing trees where access for silvicultural treatment may be difficult. Pine forests typically are adapted to survive frequent ground fires, but often become dense and more vulnerable to bark beetles (and catastrophic fire) where fire has been controlled. Fire also can scar trees and increase susceptibility to bark beetle colonization, but this effect typically

is short-lived and rarely contributes to beetle population growth (Fettig *et al.*, 2007).

Remedial options

Even when bark beetle outbreaks occur, control is not necessarily warranted. Small, local outbreaks may fail to spread for a number of reasons, including the unavailability of susceptible trees nearby (Schowalter *et al.*, 1981b), or environmental factors that preclude further population growth (Turchin *et al.*, 1999a, b). Effective management of outbreaks begins with early detection of growing populations, generally from aerial surveys or remote sensing imagery. Outbreaks revealed by these methods should be checked by ground personnel to ascertain the number of trees colonized and the density of beetle brood, if possible. Attention should be given to green trees that may be colonized but not yet symptomatic.

Several computerized models are available to predict the rate and extent of bark beetle population growth and tree mortality and evaluate the need for control efforts, including online options (Turnbow *et al.*, 1982; Stephen and Lih, 1985; Shaw and Eav, 1993; Salom *et al.*, 2003). However, the input requirements for various models must be considered in order to maximize accuracy and utility (Schowalter *et al.*, 1982). Furthermore, these models only predict beetle population size and tree mortality, i.e., numbers of host trees killed by oscillating populations of bark beetles. Evaluating the effects of tree mortality on ecosystem processes and services requires more complex models. General ecosystem models have not incorporated effects of insects, including bark beetles, on ecosystem processes and services, although several studies are pursuing this (e.g., Pfeifer *et al.*, 2011). Throop *et al.* (2004) assessed effects of N deposition and herbivory on C and N fluxes, using the CENTURY model

(Parton *et al.*, 1993), and predicted that herbivory would lead to depressed plant and soil carbon storage and N mineralization. Economic values of non-commodity services from forests also are poorly defined. Some efforts have been made to estimate values of non-commodity ecosystem services, based on user fees (e.g., for fresh water consumption, hunting licenses or recreation) (Costanza *et al.*, 1997), but require a number of controversial assumptions (Dasgupta *et al.*, 2000). Land or resource managers must depend on experience to assess the net effects of bark beetles on a variety of interacting ecosystem variables that affect management goals. If control of a bark beetle outbreak is necessary, several remedial options are available.

Insecticides generally are not a viable option for large infestations in forests, given the protection of immature stages within the subcortical habitat of trees, the short time that adults are exposed during dispersal and the toxicity of many insecticides to fish, bees and other beneficial species (Billings, 2011a, b). In fact, some chemicals registered for bark beetles are not registered for forestry settings (Billings, 2011a). Chemicals currently registered to protect trees include bifenthrin and permethrin (both pyrethroids) emulsifiable concentrates (EC). Carbaryl (a carbamate) wettable powder (WP) is registered for bark beetles and used to protect western conifers, but is not effective against the southern pine beetle (Billings, 2011a). Insecticides should be sprayed as high up the trunk of individual trees as possible, until the entire bole is wet (e.g., Billings, 2011a). Failure to soak the entire bole reduces penetration and mortality to beetles within the bark. Recent research has demonstrated that injection of individual trees with emamectin benzoate (an avermectin) water soluble (WS) or fipronil (a phenylpyrazole) EC may protect trees against bark beetles for more than one

year (Grosman and Upton, 2006; Grosman *et al.*, 2009; Billings, 2011a). Registration of these two chemicals is being pursued with U.S. Environmental Protection Agency. Given that insecticides are most effective for protecting individual, high value trees, their use will be most practical in urban and park settings.

Sanitation harvest and cut-and-leave options have been the most widely-used methods to disrupt outbreaks, depending on timber market and environmental constraints (Fettig *et al.*, 2007; Coleman *et al.*, 2008; Billings, 2011b). Salvage harvest captures some of the fiber or timber value of the wood resource. However, unscheduled salvage harvest increases the cost of forest management and may have undesired effects on wood supply for regional and global markets. Cut-and-leave involves cutting infested trees and leaving them on the ground, when removal is not feasible or permitted. Trees on the ground are exposed to high temperatures and desiccation that kill beetles in the tree (Wagner *et al.*, 1979; Gagne *et al.*, 1980). Forest managers should be aware that the window of opportunity for terminating bark beetle population growth is rather narrow, because populations reaching a release threshold by early spring may have sufficient reproductive momentum to escape normal regulatory factors (Schowalter *et al.*, 1981b). Care should be taken to ensure that all infested trees are cut, including those which may not show symptoms yet, to prevent continued population growth from remaining infested trees. Furthermore, any trees within a buffer strip, equal in width to the average tree height in the stand, in advance of the infested trees should be cut to remove resources for any beetles that remain (Billings 2011b).

Attractive or repellent chemicals can be used to protect trees or stands (Progar, 2005; Borden *et al.*, 2008; Ross and Wallin, 2008; Strom and Clarke, 2011; Xie and Lv, 2012). This strategy employs attractive

chemicals to trap-out beetles lured to baited traps or repellent chemicals to disperse beetles to non-threatening population densities. For example, β -caryophyllene plus α -pinene can be used to trap and reduce numbers of *D. armandi* in China (Xie and Lv, 2012); two repellent chemicals are registered for control of *D. frontalis* in the southern U.S., 4-allylanisole (4-AA) for protection of individual trees and verbenone for protection of stands (Hayes and Strom, 1994; Billings *et al.*, 1997; Fettig *et al.*, 2007; Sullivan *et al.*, 2007; Strom and Clarke, 2011). Local outbreaks of up to 80 trees infested by *D. frontalis* can be controlled with verbenone bags attached to newly attacked pines and adjacent uninfested trees (Goyer *et al.*, 1998). Two or more bags applied at 40 ml per 0.1 m² basal area are attached at 3-4 m height using long-handled hammers. The bags release verbenone for at least six weeks. Infestation growth was reduced about 75% and control achieved in 85% of treated stands. In larger infestations up to 120 infested trees, application of verbenone at 25 ml per 0.1 m² basal area, with felling of infested trees, reduced infestation growth 82-99% and achieved control in 80-100% of treated stands in five southern states. Although these pheromones have proven useful in the western U.S., they are not cost-effective for operational control of *D. frontalis* in the southern U.S., largely due to the short life cycle, multiple generations per year, and rapid population growth of this beetle (that create a very narrow window of opportunity for effective application) and difficulties with formulation consistency, cost, durability and elution rates (Sullivan *et al.*, 2007; Strom and Clarke, 2011). Furthermore, this tactic will not protect stressed or weakened trees or trees near large populations of bark beetles (Strom *et al.*, 2004).

A large number of competitors, predators and parasites are known to cause high mortality to bark beetle brood,

and some may be important in the collapse of bark beetle epidemics (Stephen *et al.*, 1993; Turchin *et al.*, 1999b; Gilbert and Grégoire, 2003; Berisford, 2011; Reeve, 2011; Stephen and Clarke, 2011). However, biological control generally is not feasible, given the rapid rate of bark beetle movement and difficulty of mass rearing appropriate predators or parasitoids (Stephen and Berisford, 2011), although Gilbert and Grégoire (2003) reported an inverse correlation between abundances of *D. micans* and of *Rhizophagus grandis* released for biological control. At this time, protection of natural enemy populations has been the primary focus of biological control efforts in the southern and western U.S. For example, aerial application of an artificial nutritive source could increase parasitoid longevity, fecundity and effectiveness against bark beetles (Stephen and Berisford, 2011).

Finally, painting tree boles white can disrupt their outline and prevent attraction of bark beetles to dark vertical silhouettes (Strom *et al.*, 1999). A combination of white paint and 4-AA repellent reduced the number of southern pine beetles collected in traps by 83-97% in experiments in Florida and Louisiana (Strom *et al.*, 1999). Obviously, this tactic is more expensive than alternatives for protection of multiple trees but may be feasible for preventing aggregation on individual high-value trees, especially in parks or urban situations.

Given the high cost of control, relative to the marginal profits of timber production, default management typically has favored short rotation schedules. Stands typically are harvested before they become most vulnerable to bark beetles. Although this strategy may be appropriate for private forests managed primarily for fiber or timber production, it is less practical on public forests managed for multiple uses, which include habitat values provided only by older trees that often are more vulnerable to bark beetles (Eckhardt and

Menard, 2008). The most appropriate management in public forests emphasizes preventative options and restricts remedial tactics to targeted, high-value sites, such as parks or endangered species habitats, with acceptance of risk and treatment of individual spots at a threshold of ten trees in the surrounding forest matrix.

Conclusions and recommendations

Bark beetles have been a primary factor affecting the structure of pine forests. Although tree mortality to bark beetles often detracts from forest management goals, especially in commercial plantations, or residential values, bark beetles also can enhance water resources, fish and wildlife in ways that should be considered in making management decisions.

Prevention of bark beetle outbreaks exploits beetle sensitivity to host tree condition and spacing. Maintaining healthy trees and thinning, as necessary, to create barriers to beetle population growth and spread will reduce tree mortality and control costs. Salvage harvest, protection of individual trees with insecticides or white paint to disrupt the dark silhouette of the bole, and pheromones for trap-out or disruption of host location can limit tree mortality but are labor intensive and increase costs of fiber and timber production. These tactics are less appropriate in public forests managed for values provided by older, more vulnerable trees. High-value sites for cultural or endangered species protection may require use of more expensive management options.

Future needs include improved information on effects of bark beetles on multiple ecosystem services and trade-offs among effects in public forests. Research also should provide more effective options for protecting high value trees, including systemic insecticides, while minimizing non-target effects.

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小蠹蟲的生態和管理

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摘要

小蠹蟲 (bark beetle) (鞘翅目：象鼻蟲科：小蠹亞科) 被認為是威脅整個北半球森林的主要害蟲。儘管小蠹蟲造成的樹木死亡率往往會減損森林管理的目標，但是小蠹蟲具有一些天然的作用，它們能夠使林冠疏開、疏伐及林分結構和組成多樣化，這些作用能夠為多目標利用的森林管理提供一些生態系統服務。預防小蠹蟲大發生的策略乃利用其對寄主樹木的條件和間距的敏感性，及其依賴費洛蒙誘引足夠數目的小蠹蟲來壓制樹木的防衛。種植時樹種的選擇或選擇性疏伐都有助於樹種更能容忍生育地條件及抵抗小蠹蟲。早期商業性疏伐或商業性疏伐可以增強樹木的條件，並創建甲蟲族群增長和擴散的障礙。補救措施包括殘材伐採、費洛蒙誘殺，或破壞其對寄主的定位，及樹幹塗白漆以消除樹幹較暗的輪廓。基於人力成本以及採用的方法與纖維和木材生產的邊際利潤之間的權衡，在小蠹蟲攻擊前伐採，或在攻擊後殘材伐採，都是可行的管理策略。然而，此策略不適用管理公有林中價值高但樹齡大及較脆弱的樹木。具文化或瀕危物種保護的高價值生育地，可能需要使用更昂貴的管理措施。

關鍵詞：小蠹亞科、擾亂、族群動態、生態系統服務、寄主密度。

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