



Ecology and Management of Bark Beetles (Coleoptera: Curculionidae: Scolytinae) in Southern Pine Forests

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ABSTRACT. Bark beetles (Coleoptera: Curculionidae: Scolytinae) have been an important historic and current factor affecting pine forest production in the southern United States. 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 spacing and reliance on pheromones to attract sufficient numbers to overwhelm tree defenses. Tree species selection at planting or through selective thinning can favor pine species that are more tolerant of site conditions and resistant to bark beetles. Precommercial 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 or endangered species protection may require use of more expensive management options.

Key Words: *Dendroctonus frontalis*, *Ips*, thinning, pheromones, sanitation harvest

Historically, bark beetles (Coleoptera: Curculionidae: Scolytinae) have been the primary threat to mature pine forests and forest management in the southeastern United States (Fettig et al. 2007). Periodic outbreaks of bark beetles cause annual losses of millions of dollars and pose serious challenges for forest managers (Price et al. 1998), 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.

Several aspects of bark beetle ecology should be considered in planning bark beetle management in southern pine forests. First, effects of these beetles on ecosystem services are not necessarily destructive and, in some cases, may contribute to management objectives in multiple-use forests. Second, these beetles are controlled naturally by environmental factors that can be manipulated through management practices. Although preventative measures are most effective in minimizing losses to these beetles, several remedial options can help to suppress outbreaks.

Historical Perspective

The southern pine region, from Virginia to Texas, is divided into two major subregions with relatively distinct forest conditions and vulnerability to bark beetles (Schowalter et al. 1981a). The Coastal Plain is a relatively flat lowland with poor drainage and seasonal flooding. Historically, loblolly pine, *Pinus taeda* L., codominated lowland forests with oaks, *Quercus* spp.; sweetgum, *Liquidambar styraciflua* L.; elm, *Ulmus americana* L.; and other hardwoods. Loblolly pine is relatively susceptible to bark beetles and is particularly susceptible to drought stress, which increases its vulnerability to bark beetles (Schowalter et al. 1981a). The Piedmont is a hilly upland, above the fall line, that is characterized by well-drained soils and propensity for drought and lightning-initiated fire. Piedmont forests historically were dominated by savannahs or open woodlands of drought- and fire-tolerant longleaf, *P. palustris* Miller, and shortleaf, *P. echinata* Miller, pines with an oak subcanopy; patches dominated by scrub oaks occurred on particularly dry sites. Longleaf pine is particularly resistant to bark beetles (Schowalter et al. 1981a).

Historically, bark beetle outbreaks were relatively rare and confined to landscape patches dominated by dense or aging pine hosts (Schowalter et al. 1981a). Under these conditions, bark beetles acted as natural thinning agents, killing injured or stressed hosts (especially where host pines grew close together and became competitively stressed) and maintaining wide spacing of host trees and a diversity of associated hardwoods, shrubs, grasses, or both (Fig. 1). Outbreaks were self-limiting, as mortality to hosts reduced resource availability across forested landscapes (Cairns et al. 2008).

As a result of changes in land use and selection for more rapidly growing pine species over the past century, much of the southern pine region is now dominated by large plantations of loblolly pine, with closely-spaced host trees that create easy access to stressed hosts for bark beetles (Schowalter and Turchin 1993). Consequently, there are relatively few barriers to spread of growing populations of these insects across landscapes, and bark beetles may kill host trees over large areas during outbreak years. Increasing concern about forest health and multiple-use management of public lands in the region have focused attention on bark beetles.

Bark Beetle Ecology

Bark beetles of greatest concern include the southern pine beetle, *Dendroctonus frontalis* Zimmerman, and several species of *Ips*: six-spined ips, *I. calligraphus* (Germar); eastern fivespined ips, *I. grandicollis* (Eichhoff); and small southern pine engraver, *I. avulsus* (Eichhoff). These species often co-occur in susceptible trees, but individual species also are capable of independent outbreaks in situations where other species are relatively rare.

All four beetle species colonize the phloem of all southern pine species, and all beetle species can colonize extensive portions of the bole in the absence of other species. However, when all four species colonize the same tree, southern pine beetles generally occur on the lower bole, sixspined ips on higher portions, five-spined ips above that, and small southern pine engraver on the highest portions and in larger branches. Southern pine beetles are monogamous, with females initiating gallery construction, whereas the *Ips* species are polygamous, with males initiating bark penetration and forming a nuptial chamber and multiple females excavating separate galleries radiating

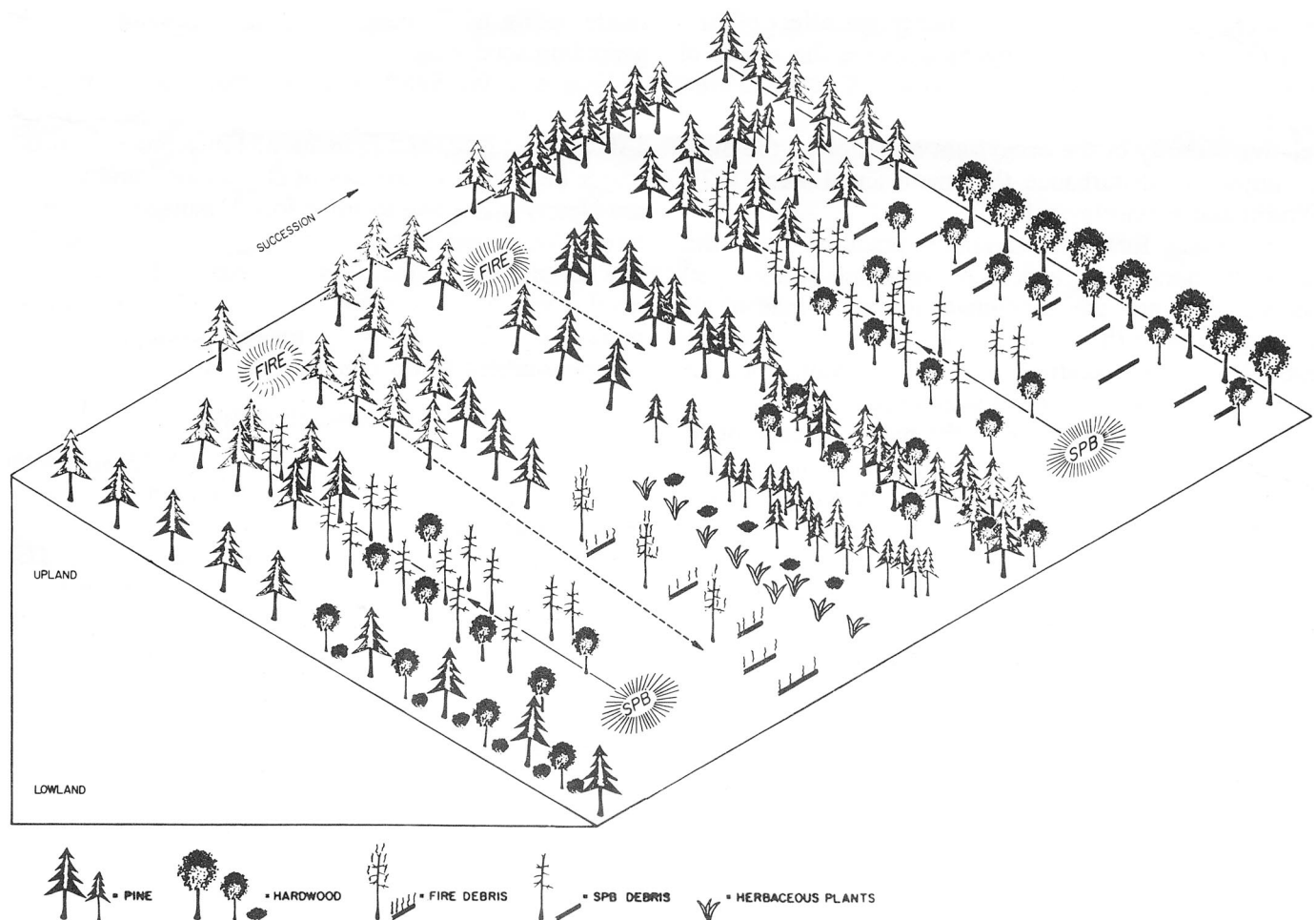


Fig. 1. Diagrammatic representation of interactions between southern pine beetle and fire in the southeastern coniferous forest. Successional transitions extend from left to right; dotted arrows indicate direction of movement. Fire is a regular feature of the generally dry uplands, but moves into generally moist lowlands where drought or southern pine beetle creates favorable conditions for combustion. Southern pine beetle is a regular feature of both forests, but is most abundant where pines occur at high density and stress levels. Fire is necessary for regeneration of pines, especially after succession to hardwoods if fire return is delayed. From Schowalter et al. (1981a).

from the nuptial chamber. Eggs are laid in niches along the gallery. Larvae feed as they excavate mines radiating from the egg galleries, eventually pupating at the ends of their mines (Fig. 2). Southern pine beetle larvae move into the outer bark to pupate.

Several aspects of bark beetle biology contribute to their ability to cause significant tree mortality. First, though small, these beetles can aggregate in large numbers on individual trees, because of effective pheromone communication (Raffa et al. 1993). The particular pheromones used to attract conspecifics differ among species, but all can be attracted to trees being attacked by others. 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). 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. However, the fungi also cause brood mortality that explains life stage adaptations to avoid infected areas. Third, these beetles are highly sensitive to tree spacing. The likelihood of mortality to nearby trees declines exponentially with distance from source trees. Trees beyond 6 m (20 feet) from source trees are unlikely to be attacked, except at very high beetle population sizes (Schowalter et al. 1981b).

Although bark beetles often are blamed for forest health problems, healthy trees are capable of defense against bark beetles. Therefore, outbreaks of bark beetles are less a threat to forest health than a

symptom of abundant trees in poor health. Healthy pine trees defend themselves through a combination of 1) resin (pitch) flow, which prevents attacking beetles from penetrating the bark barrier (Fig. 3) (Schowalter 2011, Tisdale et al. 2003); and 2) 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. Injured or stressed trees have impaired defensive ability and become vulnerable to bark beetle colonization (Lorio 1993, Nebeker et al. 1993, Lombardero et al. 2006). Fewer beetles are necessary to overwhelm the defensive capability of weakened trees, compared with healthy trees. For example, at least 100 beetles per m² bark surface area are necessary to overcome the defenses of the “average” loblolly or shortleaf pine (Hodges et al. 1979).

Disturbances are especially important as triggers for bark beetle outbreaks. Widespread tree injury or stress as a result of storm damage (Nebeker et al. 1993), fire (Lombardero et al. 2006), or drought (Mattson and Haack 1987) increases the availability of susceptible trees near bark beetle refuge trees. Ironically, the most rapidly-growing loblolly pines also are highly vulnerable 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.



Fig. 2. Gallery structure of the southern pine beetle in loblolly pine bark, viewed outward from the phloem-cambium interface.

As a result of tree defensive ability, endemic bark beetle populations are restricted to isolated injured trees, especially those trees that are lightning-struck or diseased (Flamm et al. 1993, Paine and Baker 1993). Widespread tree injury or stress during storms, fire, or drought periods allow small populations to grow sufficiently in weakened trees to kill surrounding live trees within 6 m, initiating a “spot” (Fig. 4) (Schowalter and Turchin 1993). Beetle-killed trees can be distinguished by the reddish color of their foliage, compared with yellow for trees dying from other causes (Fig. 4). 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 (Fig. 5).

Effects on Forest Ecosystem Services

Forests provide a number of important ecosystem services that are affected by bark beetles. 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, Jenkins et al. 2008). Whereas bark beetles promote succession to nonhost hardwoods, fire truncates succession at the pine forest stage (Fig. 6) (Schowalter et al. 1981a, Brose and Waldrop 2010). Bark beetles



Fig. 3. The oleoresin, or pitch, flowing from severed resin ducts constitutes a physical-chemical defense that hinders penetration of the bark barrier by insects and pathogens. From Schowalter (2011) with permission from Elsevier.



Fig. 4. Southern pine beetle “spot” in an even-aged loblolly pine plantation. U.S. Forest Service photo.

thereby diversify the landscape and reduce the likelihood of future outbreaks (Cairns et al. 2008, Coleman et al. 2008).

Fiber and timber production have the best defined 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-yr period. Accelerated harvest reduces wood prices, gaining wood users about \$837 million, or \$30 million per year, over that period. Hardwood species that replace beetle-killed pines have lower commercial value. Therefore, in addition to lost timber production, pine mortality to bark beetles in commercial forests requires unscheduled salvage harvest and replanting, which increase costs relative to revenue. However, public forests in North America are managed for multiple uses, including fiber and timber production, watersheds, fish and wildlife, recreation and, more recently, carbon sequestration. 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. Tree mortality during bark beetle outbreaks increases water yields as a result of reduced foliage area and evapotranspiration (Leuschner 1980, Tchakerian and Coulson 2011). The extent to which such changes in water yield are positive or negative depends on the needs of downstream communities. For example, increased water yield during a drought, a typical trigger for outbreaks (Mattson and Haack 1987, Schowalter 2011), could be perceived as a benefit to the extent that it maintains a more constant water supply to municipalities compared with 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. Many woodpecker species, including the red-cockaded woodpecker, *Picoides borealis* Vieillot, and pileated woodpecker, *Dryocopus pileatus* (L.), feed directly on bark beetles and may select bark beetle-killed trees for cavity nest sites



Fig. 5. Coalescing spots of southern pine beetle infestation in loblolly pine forest. U.S. Forest Service photo.



Fig. 6. Successional transition from pine-dominated forest to hardwood forest in the wake of southern pine beetle infestation. In the absence of fire, shade-tolerant hardwoods eventually replace shade-intolerant pines naturally.

(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 (Fradley 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). 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 $\approx 10\%$ of visual landscape affected than it did above this threshold. Furthermore, visual preference was affected relatively little by a subject's awareness of the cause. These results suggest that visual impact of an outbreak on viewers' perception peaks relatively early and that education has relatively little effect on public perception.

Large-scale pine mortality during outbreaks of bark beetles can reduce carbon uptake and increase carbon emission from decaying trees, resulting in a net flux of CO_2 from forests to the atmosphere (Kurz et al. 2008). However, Brown et al. (2010) noted that forests recovering from mortality to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, 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 10 yr 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.

Management Options

The keys to managing bark beetles are maintaining healthy, site-adapted tree species and adequate spacing between host trees. Maintaining healthy trees over large areas is difficult or impossible, espe-

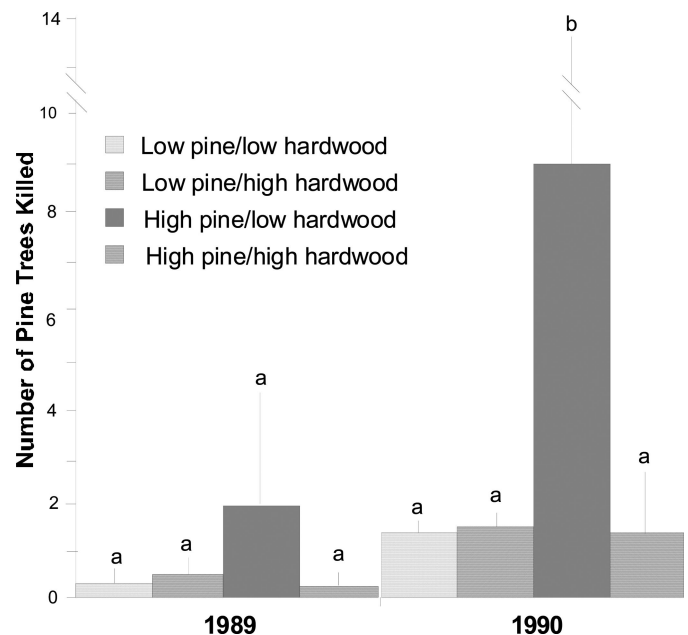


Fig. 7. Effect of host (pine) and nonhost (hardwood) densities on population growth of the southern pine beetle, measured as pine mortality in 1989 (Mississippi) and 1990 (Louisiana). Low pine basal area is 11–14 m^2/ha (50 $\text{feet}^2/\text{acre}$); high pine basal area is 23–29 m^2/ha (100 $\text{feet}^2/\text{acre}$); low hardwood basal area is 0–4 m^2/ha (15 $\text{feet}^2/\text{acre}$); high hardwood basal area is 9–14 m^2/ha (45 $\text{feet}^2/\text{acre}$). Vertical lines indicate standard error of the mean. Bars within same letter did not differ at an experiment-wise error rate of $P < 0.05$ for data combined for the 2 yr. From Schowalter and Turchin (1993) with permission from the Society of American Foresters.

cially during severe, large-scale droughts or storms (e.g., hurricanes). However, appropriate tree species selection and stand thinning minimize the probability of environmental stress and have been used successfully to prevent bark beetle outbreaks. Such options address the conditions that lead to outbreaks and are, therefore, the best means of preventing outbreaks. Should these options fail to prevent an outbreak, several remedial options also have had some success in terminating outbreaks.

Preventative Options. Tree species selection, either at planting or through vegetation management, can influence bark beetle populations. Tree species introduced on sites where they did not occur historically become exposed to environmental conditions to which they are not adapted and often become susceptible to bark beetles. For example, loblolly pine planted on dry upland sites is likely to become stressed by water limitation. Replacing loblolly pine plantations with longleaf pine on upland sites in several public forests has restored historic forest structure to these sites. Longleaf pine is more tolerant of drought and fire and resistant to bark beetles, compared with loblolly pine, thereby reducing the incidence and extent of bark beetle outbreaks on these sites. Pine forests typically are adapted to survive frequent ground fires. Periodic prescribed fires can reduce density and growth of competing trees. Fire also can scar trees and increase susceptibility to bark beetle colonization, but this effect is short-lived and rarely contributes to population growth (Fettig et al. 2007).

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 southern pine beetle populations. Tree mortality was

significantly higher in dense, pure pine stands, compared with low density pine stands, regardless of hardwood density (Fig. 7).

Selective thinning to reduce pine density also reduces the risk of outbreaks and their spread across forest landscapes (Brown et al. 1987, Schowalter and Turchin 1993, Turchin et al. 1999, Fettig et al. 2007). Thinning reduces susceptibility to bark beetles in several ways (Fettig et al. 2007): 1) Reduced host density directly reduces resource availability for beetle populations; 2) increased tree spacing reduces competition between trees for water and nutrients, minimizing and delaying effects of drought (Brown et al. 1987); and 3) a more open canopy reduces the effectiveness of pheromone communication between host-seeking beetles and beetles at colonized trees and raises stand temperatures to levels that can reduce beetle survival (Fares et al. 1980, Amman et al. 1988). Studies of southern pine 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 (20 feet) (Schowalter et al. 1981b, Schowalter and Turchin 1993).

Pine stands typically are harvested by clearcutting (all trees cut), although shelterwood cutting (scattered trees left to provide natural seed source) also is practiced. Clearcutting requires replanting of pine seedlings. 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 composition and future susceptibility to bark beetles. Shelterwood cutting and natural seedling produce a more uneven-aged forest with greater variation in future susceptibility to bark beetles.

Remedial Options. Even when bark beetle spots develop, control is not necessarily warranted. Spots may fail to grow beyond a certain size 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. 1999). Effective management of outbreaks begins with early detection of growing spots, generally from aerial surveys or remote sensing imagery. Spots revealed by these methods should be checked by ground personnel to ascertain the number of trees infested and density of beetle brood, if possible. Attention should be given to green trees that may be infested 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, Salom et al. 2003). However, the input requirements for various models must be considered to maximize accuracy and utility (Schowalter et al. 1982). Furthermore, these models only predict beetle population size and tree mortality (i.e., numbers of pine trees killed by oscillating populations of bark beetles). Evaluating the effects of tree mortality on ecosystem processes and services requires more complex models, which have not been developed for southern pine forests. General ecosystem models have not incorporated effects of insects, including bark beetles, on ecosystem processes and services. One exception is Throop et al. (2004), who 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 noncommodity services from pine forests also are poorly defined. Some efforts have been made to estimate values of noncommodity 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, 2011b). In fact, some chemicals registered for bark beetles are not registered for forestry settings (Billings 2011a). Chemicals currently registered to protect southern pines include bifenthrin and permethrin (both pyrethroids) emulsifiable concentrates (EC). Although carbaryl (a carbamate) wettable powder (WP) is registered for bark beetles and used to protect western pines, it 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 (Billings 2011a). Failure to soak the entire bole reduces penetration and mortality to insects 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 1 yr (Grosman and Upton 2006, Grosman et al. 2009, Billings 2011a). Registration of these two chemicals is being pursued with the 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 spot growth, 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 threshold of $\approx 100,000$ beetles in a 10-tree spot by early June may have sufficient reproductive momentum to escape normal regulatory factors (Schowalter et al. 1981b). Population growth generally can be truncated by cutting infested trees when a spot reaches a size of 10 infested trees. However, care should be taken to ensure that all infested trees are cut, including those trees that may not show symptoms yet, to prevent continued population growth from remaining infested trees. Consequently, all trees within a buffer zone 10 m in advance of the infested spot generally are cut (Fig. 8).

Bark beetle pheromones can be used to protect trees or stands (Strom and Clarke 2011). This strategy employs attractive pheromones to trap-out beetles lured to baited traps or repellent pheromones to disperse beetles to nonthreatening population densities. Two pher-



Fig. 8. Control of southern pine beetle infestation in a loblolly pine plantation by means of a 10-m (30 feet) barrier to prevent continued spread. Note the greater degree of tree mortality in the even-aged pine plantation compared with the older, more diverse infestation source across the road. U.S. Forest Service photo.

omones are registered for control of southern pine beetle, 4-allylani-sole (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). Small spots of up to 80 infested trees 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 (0.5 oz. per ft²) basal area are attached at 3–4 m (10–12 feet) height using long-handled hammers. The bags release verbenone for at least 6 wk. Infestation growth was reduced ≈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 (0.87 oz. per ft²) 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. However, at this time, these pheromones have not proven to be cost-effective for operational control of southern pine beetle, largely because of the short life cycle and rapid spot 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 associated with southern bark beetles (Stephen et al. 1993, Stephen and Clarke 2011). Several species are known to cause high mortality to bark beetle brood, and some may be important in the collapse of bark beetle epidemics. However, manipulation of biocontrol agent abundance has not proven to be feasible, given the rapid rate of bark beetle movement and difficulty of mass rearing appropriate predators or parasitoids (Stephen and Berisford 2011). At this time, protection of natural enemy populations has been the primary focus of biological control efforts. 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 red-cockaded woodpecker habitats, with acceptance of risk and treatment of individual spots at a threshold of 10 trees in the surrounding forest matrix.

Conclusions and Recommendations

Bark beetles have been a primary factor affecting the structure of pine forests in the southern United States. 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, although minimizing nontarget effects.

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