SOUTHERN PINE BEETLE II

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Southern Pine Beetle II

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Preface

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) has been studied extensively from a variety of perspectives since the early 1960s. Much of the emphasis has been directed to research (the acquisition of new knowledge), development (integration and interpretation of existing knowledge), and application (use of knowledge for planning, problem solving, and decision support). The southern pine beetle was the focus of two major federally funded programs conducted between 1973 and 1985: the Expanded Southern Pine Beetle Research and Application Program (ESPBRAP) and the Integrated Pest Management Program (IPM Program). Two seminal publications were produced from these efforts:

Thatcher, R.C.; Searcy, J.L.; Coster, J.E.; Hertel, G.D., eds. 1980. The southern pine beetle. Tech. Bull. 1631. Washington, DC: U.S. Department of Agriculture Forest Service, Expanded Southern Pine Beetle Research and Applications Program. 265 p.

Branham, S.J.; Thatcher, R.C., eds. 1985. Integrated pest management research symposium: the proceedings. Gen. Tech. Rep. SO-56. New Orleans, LA: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 383 p.

The Thatcher and others (1980) document was intended to be an interpreted synthesis of the current state of knowledge on the southern pine beetle, and it is highly regarded today for accomplishing this end. The Branham and Thatcher (1985) document was a comprehensive report for the projects associated with the IPM Program, and for this reason, it did not provide an updated interpretation of knowledge, although it is a very useful contribution. In the nearly 30 years since the last synthesis of knowledge on the southern pine beetle, the insect has continued to be a significant pest organism and consequently the object of considerable investigation. In this interim, the nature of the research arena and the forest environment changed significantly. The tools and technologies from the digital age were mainstreamed into scientific inquiry, and new discoveries followed. The nature of the forest changed dramatically as industrial ownership diminished, human populations encroached into the forest environment, and recreational demands on the forest landscape expanded. These changes affected the economic, ecological, social, and political impacts of the southern pine beetle in unique and undefined ways. Finally, an additional significant research initiative was funded by the USDA Forest Service, Southern Research Station, in the early 2000s to address southern pine beetle biology and management within this new context. Consequently, the project presented here was initiated to provide a contemporary and freshly interpreted summary of the state of knowledge of the southern pine beetle. The following volume, *The Southern Pine Beetle II*, was produced from the labors of a suite of knowledgeable authorities representing both scientists and practitioners.

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Introduction

The knowledge base for the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae), has increased dramatically since the last comprehensive and interpretative summary (Thatcher and others 1980). This insect continues to be a significant pest affecting the forest environment of the Southern United States and adjoining States, and it is also the subject of considerable ongoing basic research. The knowledge base for the SPB is therefore broad-based and ranges from practical information that forms the foundation for integrated pest management (IPM) to basic discoveries that define scientific understanding of the roles this organism plays in the natural environment. Accordingly, the goal of *The Southern Pine Beetle II* is to provide a synthesis of new and existing knowledge to address both practical application as well as advancement of scientific understanding.

The subject content of *The Southern Pine Beetle II* is illustrated in Figure 1. At the onset of the project, the technical substance and organization of the volume was critically examined and subsequently defined by the editors (Robert N. Coulson and Kier D. Klepzig) and a knowledgeable steering committee that included Matthew P. Ayres (Dartmouth College), Fred P. Hain (North Carolina State University), James R. Meeker (USDA Forest Service, FHP), and Frederick M. Stephen (University of Arkansas). This committee also identified authors for the individual chapters that collectively define the volume. This approach to the organization of *The Southern Pine Beetle II* was taken to provide an integrative structure to the volume as well as a comprehensive summary of technical knowledge; i.e., the vision was for the sum to be more than the individual parts.

The Southern Pine Beetle II consists of five basic sections: Ecology, Impact, Silviculture and Management, Treatment Tactics and Strategies, and Integrated Pest Management. The first section dealing with SPB ecology consists of three subsections that include chapters addressing the SPB from different levels of integration: individuals (systematics, natural history, and behavior), populations (within-tree, within-stand, within-landscape, and within-ecoregion), and communities (parasites, symbionts, predators, mutualists and phorants, competitors, and the bark beetle guild). The second section addresses SPB impact and includes two separate subsections: impact assessment (economic, ecological, social, and political) and monitoring (state and private forests and the public forests). The subsection dealing with state and private forests contains one chapter. The subsection on public forest monitoring consists of four chapters: aerial sketchmapping, survey, database management, and operational use of survey information. The third section deals with silviculture and management and includes chapters on risk and hazard assessment, forest establishment, and restoration. The fourth section considers the various treatment tactics and strategies applied for suppression of population and prevention of outbreaks of the insect. It includes chapters dealing with chemical pesticides, semiochemical (behavioral chemicals), and mechanical methods for control. The fifth and final section deals with integrated pest management. It draws together the extant scientific and technical information useful in managing the impacts of the SPB forest landscapes of the South.

The authors who contributed the individual chapters of *The Southern Pine Beetle II* are recognized authorities in the respective domains of their contributions. The authors represent a blend of individuals who have, in some cases, devoted a significant portion of their professional careers to investigations of the SPB and new personalities who have brought fresh perspectives to the research arena. The chapters have been peer reviewed, but judgments on content and interpretation remain those of the authors. Beyond their economic importance, bark beetles are fascinating organisms that have captured the interests of prominent forest entomologists for more than a century. The SPB is among the most thoroughly studied forest insects, and this volume is intended to summarize and interpret the knowledge base for this species.

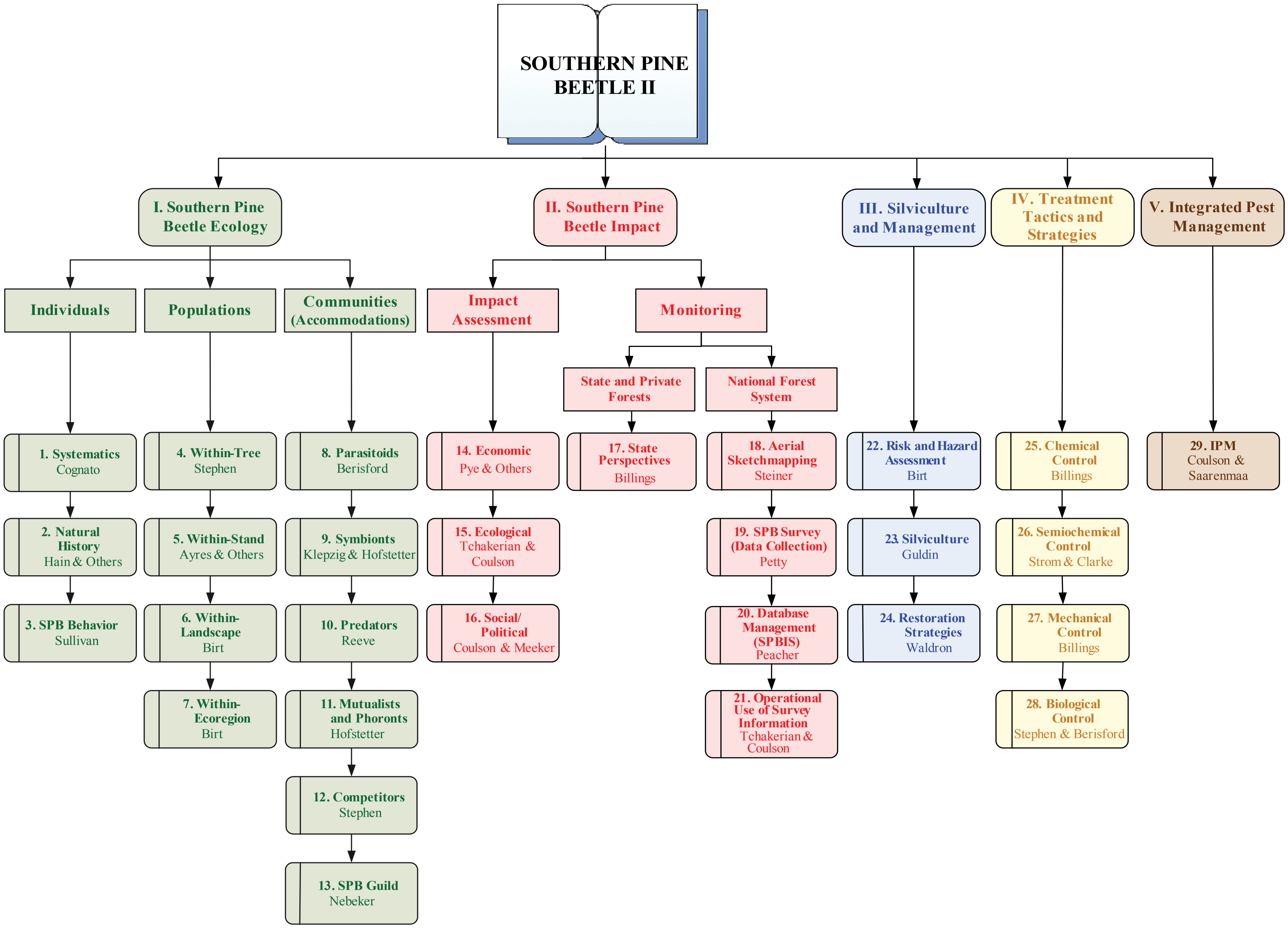

Figure 1— Diagrammatic representation of the organization and content of *The Southern Pine Beetle II*. The text is organized into five sections and 28 chapters that address southern pine beetle ecology impact, silviculture and management, treatment tactics and strategies, and integrated pest management.

Section I

I. Southern Pine Beetle Ecology

Section I addresses southern pine beetle ecology. This section is organized topically into three units and includes chapters associated with individual organisms, populations, and communities (Figure I.1). The unit that addresses individuals (the autecology of the southern pine beetle) contains three chapters that consider the systematic placement of the insect, natural history, and general behavior. This overview is intended as a prelude to the more detailed and technical chapters that follow in the remaining sections. The second unit deals with population dynamics of the southern pine beetle. Historically, studies of population dynamics (causes for change in the distribution and abundance of the southern pine beetle) have been organized around spatial and temporal extent and include investigations of the insect occurring within trees, within stands (infestations), within landscapes, and within ecoregion (the southern pine forest). Individual chapters are devoted to each of these topics. The third unit deals with community relationships; i.e., the assemblage of populations of organisms associated with the southern pine beetle and the accommodations that the different species make for each other. This unit contains six chapters and includes an examination of parasites, symbionts, predators, mutualists and phoronts, competitors, and the southern pine bark beetle guild.

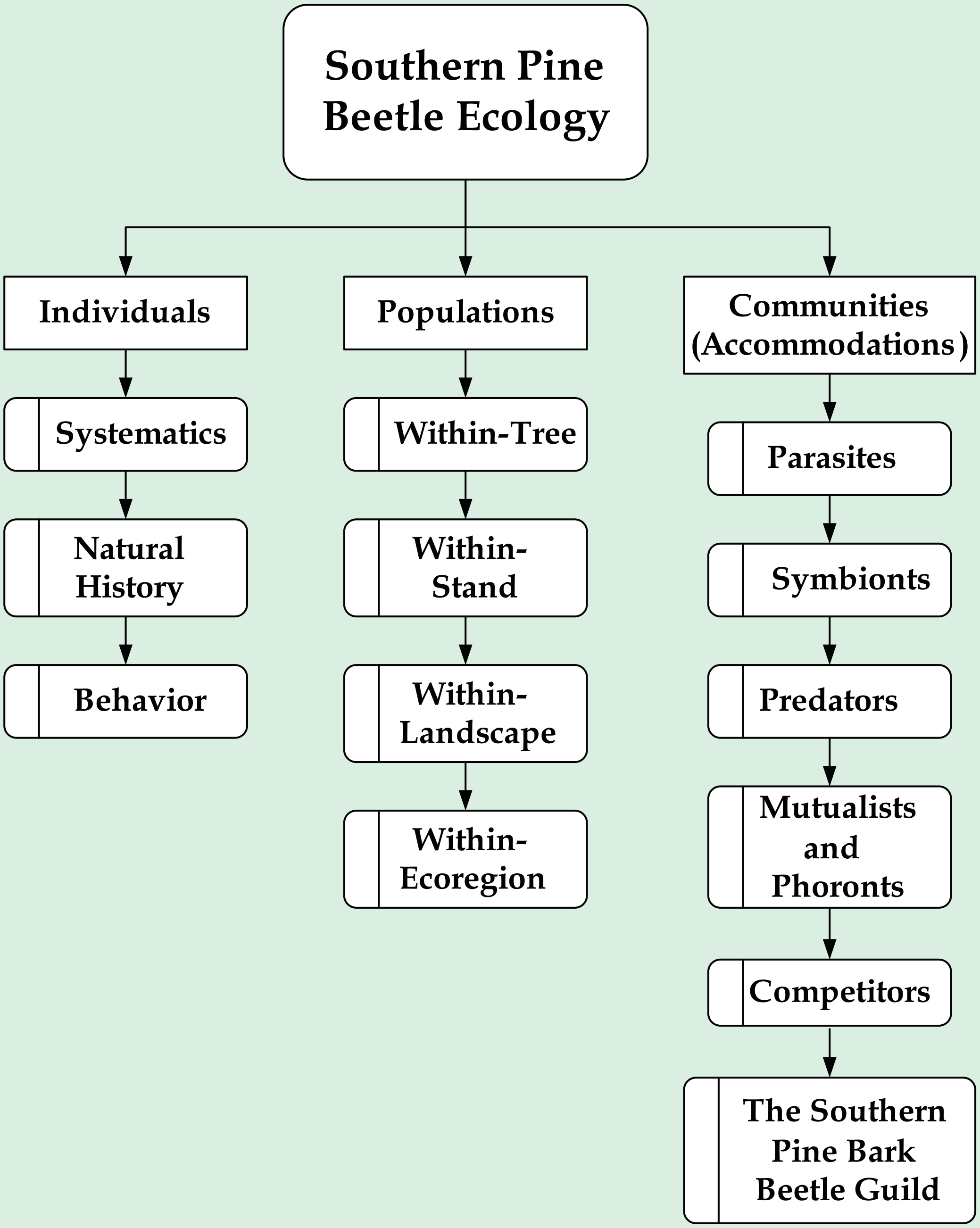

Figure I.1—Diagrammatic representation of the organization of Section I of *The Southern Pine Beetle II* dealing with ecology. The unit is organized into three subsections and 13 chapters that address individuals (systematic, natural history, and behavior), populations (within tree, within stand, within landscape, and within ecoregion), and communities (parasites, symbionts, predators, mutualists and phorants, competitors, and the southern pine bark beetle guild). This section addresses ecology of the southern pine beetle.

1

A Review of *Dendroctonus frontalis* Zimmermann Systematics

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Keywords

diagnostic characters
molecular phylogeny
Scolytidae
southern pine beetle
taxonomy

Abstract

The systematic history of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, is reviewed. Morphological, biological, karyological, and molecular data clearly define and diagnose the species limits of *D. frontalis*. More complete phylogenetic analysis and characterization of population genetic variation will further clarify the evolutionary history of the *D. frontalis*.

1.1. TAXONOMIC HISTORY

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is one of the most important bark beetle pests in the United States. As a consequence of its economic impact, this species has been the subject of intensive taxonomic study. The original description (Zimmermann 1868) was brief and based on merely a few specimens limited to Southeastern United States, and it would be another 120 years before the species concept of *D. frontalis* was solidified. The taxonomy of *D. frontalis* has often fluctuated because morphological character states such as body size, and abundance and size of punctures and setae vary geographically and often overlap with closely related species. Collection of hundreds of *Dendroctonus* specimens during the early 1900s in the Western United States and Mexico allowed for the first comprehensive revision of the genus. *Dendroctonus frontalis* was first synonymized with *D. brevicomis* LeConte (Dietz 1890). However, Hopkins (1902, 1909) resurrected *D. frontalis* based on the study of a larger series of specimens and diagnosed *D. frontalis* by the presence of long setae on the elytral declivity. Two species, *D. arizonicus* Hopkins and *D. mexicanus* Hopkins, were described for specimens from the Southwestern United States and Mexico, respectively (Hopkins 1905, 1909). Wood (1963) completed a second large revision of the genus. He was systematically more conservative than Hopkins and synonymized *D. arizonicus* and *D. mexicanus* with *D. frontalis* based on the gradation of anatomical characters among southeastern, southwestern, and Mexican populations. Years later, several studies re-examined the validity of *Dendroctonus* species based on new morphological (i.e., male genitalia), ecological, and karyological data (Vité and others 1974, 1975; Wood 1974, 1982b). As a result, *D. mexicanus* was resurrected (Wood 1974) and a new species, *D. vitei*, was described for Guatemalan specimens of *D. frontalis* (Wood 1974). Thus Wood (1982b) defined *D. frontalis* as a small species occurring in Southeastern United States, Arizona, and Honduras (at elevations below 1,000 m) and having a flatter female frons with finer punctation than *D. mexicanus*.

1.2. BIOSYSTEMATICS

The extensive biosystematic study of the *D. frontalis* species complex (*D. frontalis*, *D. brevicomis*, *D. mexicanus*, *D. vitei* Wood, *D. approximatus* Dietz, and *D. adjunctus* Blandford) redefined the species limits of *D. frontalis* (Lanier and others 1988). This study extensively examined intra- and interspecific variation of male genitalia, body size, external morphology, karyology, and fertility. Diagnostic characters were found for the closely related sympatric species *D. frontalis*, *D. mexicanus*, and *D. vitei*.

Male genitalia were taxonomically informative for this species complex. Examination of nearly 260 individuals representing many populations for each species revealed major interspecific differences in the seminal rod structure allowing for indisputable diagnosis of male specimens (Figure 21 in Lanier and others 1988). Generally, little intraspecific variation was observed. Some *D. frontalis* individuals from Guatemala, Honduras, Mexico, and Arizona possessed a relatively longer seminal rod process; however, this character was not diagnostic for these populations.

Pronotal width varies considerably within species, but the mean pronotal width measured from a series *D. frontalis* specimens was significantly different from other sympatric *Dendroctonus* species (Table 5 in Lanier and others 1988). Nonetheless, size and external morphology were not consistently associated with seminal rod shape in the *D. frontalis* complex. The size ranges of *D. frontalis*, *D. mexicanus*, and *D. vitei* overlap substantially, and external morphology, specifically the size and density of setation on the elytral declivity, correctly identified only 75 percent of a series of *D. frontalis* and *D. mexicanus* specimens. However, *D. frontalis* was confidently distinguished from *D. vitei* when an additional character, the lighter hue of the elytra relative to the pronotum and head in *D. frontalis*, was also considered.

Karyology also demonstrated diagnostic characters for *D. frontalis* (Figure 17 in Lanier and others 1988). Meiotic metaphase I cells in males had a karyotypic formula of seven pairs of autosomes and a parachute-shaped sex bivalent chromosome. The only observed intraspecific variation was meiotic abnormalities in one individual. Morphologically similar species *D. mexicanus* and *D. brevicomis* had a meiotic karyotypic formula of five pairs of autosomes and a parachute-shaped sex bivalent chromosome, although some variation in the sex chromosome was observed for *D. brevicomis*.

Breeding experiments tested intra- and interspecific fertility among *D. frontalis* individuals from 16 populations taken from the Southeastern United States, Arizona, and Mexico, *D. mexicanus*, *D. brevicomis*, and *D. vitei* (Lanier and others 1988, Vité and others 1974). Intraspecific fertility among individuals from different populations was similar to individuals from the same population. However, female F1 with one parent from a Mexico population had a low hatchability of laid eggs, whereas males from these crosses produced fertile offspring. These hybrids did not exhibit morphological irregularities that would preclude interbreeding between these populations. Interspecific fertility tests demonstrated that most pairings produced either no eggs or sterile eggs (Lanier and others 1988, Vité and others 1974). Interspecific pairings were also uncommon; that is, males were resistant to join heterospecific females, and often males had to be forced into the females' nuptial chambers (Lanier and others 1988).

This study of Lanier and others (1988) provided much evidence for the taxonomic limits of *D. frontalis*. It also demonstrated that individuals from disjunct populations were capable of interbreeding and that pre- and post-zygotic barriers exist among sympatric species, of the *D. frontalis* species complex (Figure 1.1). Thus *D. frontalis* is currently defined as the smallest species in the *D. frontalis* species complex that possesses a seminal rod with a dorsal process and rounded ventral bulb, short and long setae on strial interspaces 1-3 of the elytral declivity (Figures 1.2 and 1.3), a meiotic formula of 7AA + Xyp, and a range that includes Southeastern United States, the Southern Rocky Mountains of the United States, Mexico (coastal facing slopes, 1300-1800 m), and Central America (at elevations between 900-1300 m) (Figure 1.1).

1.3. MOLECULAR PHYLOGENETICS

1.3.1. Intraspecific Variation

Intraspecific genetic variation has been investigated for *D. frontalis,* although these studies are mostly limited to electrophoretic investigations and to merely a few populations. Electrophoretic analysis of six enzyme loci and five populations (Virginia, Georgia, Texas, Arizona, and Mexico) provided the most geographically extensive survey of genetic variation among *D. frontalis* populations to date

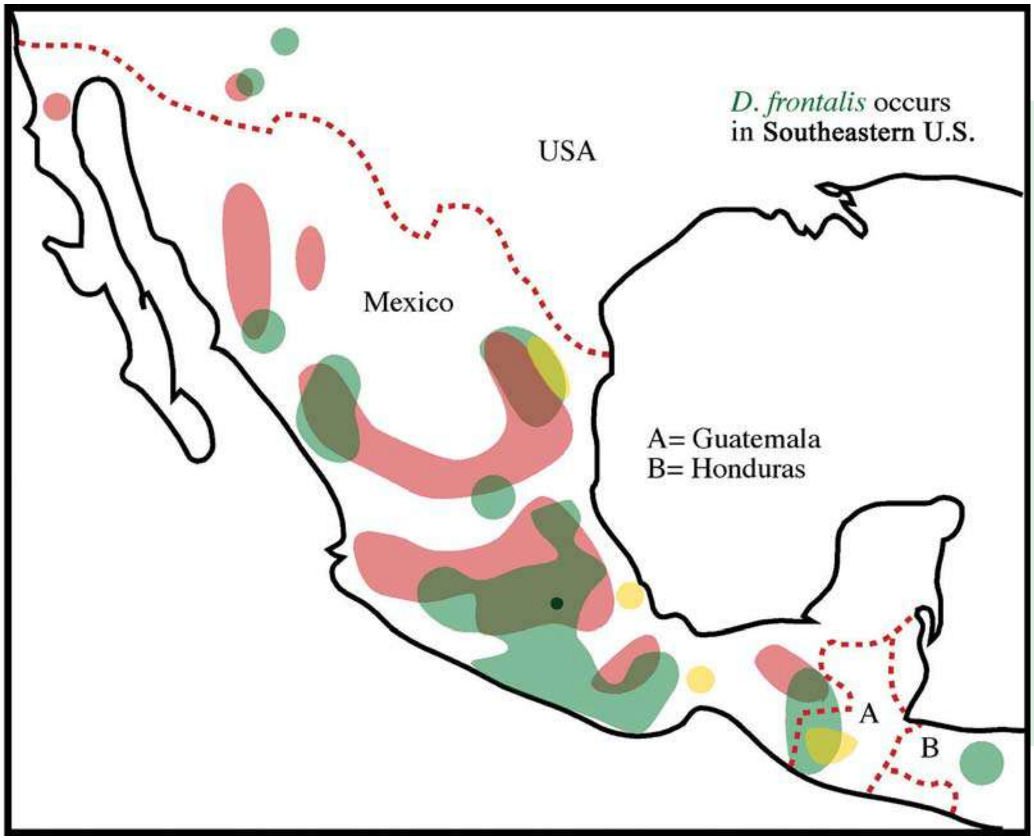

Figure 1.1—Approximate distribution of related species *D. frontalis* (green), *D. mexicanus* (red), and *D. vitei* (yellow) in the United States, Mexico, and Central America. *Dendroctonus frontalis* primarily occurs in Mexico on coastal facing slopes (1300-1800 m) and in Central America (900-1300 m); *D. mexicanus* occurs in Mexico in semiarid forests (1800-2500 m); and *D. vitei* occurs in Mexico on coastal facing slopes (1000-1500 m) and in Central America (less than 2500 m). (redrawn from Salinas-Moreno and others 2004, Lanier and others 1988)

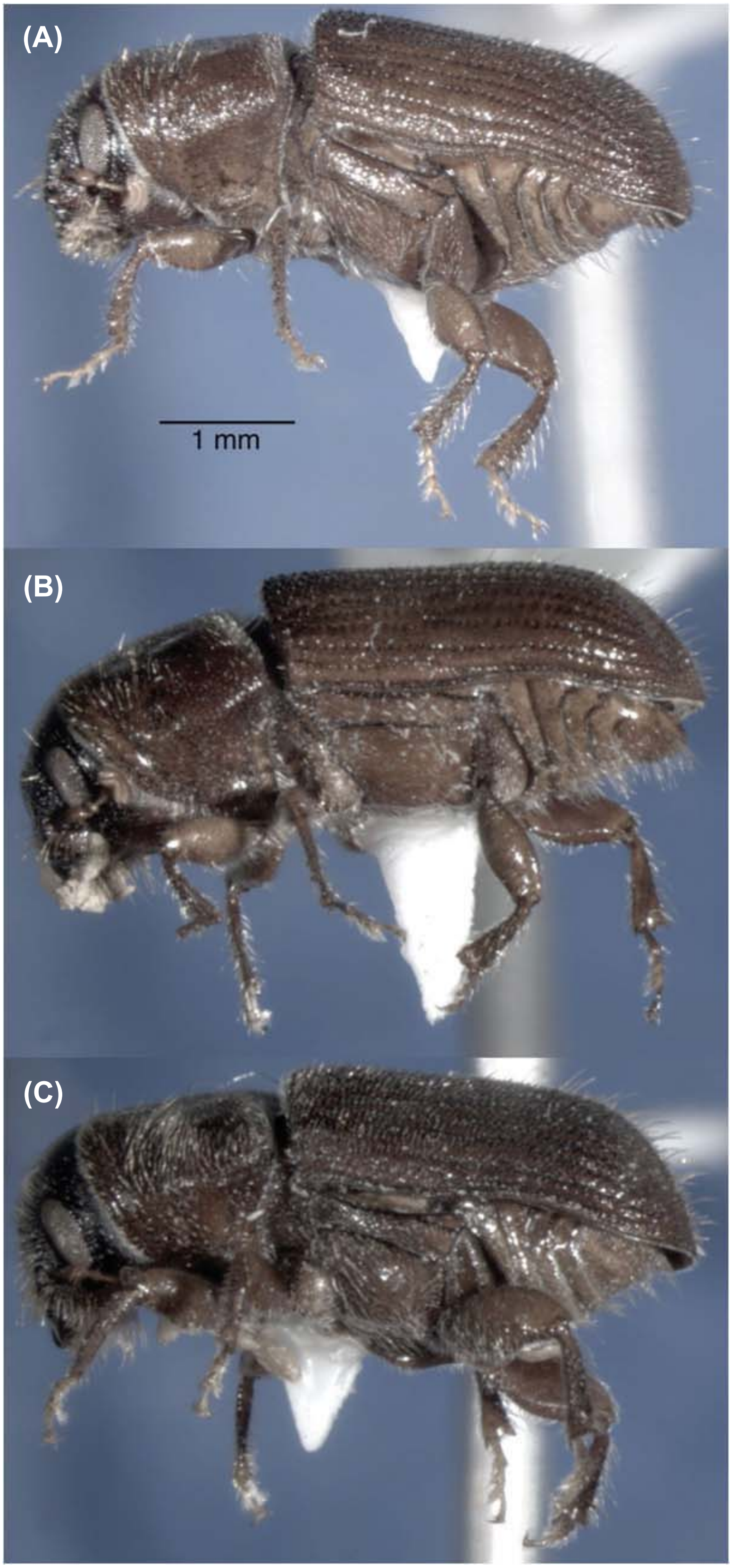

Figure 1.2—Lateral view of three related *Dendroctonus* species, (A) *D. frontalis*, (B) *D. mexicanus*, and (C) *D. vitei*. (photograph by A.I. Cognato)

(Anderson and others 1979). The frequencies of alleles varied across populations and were generally in Hardy-Weinberg proportion, which suggested that factors such as non-random mating, selection, migration, and flawed sampling were not issues for this study. Significant differences in allele frequencies were observed between eastern and western populations. The *D. frontalis* individuals from Mexico and Arizona differed genetically both from each other and from Texas, Georgia, and Virginia beetles, suggesting a historical separation of these three populations. The significant difference of allele frequencies between eastern and western populations was confirmed by another study that examined the genetic variation among individuals in Virginia, North Carolina, Georgia, Louisiana, Texas, and Arizona (Namkoong and others 1979). Allele heterogeneity was observed among these populations and was confirmed by a subsequent study (Roberds and others 1987).

While isozymes allow for a coarse assessment of genetic variation, microsatellites and nucleotide variation of specific genes allows for inferences of population structure on a smaller geographic scale (Avise 2004). Microsatellite loci have been characterized for *D. frontalis* (Schrey and others 2007). The allelic variation of these loci showed no population structure among six localities in Mississippi, suggesting that *D. frontalis* throughout this State represented a cohesive genetic unit (Schrey and others 2008). However, heterogeneity likely exists for disjunct populations separated by greater distance.

Intraspecific nucleotide variation for specific genes is not well characterized for *D. frontalis*. Kelley and Farrell (1998) included three individuals from Texas and Michoacan, Mexico, in their phylogenetic analysis of *Dendroctonus* based on mitochondrial cytochrome oxidase I (COI) DNA sequence. They reported that these sequences exhibited less than 1 percent difference. Given the limited sample size, it is premature to characterize *D. frontalis* as having low COI nucleotide diversity because more extensive studies have revealed much intraspecific COI DNA variation (>4 percent) for other *Dendroctonus* species (Cognato 2006, Cognato and others 2005, Kelley and others 1999, Maroja and others 2007).

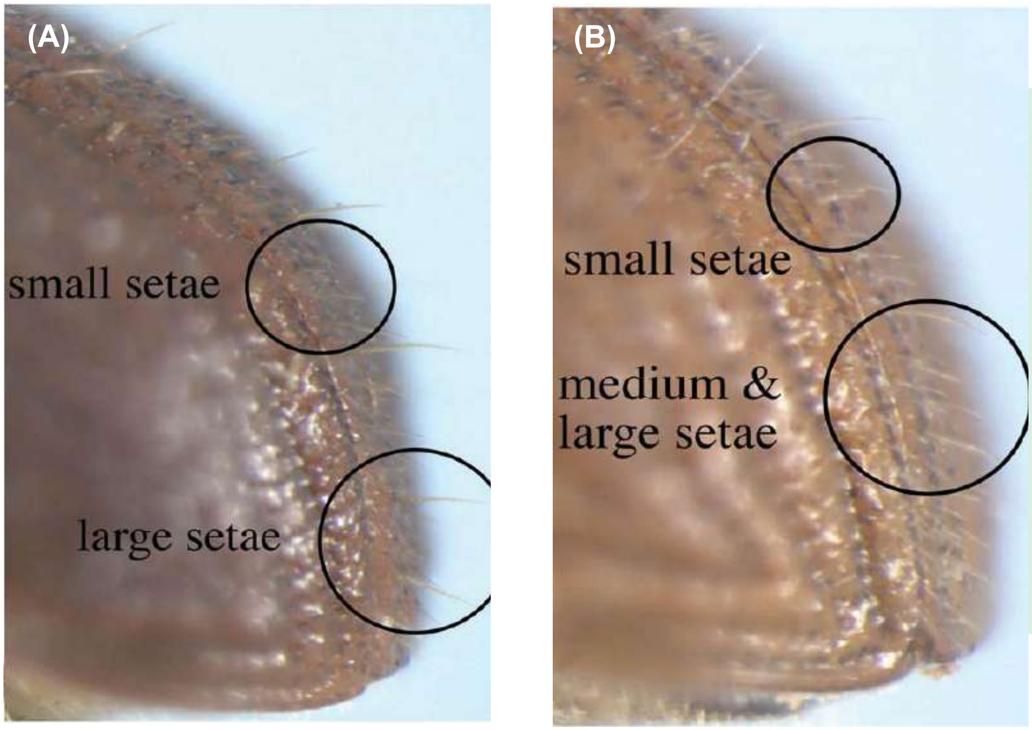

Figure 1.3—Oblique angle of the elytral declivity of (A) *D. frontalis* and (B) *D. mexicanus*. *Dendroctonus frontalis* is diagnosed by short and long setae on strial interspaces 1-3 of the elytral declivity as compared to *D. mexicanus*, which is diagnosed by short, medium, and long setae on strial interspaces 1-3 of the elytral declivity. *D. vitei* is diagnosed by larger mean size and darker coloration. (photograph by Lanier and others 1988)

1.3.2. Interspecific Variation

Electrophoretic data provided the first phylogenetic evidence for the relationship of *D. frontalis* with congeners. Wagner distance analysis of the allele frequencies of 18 gene loci revealed a relationship between *D. frontalis* and *D. brevicomis* (Bentz and Stock 1986) as predicted by morphological similarity (Wood 1963). A Nei distance of 0.675 between these species suggested that they were not closely related. Kelley and Farrell (1998) provided the first comprehensive phylogeny based on mitochondrial COI DNA nucleotides that included most valid *Dendroctonus* species. One most parsimonious tree revealed a sister relationship between *D. frontalis* and *D. vitei*, and *D. mexicanus* was basal to these species. However, the authors suggested that the relationship between *D. frontalis* and *D. vitei* might have been an artifact of the incomplete sequence of *D. vitei,* and suggested a possible sister relationship between *D. frontalis* and *D. mexicanus* that is consistent with morphological data. The *D. frontalis* species complex as defined by Lanier and others (1988) was monophyletic.

Dendroctonus frontalis has also been included in higher-level phylogenetic analyses of scolytines (Sequeira and Farrell 2001, Sequeira and others 2000). These studies used various single copy nuclear and ribosomal genes to reconstruct, in part, phylogenies of eight *Dendroctonus* species, including members of the *D. frontalis* species complex. The phylogenies resulting from these separate gene analyses differed in the arrangement of some species. Notably, the author of this chapter conducted a parsimony analysis including 4,684 nucleotides from five genes (small nuclear ribosomal subunit 18S, large nuclear ribosomal subunit 28S, elongation factor-1alpha, enolase, and COI) for eight *Dendroctonus* species including *D. frontalis* (for GenBank numbers see Sequeira and Farrell 2001, Sequeira and others 2000). An exhaustive tree search using default settings in PAUP* (Phylogenetic Analysis Using Parsimony [*and other methods]) version 4 (Swofford 2002) resulted in one most parsimonious tree (Figure 1.4). High bootstrap values were found for all clades within the tree (Figure 1.4). A close relationship between *D. frontalis* and *D. mexicanus* was recovered, and relationships of the remaining species were similar to those that were predicted by biological data (Lanier and others 1988).

1.4. CONCLUSION

We have a good understanding of the state of *D. frontalis* systematics. The species is concretely defined by morphological and molecular data. Future systematic research on

D. frontalis would best focus on phylogenetics and population genetics. A phylogenetic analysis using the above nucleotide data and morphological characters for all *Dendroctonus* species, especially *D. vitei,* would firmly fix the relationship of *D. frontalis* among the other species. A detailed examination of intraspecific genetic variation would allow for inference of contemporary gene flow and the evolutionary processes that shaped the biology and ecology of *D. frontalis*.

1.5. ACKNOWLEDGMENTS

I thank Bob Coulson for the invitation to contribute to the Southern Pine Beetle II.

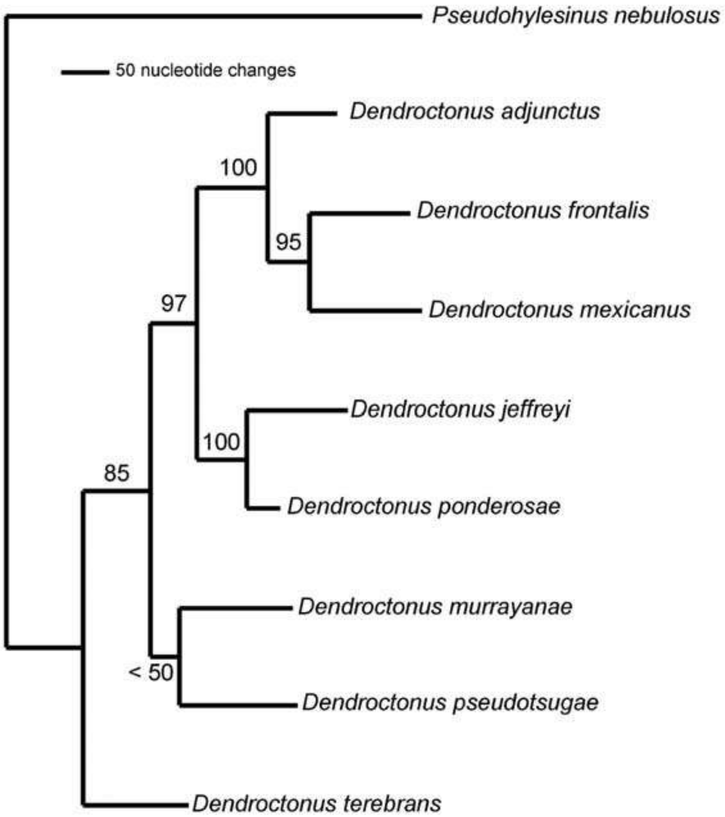

Figure 1.4—Molecular phylogen of *Dendroctonus* species reconstructed with 401 parsimony-informative characters derived from 4,684 nucleotides from 18S ribosomal subunit (1666 bp), 28S ribosomal subunit (684 bp), elongation factor-1alpha (865 bp), enolase (423 bp), and COI (1046 bp). An exhaustive search recovered one most parsimonious tree. Bootstrap values calculated with 1,000 pseudo-replicates are given at the branches, and branch lengths are equal to number of character state changes.

2

Natural History of the Southern Pine Beetle

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Abstract

The southern pine beetle (SPB) is a tree killer of southern yellow pines. All life stages—eggs, larvae, pupae, and adults—infest the inner bark or phloem tissue of the host tree. Adult beetles overcome the tree's defenses through a mass-attack phenomenon. They are attracted to the tree by a pheromone system consisting of volatiles produced by the beetles and the host. The pheromone system also prevents the beetles from over-colonizing the tree. Once inside the tree, parent adults construct serpentine egg galleries in the inner bark tissue. Individual eggs are deposited in egg niches along the egg gallery. After eclosion, the larvae develop on host tissue, and development is aided by mycangial fungi deposited in the egg galleries by the adult females. Pupation occurs in the outer bark, and brood adults emerge to attack another nearby tree. As this process continues infestation spots of dead and dying trees can be created. Generally an SPB spot gets its start on stressed and weakened tress. Depending upon climate, the number of SPB generations per year can vary from one to nine. The SPB has the capacity to cause periodic large-scale eruptions that encompass entire regions of the South. Host resistance, predators, parasites, diseases, and competitors all keep SPB populations in check during nonepidemic years.

Keywords

behavior
colonization
Dendroctonus frontalis
geographic and host range
Pinus
population cycles

2.1. INTRODUCTION

The natural history of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is one of the most fascinating stories in the world of biology (Thatcher and others 1980). While not a true social insect, SPB does have the capacity, through a sophisticated pheromone system, to amass an army of attacking beetles capable of overcoming the chemical defenses of trees thousands of times larger than an individual beetle, which is about the size of a grain of rice. This is a life or death struggle between the beetle and its host. As its generic name (*Dendroctonus*) indicates, the SPB is an obligate tree killer. However, the tree's defense includes a large reservoir of toxic chemicals, and the ability to increase production in response to damage. If the tree survives, many beetles either die or fly off in search of another host. The story does not end with the death of the host. When the SPB successfully colonizes a tree, over-colonization and resource depletion are avoided when the pheromone system inhibits further attacks, causing incoming flying beetles to search for another host. Furthermore, in a heavily attacked tree, as the female excavates an egg gallery and lays her eggs, she may reemerge before laying her full complement of eggs and seek another host. This system helps insure the survival of the next generation by regulating the within-tree population size, a remarkable phenomenon in the world of biology.

In a successfully attacked tree, other players engage in complex interactions with the SPB that have positive and negative effects on brood survival. These players include mycangial fungi, phoretic mites, blue stain fungi, bacteria, predators, parasites, competitors, and diseases. While the SPB do not tend their young as a social insect such as the honeybee does, they do provide their offspring with sustenance in the form of mycangial fungi that are maintained in special thoracic pouches called mycangia. The adult female actively inoculates the egg galleries with the fungi, and by doing so enhances the survival of the larval stage.

When all is in balance, SPB eggs hatch, and larvae develop in short larval galleries, move to the outer bark to avoid competitors, pupate to adults, and emerge to continue this cycle into the next generation and up to as many as eight generations in a given year. However, sometimes the interactions of the various SPB associates are not in balance. The SPB pheromones also attract natural enemies that come to prey upon or parasitize the beetle directly. They can also attract competitors that desire the nutritious inner bark tissue. These enemies can exact a serious toll on the SPB's survival. For instance, there may be too many phoretic mites carrying the blue stain fungi that compete with SPB's mycangial fungi. The blue stain fungi may prevent the SPB larvae from developing normally, resulting in much longer larval galleries and greater mortality. Other, less understood pathogens are sometimes also involved.

Despite all of these complications, the SPB can periodically create highly eruptive populations capable of killing thousands of healthy pines. Obviously, this is an unusual case, or we would not have any southern yellow pines. Most of the time, the SPB is a scavenger that survives on trees under stress from lightning strikes, storm damage, disease, or suppression by other trees. At these times the beetle is competing with all of the factors mentioned above plus other, less aggressive bark beetles. At low population levels the struggle for survival is difficult; yet the SPB's tenacious nature prevents extinction as it lies in wait for a confluence of conditions to trigger the next epidemic.

This is the story of a remarkable and highly destructive insect that forest managers must cope with. When forests are managed correctly, damage by this insect can be minimized. In order to minimize the hazard, we must understand this insect. Here is what we know.

2.2. BACKGROUND

The SPB is a minute insect ~3 mm long that infests southern yellow pines, especially loblolly (*Pinus taeda* L.) and shortleaf (*P. echinata* Mill), although virtually any pine species can be subject to attack. Southern pines have evolved extensive and potent defense mechanisms (Franceschi and others 2005), but the beetles are very resistant to the defensive chemicals in the trees' resin. With enough attacking beetles the mass-attack strategy of the SPB allows the insect to overcome the defenses of even the healthiest trees. As a result, the SPB has the capacity to create eruptive populations that can cause widescale mortality of southern yellow pines, making this insect the most destructive pest of its hosts. Its destructive potential is aided by the production of multiple overlapping generations each year.

The SPB is a native pest, and so the host and the insect share an evolutionary history. However, it is important to understand that the landscape the beetle currently inhabits is very different from the landscape of its evolutionary past. Throughout the South most pine forests are unmanaged, on private land in small holdings, and on old agricultural sites with depleted soils (Smith 1976). Prior to the arrival of Europeans, much of the southern forest land was composed of late successional trees such as oak, hickory, and SPB-resistant longleaf pine. These forests were cut down for agricultural production. Once the soils were depleted or eroded away, the land was abandoned, and early successional trees eventually colonized the sites. The forests were transformed to early successional loblolly and shortleaf pines on unmanaged sites with poor soils. In addition, fire was removed from the landscape, allowing loblolly and shortleaf to dominate in many locations where longleaf pine historically grew. Much of the southern forests can now be described as overstocked and in poor health. This alteration of the historic landscape pattern and species composition has created a landscape that allows the SPB to be a major pest.

In endemic situations beetles require very susceptible hosts that are unable to repel attack even at low beetle densities. Lightning-struck trees appear to be a particularly important susceptible host (Lorio 1986) that are found at a rate of about one per kilometer of forest (Coulson and others 1999b, Flamm and others 1993). Lightning-struck trees are abundant enough and stay attractive long enough for searching beetles to find and colonize them (Coulson and others 1999b). Such material as diseased trees, storm damaged trees, and trees infested by other insects may also provide places where dispersed populations can subsist (Gara and others 1965).

2.3. SPB LIFE STAGES

The SPB was originally described in 1868. The SPB is multivoltine with complete metamorphosis consisting of egg, larval, pupal, and adult stages (Dixon and Osgood 1961, Hopkins 1909, Thatcher 1960).

2.3.1. Egg

The adult SPB attack living host trees by boring through the outer bark and constructing serpentine egg galleries (Figure 2.1) in the inner bark or phloem tissue of the host tree (Thatcher and others 1980). Eggs are laid in single egg niches along the main gallery (Figure 2.2). The egg is slightly oblong to oval, opaque, and shiny white, measuring about 1.5 mm long by 1 mm wide. The egg stage lasts from 3 to 34 days at temperatures ranging from 30^{o} to 10 ^{o}C (Gagne and others 1980, and Wagner and others 1984a). Approximately one day before eclosion the larval mandibles are visible through the egg covering.

2.3.2. Larva

After egg eclosion the larvae (Figure 2.3) consume the plant tissue in the immediate area of the egg niche along with mycangial fungi left by the mother. The larva is a subcylindrical,

Figure 2.1—SPB egg galleries with larvae. (photography by Ron Billings, Texas Forest Service, www.forestryimages.com)

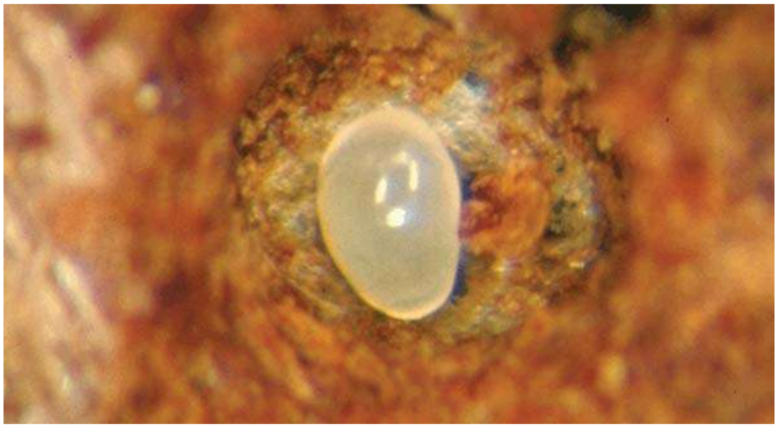

Figure 2.2—SPB egg. (reproduced from Payne 1980)

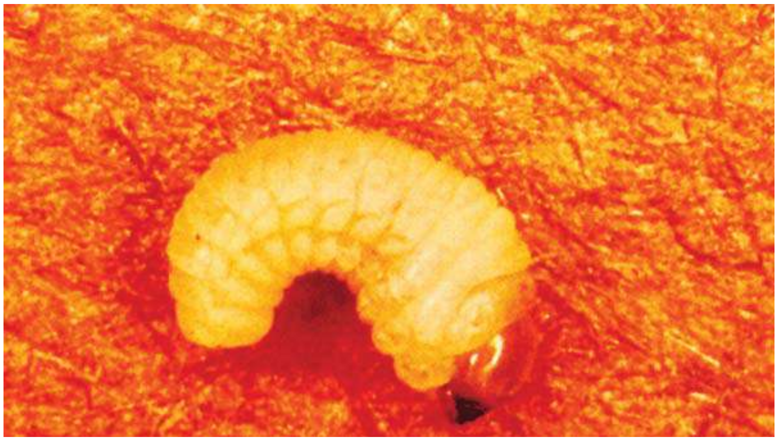

Figure 2.3—SPB larva. (reproduced from Payne 1980)

Figure 2.4—SPB pupa. (reproduced from Payne 1980)

curved, legless grub with 3 thoracic and 10 abdominal segments. The first instar is approximately 2 mm long, and yellowish white in color, with a prominent head and well-developed mouthparts. The mature larva is 5-7 mm long, with a reddish head and small antenna situated in depressions just above the bases of the mandibles. There are four larval instars (Fronk 1947, Goldman and Franklin 1977, Mizell and Nebeker 1979). The overall larval stage lasts from 15 to 40 days, over temperatures of 25° to 15 °C (Gagne and others 1980, Wagner and others 1984a).

2.3.3. Pupa

The yellowish white pupa (Figure 2.4) has the form of the adult, but with wing pads and folded legs. Pupae range in size from 3 to 4 mm in length. The pupal stage lasts 5 to 17 days over a temperature of 30° to 15 °C (Gagne and others 1980, Wagner and others 1984a).

2.3.4. Adult

The callow adults (Figure 2.5) start out yellowish white to reddish brown, and finally become dark brown (scleritized) about one week before (Figure 2.6) emergence from the host tree. This stage lasts from 6 to 14 days over temperatures ranging from 30° to 15 °C (Gagne and others 1980, Wagner and others 1984a). The adult is cylindrical and elongated, 2-4 mm in length, and brownish to black in color. The head is broad and prominent, with well-developed chewing mouthparts and tubercles that form a distinct frontal groove. The tubercles are rougher and more acute on the male, while the middle front of the female's head is more convex and shiny (Payne 1980).

The compound eyes are situated behind the base of each seven-segmented clubbed antenna. The prothorax is slightly narrowed at the head. The elytral declivity at the posterior is convex. Males and females can be differentiated by a transverse ridge, the mycangium, found only on the anterior pronotum of the female where the mycangial fungi are cultured. Males lack this structure but have a pronounced frontal suture (Bunt and others 1980).

2.3.5. Generations

The number of generations per year varies considerably depending upon climatic conditions. In the northern extreme of the SPB range perhaps only one or two generations will occur within a single year, while seven to nine may occur along the Gulf Coast (Thatcher 1960). In North Carolina, for example, typically three to four generations occur in a year's time. As the number of generations increases moving south, overlap between generations increases to the point that there is a continuous presence of SPB adults in the forest environment during the summer and fall months. The reemergence of the female after initial attack further minimizes distinct generations. Depending upon the season and location, SPB develop from egg to adult in 26-54 days (Thatcher 1960, 1967).

For the SPB the lower lethal temperature is about –12 °C. Complete SPB mortality occurs when the insect is exposed to air temperatures of –16 °C or less (Ayres and others 2000). At temperatures between 12.5° and 30 °C beetle survival was 90 percent under lab conditions, but above 30 °C survival dropped (Gagne and others 1982). The greatest time between attack and emergence occurred at 12.5 °C and the shortest occurred at 27 °C. The average period between first attack and mean eggs was 19.1 days, ranging between 15.4 and 24.6 days (Wagner and others 1979).

2.4. HOST SELECTION

The first beetles to arrive at a selected tree are commonly referred to as "pioneer" beetles (Borden 1974). These are females that locate a host without the aid of secondary attractants. Male SPBs are attracted to the host after the females have successfully attacked and initiated secondary attraction. It is not clear how pioneer beetles find a suitable host tree. One hypothesis states that a primary attraction given off by stressed trees attracts the pioneers. The attractant is in the form of volatile compounds resulting from the deterioration of the plant tissues (Heikkenen 1977, Person 1931). This hypothesis is difficult to test because once a pioneer beetle begins attacking the tree, secondary attraction in the form of the insect's pheromones, is introduced. The SPB begin to produce aggregation pheromones when they come in contact with new host tissue (Vité and Crozier 1968, Vité and Rudinsky 1960).

An alternative hypothesis is that the pioneer beetles randomly land on vertical objects (Gara and others 1965) and test the tree for chemical stimuli that indicate a suitable host. If the tree is suitable, the female begins boring, and the aggregation phase begins. If the tree is not suitable, the insect flies off in search of another host (Gara and others 1965).

Attacks by emerging beetles begin in the spring as soon as temperatures warm (Gara 1967). Flying beetles orient to the secondary attractant, when present, utilizing any vertical object near the center of the pheromone plume as landing space (Gara and others 1965). After landing the SPB show negative geotaxis as they search for a suitable location to enter the tree (Bunt and others 1980). A beetle may walk until it encounters a predator, drops off the tree, or bores into the tree. Once beetles begin searching they are unlikely to leave the tree. When the SPB encounter each other, fighting may take place with the smaller insect being driven off and/or losing an appendage.

Figure 2.5—SPB callow adult. (reproduced from Payne 1980)

Figure 2.6—SPB adult. (photograph by Texas Agriculture Extension Service Archive, Texas A&M University)

During the initial phase of infestation the insect must overcome the host's resin production, which can kill or push the insect out of the tree. The beetle works to get through the resin; if not successful then beetle survival is not likely (Bunt and others 1980, Gara and others 1965). If successful, the beetle excavates resin faster than it is exuded, forming a pitch tube of resin on the bark surface (Figure 2.7). Entering a host quickly is important because it decreases the tree's ability to produce more resin, confers an advantage against competing conspecifics in securing adequate space and resources for the beetle's progeny, and minimizes the risk posed by predators that are also attracted to the secondary attractants (Wallin and Raffa 2002).

2.4.1. Host Condition

Tree physiology, site, and stand parameters affect host susceptibility and suitability to SPB attack and development (Hodges and others 1979). Trees under stress as a result of high stand density, disease, lightning strikes, flooding, drought, wind damage, or mechanical damage may have insufficient resources to mount a successful defense against SPB attack. Overstocked stands are commonly associated with SPB infestations (Bennett 1968, Leuschner and others 1976, Lorio and Bennett 1974). Overstocking causes reduced tree vigor due to increased between-tree competition (Hicks and others 1978). Even in overstocked mixed pine/hardwood stands, SPB infestations are common. Poor tree vigor is expressed in reduced radial growth (Bennett 1968, 1971) and is consistently associated with SPB infestations (Coulson and others 1974).

Figure 2.7—Pitch tubes formed on tree attacked by SPB. (photograph by Erich G. Vallery, USDA Forest Service, SRS-4252, www. forestryimages.org)

The SPB uses visual and chemical cues to find appropriate hosts. Visually the insect orients to vertical objects (Gara and others 1965). Once on a tree, the beetle's choice of an entry point is based on very specific host cues (Gara and others 1965, Vité and Pitman 1969b). Inside the tree the SPBs orient toward regions where there are relatively low monoterpene concentrations and thus avoid resin ducts during gallery construction (Wallin and Raffa 2002).

2.4.2. Pheromone System

As beetles begin to bore into a tree, pheromones are produced that attract more beetles. Olfaction is a strong stimulus orienting beetle flight (Gara and others 1965, Turchin and Thoeny 1993). This is an essential process because, even for the weakest trees, a substantial number of attackers must arrive at the tree over a short period of time to successfully overcome the tree's resistance. The pulse of attacks distributes tree defenses, so the number of attackers required is correlated with tree strength. If enough beetles attack, even the strongest tree will succumb and the SPB will successfully colonize the host. The SPB may also orient to trees with exposed resin or an *Ips* infestation (Gara and others 1965, Wermelinger 2004).

Secondary attraction involves both beetle- and host-produced volatiles that attract flying SPBs (Payne 1979). The beetle's olfactory organs (sensilla) located on the distal segment (club) of the antennae detect these volatiles (Dickens and Payne 1978b). The SPBs follow the pheromone clues, and as they get close to the pheromone source they begin landing on vertical objects. The number of beetles flying also increases towards the source of pheromones (Coster and Gara 1968, Gara and Coster 1968). Termination of mass attack on a host is likely mediated by changes in olfactory cues as well; either the reduction or increase in the concentration of attractant compounds may inhibit further attraction.

2.4.3. Behavior

At the early stages of an attack the sex ratio of arriving beetles favors males. Generally, a tree is first attacked at mid-bole, and as more beetles arrive the attacks spread to the upper and lower levels of the bole (Coster and others 1977a, Fargo and others 1979). Highest beetle densities occur at 2-3.5 m (Flamm and others 1993). There may be some seasonal variation both to this pattern of vertical distribution (Thatcher and Pickard 1964) and to the diurnal pattern of attack (Coster and others 1977a, 1977b; Vité and others 1964). When the density of attacking beetles approaches some maximum for the tree, the flying beetles in the area switch (Gara and Coster 1968) their focus of aggregation and attack to an adjacent host tree, beginning anew the attack process.

The timing of an attack is dependent on the number of beetles available in the area. In epidemic areas, infestation occurs by the second day of attractive material being presented. During the summer months a host tree can be completely mass attacked within three to five days after the first pioneer beetles land on the tree (Coster and others 1977a, Fargo and others 1979). Inter-tree distance is very important (Gara and Coster 1968) as the attacks switch from tree to tree. Trees within 5 feet of the pheromone source received 3.6 times as many attacks as trees 15 feet away. Trees more than 15 feet away from a pheromone source are not likely to be attacked (Gara and Coster 1968, Johnson and Coster 1978). The dynamic aggregation phase of the SPB life cycle, the rapid increase in beetle attacks followed by the equally rapid decline, can be attributed to the relative amounts of behavioral chemicals present over the aggregation and attacking period (Payne 1980).

2.4.4. Colonization

Mating takes place in the nuptial chamber, which is just inside the entrance hole (Payne 1980). Sometimes resin will continue to flow into the chamber, forcing the female and male to continue excavation of the site (Hopkins 1899). If unsuccessful they may become entombed in the resin. If successful, mating takes place. The male backs into the nuptial chamber, and the beetles mate end to end. The SPB is considered monogamous because generally only one male and one female are found in a gallery. However, in laboratory experiments females mated multiple times (Yu and Taso 1967).

After mating the female constructs a serpentine, branchless egg gallery in the cambium, sometimes lightly scoring the sapwood (Figure 2.8). The male follows behind, removing boring particles from the area of current activity. A space of 15-25 mm is kept clear of frass (Hopkins 1899, Thatcher 1960, Yu and Tsao 1967). After constructing 2-3 cm of gallery, the female begins cutting egg niches into the gallery walls. A single egg is deposited in each niche and held in place by tightly packed borings (Fronk 1947).

Egg densities within the egg gallery average about 1.59 eggs per cm of gallery, with up to 30 eggs laid per gallery. Attacking beetle densities range from 1 to 3.5 beetles/dm^2 of bark area. (Lashomb and Nebeker 1979, Wagner and others 1979). As the attack proceeds in a stand, beetle densities, and thus gallery densities, per tree may increase but gallery length per beetle will be reduced. This indicates there may be a density-dependent compensatory feedback mechanism that regulates SPB egg densities (Fargo and others 1979, Gagne and others 1982). One potential explanation for this is that beetles may be detecting vibrations from gallery construction. Beetle densities are also maximized by beetles switching from trees already under attack to newly attacked trees (Wallin and Raffa 2002). Peak gallery density in trees ranges from 1.1 to 30.9 cm/dm^2 of bark area (Feldman and others 1981b, Flamm and others 1993).

As the female constructs the egg gallery, she inoculates the gallery with mycangial fungi. The fungi increases the insect's growth efficiency by concentrating the nitrogen from the surrounding cambium (Ayres and others 2000). The fungus *Entomocorticium* is able to concentrate nitrogen to levels significantly higher than that of the other mycangial species (Ayres and others 2000).

The eggs hatch in two to nine days, and the first instar larvae enter the cambium layer of the host (Fronk 1947). The larval galleries are a few centimeters long and are formed perpendicular to the adult gallery (Figure 2.8). In later instars the larval galleries are enlarged and enter the inner bark. In the fourth instar the larvae bore into the outer bark where pupation occurs (Goldman and Franklin 1977). When the mycangial fungi are well established, the larval galleries are relatively short. However, when the larvae are feeding in areas colonized by the blue stain fungus, *Ophiostoma minus*, the larvae

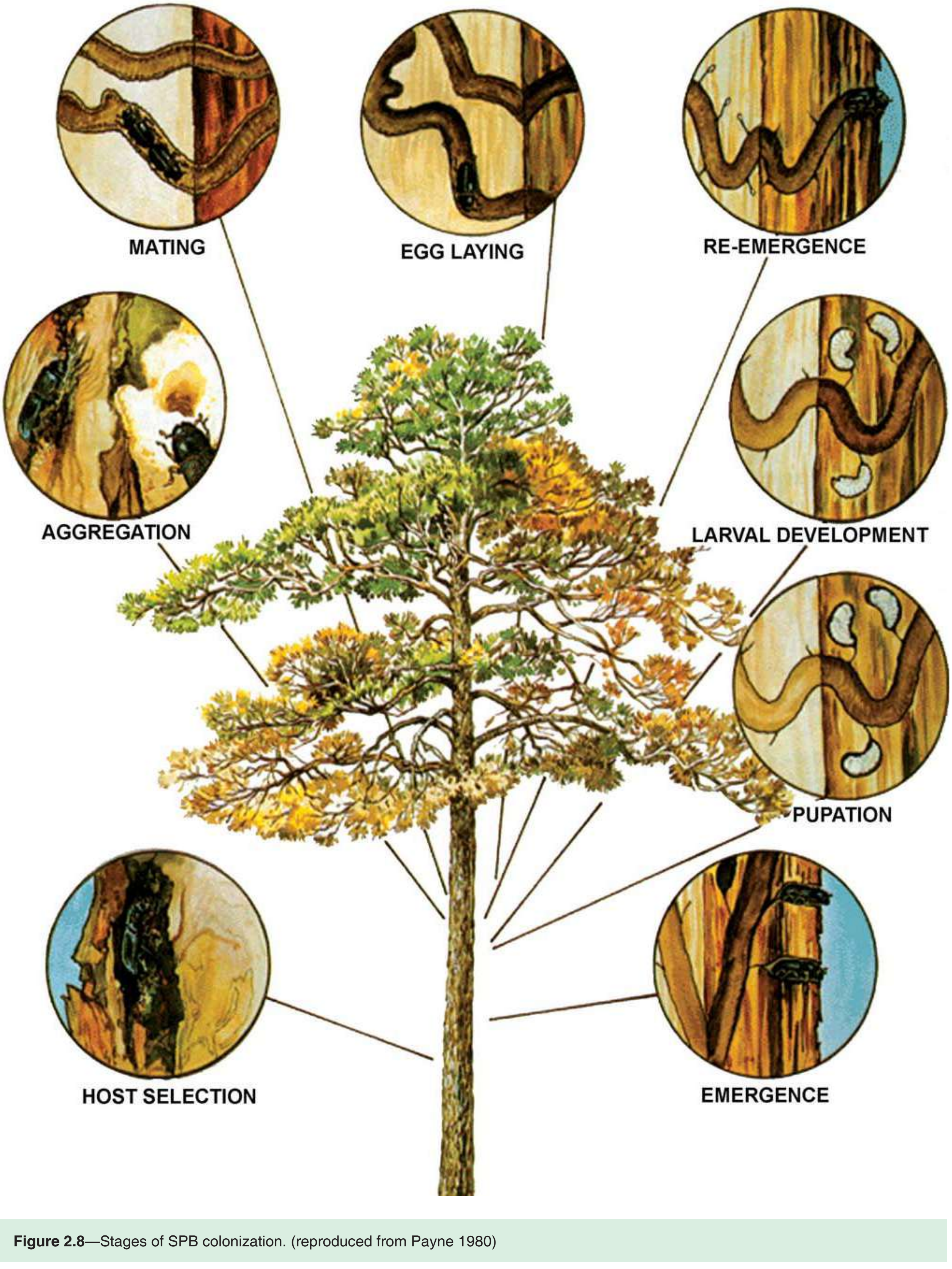

Figure 2.8—Stages of SPB colonization. (reproduced from Payne 1980)

create meandering tunnels rather than the small feeding chamber typical of successful larvae. The larvae frequently die in areas dominated by blue stain. Survival to adulthood is most strongly related to larval survival rates (Gagne and others 1980).

In the dead tissue of the outer bark, the fourth instar larvae construct an oblong pupal cell and transform into pupae (Figure 2.8). The pupa first develops into a callow adult that generally stays under the bark while its exoskeleton completes scleritization (Thatcher and others 1980). This is evident in the color change of the exoskeleton from yellowish tan (callow adult) to reddish brown to black-brown (fully mature adult).

2.5. REEMERGENCE AND EMERGENCE

The SPB emerge from an infested tree in two waves (Figure 2.8). First, parent insects reemerge after successfully excavating a gallery and laying eggs, and second, the progeny emerge once they reach adulthood. Under normal environmental conditions, adult entry and reemergence occurs over a 14-day period and the progeny emerge in 28 days (Coulson and others 1979b). Beetles can reemerge in as few as eight days after female attack, but at lower densities beetles stayed in the trees longer to create more extensive galleries (Gagne and others 1982). The reemerged parent adults continue to play a vital role in the infestation's dynamics by receiving olfactory signals, attacking new hosts, producing pheromones, mating, and laying eggs (Cooper and Stephen 1978, Coulson and others 1978, Franklin 1970b). While there is a distribution of insect development and overlapping of generations, there are definite peaks in dispersal. These peaks insure that sufficient numbers of SPBs are available to overcome host resistance by mass attack (Coulson and others 1979b).

The adults reemerge from a tree by boring a clean-cut circular exit hole through the outer bark. Unfavorable conditions, such as cold temperatures, may cause the adult to remain under the bark for some time (Kinn 1978). Emergence follows a typical bell-shaped curve with a few emerging at first, followed by a mass emergence, and then declining emergence. Once SPB adults emerge they must fly to find new host trees, either near their brood tree or in a new location. In both cases, they must arrive at the new host in sufficient numbers to complete a mass attack. The distance that the beetles can disperse when leaving a brood tree can be further than 1 km, although only about one-third of the beetles have this range (Turchin and Thoeny 1993). During the winter, emerging beetles may reattack the upper bole of the same tree (Thatcher and Pickard 1964). The SPB overwinters in all life stages, and during a mild winter, development can continue throughout the year.

2.6. SEASONAL BEHAVIOR

The behavior of the SPB changes with the season. In the fall the beetles have the highest average fat content, providing them with the resources for dispersal outside of a current infestation (Billings 1979, Franklin 1970b, Hedden and Billings 1977, Lorio 1986, Thatcher and Pickard 1967). During midsummer, when beetle fat content is lowest and tree resistance is greatest, beetles are more likely to increase the current spot infestation rather than undergoing long distance dispersal (Turchin and Thoeny 1993). In the fall and spring dispersing SPB select host material without the benefit of secondary attractants, while in the summer emerging beetles are likely to be affected by the more or less continuous presence of secondary attractants from newly attacked trees (Gara 1967). Since dispersal losses will be small during the summer, greater numbers of beetles will be available to overcome the resistance of the host trees. During the summer, brood development accelerates, the beetles remain within the infestation area, and consequently spot expansion is accelerated.

During an outbreak infested spots are frequent, meaning that beetles spend less time searching and dispersing and more time continuing spot growth (Turchin and Thoeny 1993). One-third of all beetles disperse further than 1 km during the fall, while dispersal during the summer is only about half as far. As an attack progresses beetles must switch from attacking a single tree to attacking nearby trees in order to provide their offspring with sufficient resources. As a tree is attacked and gallery construction increases, the proportion of beetles that attack the tree decreases, increasing attacks on uninfested neighbors. An average tree must be attacked by 5,000-15,000 beetles over a period of 5-15 days to establish a suitable habitat for larval survival and development (Gara and others 1965).

2.7. SPB ASSOCIATES

Natural enemies of the SPB are also attracted to infested trees (Dixon and Payne 1980). Predators include *Thanasimus dubius* (F.) (Coleoptera:Cleridae), *Medetera bistriata* Parent (Diptera:Dolichopodidae), and *Scolopscelis mississippensis* Drake and Harris (Hemiptera:Anthocoridae). Four common parasitoids are *Heydenia unica* Cook and Davis (Hymenoptera: Pteromalidae), *Spathius pallidus* Ashmead (Hymenoptera: Braconidae), *Coeloides pissodis* (Ashmead) (Hymenoptera: Braconidae) and *Roptrocerus eccoptogastri* (Ratz.) (Hymenoptera: Braconidae). These parasitoids attack eggs and larvae, and thus are generally present after the tree has been attacked and pheromone signals have decreased. The SPB can also face competition from other insects over the inner bark resources of pines. *Ips* species are attracted to SPB-infested trees (Dixon and Payne 1980). When the SPB and *Ips* infest the same tree with similar population densities, the SPB dominate in the majority of the bole while *Ips* tend to infest the upper bole and large branches. At low SPB densities, *Ips* can compete for the entire bole (Flamm and others 1993), and on occasions the SPB is the secondary invader.

Perhaps the most important predator of the SPB is *Thanasimus dubius* (F.) (Coleoptera: Cleridae). Tree colonization by *T. dubius* lags behind SPB colonization by about a day, and they generally concentrate about mid-bole (Dixon and Payne 1979a). Population density of clerids does not seem to be related to SPB density alone, because sometimes there are increases in the clerids without a corresponding increase in SPB (Moser and Dell 1979b). Diurnal activity of the clerid varies (Dix and Franklin 1977, Dixon and Payne 1979a), but they appear to be most active just after SPB flight and coincide with increasing temperatures and host pheromones. Clerid larvae, on the other hand, are active on the bark surface during the night (Dix and Franklin 1977). Above 25 ºC *T. dubius* is not an effective predator and its survival time decreases (Mignot 1966). *Thanasimus dubius* is most effective at cooler temperatures (Moser and Dell 1979b). As infestations progress *T. dubius* may become more concentrated (Dixon and Payne 1979a, Moser and Dell 1979b). However, in SPB/clerid encounters, the clerid is not considered an efficient predator in handling and killing its prey (Bunt and others 1980). Clerids consume about 2.2 SPBs per day as adults, and on average about 100 SPBs over the course of their larval development (Thatcher and Pickard 1966).

There are also some facultative predators, *Corticeus glaber* and *Corticeus parallelus* (Coleoptera: Tenebrionidae), that will consume SPBs. These predators seem to prefer the frass and blue stain fungus associated with an infestation to SPB itself (Goyer and Smith 1981).

The SPB frequently carry phoretic mites that ride on the beetles from place to place, but do not purposefully harm the insect. *Tarsonemus krantzi* and *Trichouropoda australis* are two of the most common phoretic mites (Moser 1976b). Most mites are found under the elytra. Species of phoretic mites have been identified as the main sources of blue stain inoculum (Moser and Bridges 1986). These mites live and develop beneath the bark of pines and feed on blue stain fungi. The blue stain fungus, *Ophiostoma minus* (Ascomycetes: Ophiostomataceae), also colonizes the phloem and competes with the mycangial fungus (Lombardero and others 2003).

2.8. GEOGRAPHIC AND HOST RANGE

The geographic range of the SPB stretches from New Jersey south to Florida, west to central Arizona, and south again in Central America to northern Nicaragua. It has been reported in Pennsylvania, Ohio, Indiana, Illinois, and Missouri (St. George and Beal 1929). The geographic distribution consists of two large areas (Vité 1974): the Southeastern United States, where the distribution coincides with the distribution of southern yellow pines such as loblolly and shortleaf pines, and an area from Arizona to Honduras where the population is less contiguous. SPB populations between and within these two large areas do not behave as a single, large, random mating population, but rather genetic differences exist among widely separated populations (Anderson and others 1979, Namkoong and others 1979, Roberds and others 1987).

2.8.1. Preferred Host Species

The SPB infests and kills all pine species in its range (Hopkins 1909, St. George and Beal 1929, Dixon and Osgood 1961). In the Southeastern United States the preferred hosts are loblolly (*Pinus taeda* L.) and shortleaf (*P. echinata* Mill.), but the beetle also infests the following species: longleaf pine (*P. palustris* Mill.), slash pine, (*P. elliottii* Engelm.), spruce pine (*P. glabra* Walt.), pitch pine (*P. rigida* Mill.), Virginia pine (*P. virginiana* Mill.), table-mountain pine (*P. pungens* Lamb.), eastern white pine (*P. strobus* L.), Japanese red pine (*P. densiflora* Sieb. and Zucc.), red pine (*P. resinosa* Ait.) and pond pine (*P. serotina* Michx.) (Payne 1980, Drooz 1985). In Arizona and New Mexico, SPB infestations are reported on ponderosa pine (*P. ponderosae* Laws.) (Hopkins 1909, Wood 1963), and Apache pine (*P. engelmannii* Carr.) (Vité and others 1974, 1975). In Mexico, SPB has infested *P. teocote* Schiede and Deppe (Vité and others 1974), *P. oocarpa* Schiede, and Pringle pine (*P. pringlei* Shaw). In Honduras SPB has been found infesting *P. oocarpa*, and *P. pseudostrobus* Lindl. (Vité and others 1974, 1975). While the SPB can and will infest all of these pine species, in some cases fewer SPBs emerge than attack, and the host acts as a sink instead of a source.

2.8.2. Nontraditional Host Species

SPB hosts such as eastern white pine (*P. strobus* L.), red spruce (*Picea rubens* Sarg.), and Norway spruce (*P. abies* L.) have been considered exceptional or nontraditional hosts that are indiscriminately attacked during an epidemic on preferred hosts but cannot sustain the epidemic. However, during the early part of the 21st century, an epidemic raged in the southern Appalachians that killed many white pines. In rare cases Norway spruce, red spruce, and even eastern hemlock (*Tsuga canadensis* Carriére) were killed. Entire stands of white pines were destroyed, suggesting that white pine infestations of the SPB can, indeed, sustain an epidemic.

2.9. CLIMATE CHANGE

Given its wide host range, genetic plasticity, and ability to sustain epidemics in nontraditional species, it appears that the geographic range of the SPB is only constrained by host availability and climatic conditions. In the west, the Great Plains are devoid of the SPB's host type, but to the north winter climatic conditions are probably the limiting factor (McClelland and Hain 1979, Ungerer and others 1999). Air temperatures of –16 ºC cause almost total mortality of overwintering SPB populations, and the isoclines corresponding to a probability of winter temperatures of –16 ºC or colder approximate the northern limit of where the SPB has been found (Ungerer and others 1999). Since host material is abundant further north, an increase in minimum winter temperature of just a few degrees could result in a substantial increase in the geographic range of the SPB (Ungerer and others 1999).

2.10. POPULATION CYCLES

SPB populations can be classified as pulse eruptive (Berryman 1986). Outbreaks occur at irregular intervals and cause severe and rapid mortality of healthy, vigorous host trees (Figures 2.9 and 2.10). However, at low population levels, the SPB attacks are confined to weakened or dying trees as a result of high stand density, disease, lightning strikes, flooding, drought, wind damage, or mechanical damage. Most outbreaks are 2-3 years in duration and collapse as a result of natural enemies, a loss of suitable host type, climatic factors, or a combination of these factors.

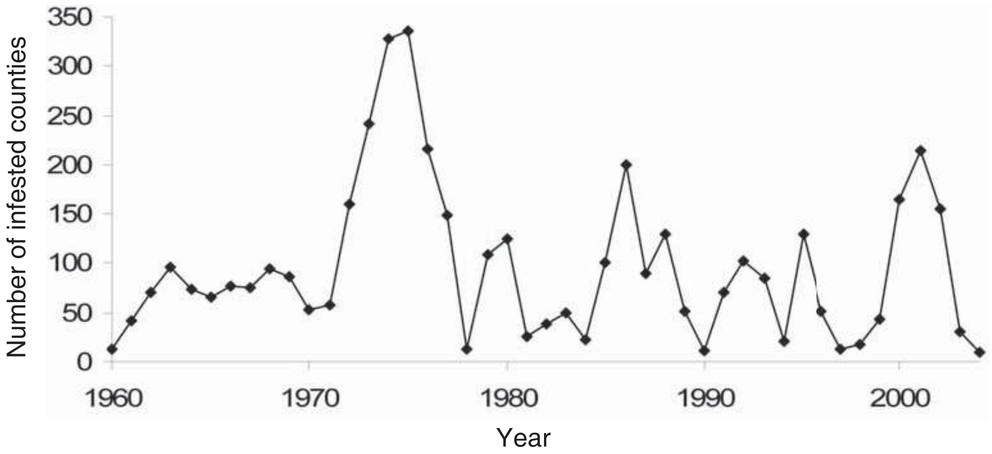

Figure 2.9—Number of SPB-infested counties in the South from 1960 to 2004. (data from Price and others 1998; updated by the USDA Forest Service through 2004)

A two-phase model describes the population shift from low-level to epidemic conditions (Mawby and others 1989). The model has three points that represent a stable low-level phase maintained by host-tree-defensive capabilities, a transient high-level phase determined by host material availability, and a threshold between the two phases. This threshold depends on local environmental and biotic factors and is rarely observed because of its transience. The SPB populations may survive for years at low levels, causing localized mortality in small spots of weakened trees, then build up to numbers approaching the threshold, and under environmentally favorable conditions, exceed the threshold, causing a pulse eruption or epidemic. The challenge for forest managers is to understand this cycle and the local environmental and biotic factors that cause populations to erupt, and establish management strategies that minimize the likelihood of this occurrence.

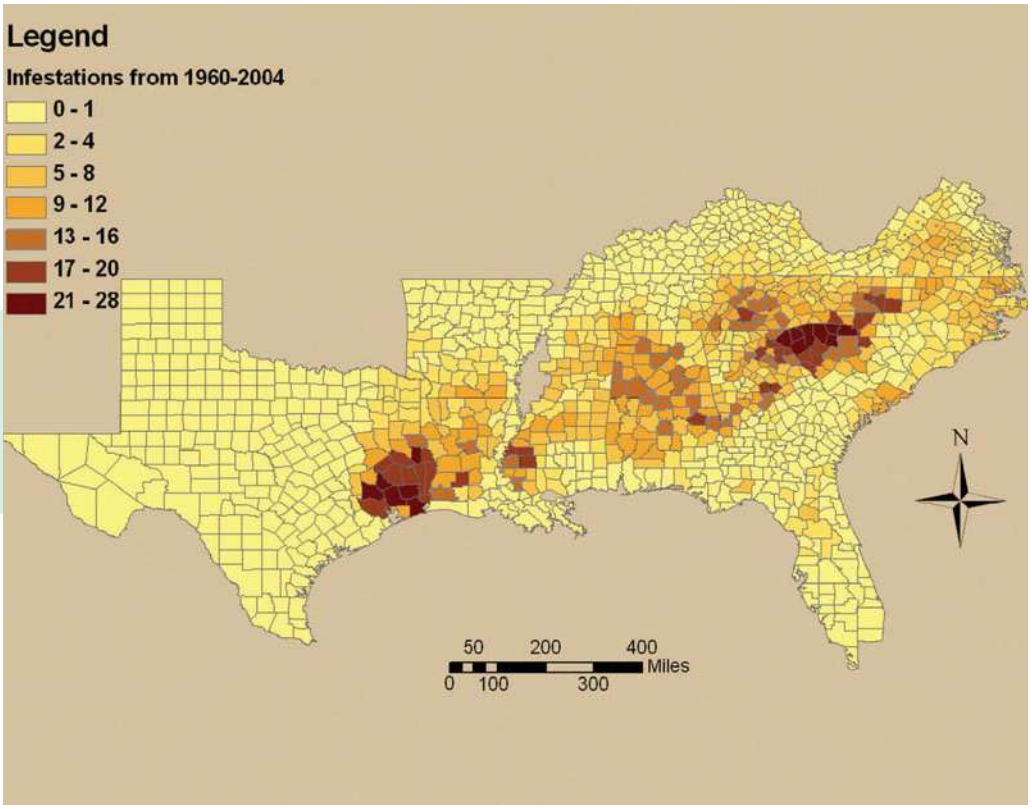

Figure 2.10—Frequency of SPB activity by county from 1960 to 2004. (data from Price and others 1998; updated by the USDA Forest Service through 2004)

3

Southern Pine Beetle Behavior and Semiochemistry

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Keywords

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semiochemical

Abstract

The southern pine beetle (SPB) feeds both as adults and larvae within the inner bark of pine trees, which invariably die as a result of colonization. Populations of the SPB erupt periodically and produce catastrophic losses of pines, while at other times the beetles persist almost undetectably in the environment. The southern pine beetle has evolved behaviors that maximize its survival and reproduction when local population densities are either high or low. When densities are high, the SPB utilizes pheromones to organize synchronous mass attacks capable of overwhelming the resin defenses of healthy, vigorous trees. They thereby render hosts available to colonization that would not be susceptible to attack by one or a few individuals. When densities are low, the SPB must find and utilize trees that have been previously rendered susceptible by either abiotic factors, particularly lightning strikes, or biotic stressing agents such as attacks by other bark beetle species. This chapter reviews existing knowledge of the behavior and chemical ecology (i.e., use of chemical signals including pheromones) of the SPB and addresses how these aspects of SPB biology may either facilitate or hinder efforts to manage this virulent forest pest.

3.1. INTRODUCTION

Damage from the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) occurs conspicuously on the landscape as patches of pines that are killed rapidly and sequentially over a period of weeks or months. Each such infestation or SPB "spot" typically consists of a zone of contiguous pines that may be dead and abandoned, currently colonized, and/or undergoing mass attack. This zone is usually surrounded by apparently uninfested trees, and newly infested trees are accumulated typically on just one side of the spot, called the spot's head. Spot growth (i.e., accumulation of new infested trees in a spot) occurs at a rate that is dependent on the number of currently infested trees, the density of adjacent suitable hosts, the season, and a variety of other factors. Individual spots may accumulate as few as one new tree every 2-3 days (Johnson and Coster 1978, Schowalter and others 1981b) or may engulf dozens of trees per day and grow to encompass hundreds of acres in a matter of weeks. Mass attacks on uninfested trees at the spot head are mediated by pheromones released both by the SPB established in adjacent, recently infested trees within the spot head, and by individuals landing on the uninfested trees.

Less conspicuously, the SPB may attack single, isolated trees in the forest, and during periods of relatively low beetle population numbers (nonoutbreak or latent population phase) this may be the only mortality attributable to this insect. However, with an adequate density of susceptible hosts and/or foraging beetles in the immediate area, spots may develop from such isolated, infested trees (Coulson and others 1985a, Franklin 1970b).

3.2. BEHAVIORAL EVENTS OF THE SPB LIFE CYCLE

The complete life cycle of the SPB can be divided into the following sequence of events: 1. dispersal, 2. host location and selection, 3. host attack and colonization, 4. parent adult reemergence, 5. brood development, and 6. brood emergence.

3.2.1. Dispersal

Upon emergence, the SPB takes flight in search of a host tree. Unlike many other species of aggressive bark beetle (Borden 1982), newly emerged SPB do not require a period of flight exercise before they respond to attractants (Gara and others 1965, Payne and others 1976), although flight exercise has been shown to enhance responsiveness in walking beetles (Andryszak and others 1982). The SPB apparently does not feed to replenish energy reserves during dispersal, and they can survive merely 1-2 weeks while outside of a host tree and exposed to air temperatures suitable for flight (Wagner and others 1984a). Thus, individuals that are to survive and reproduce must locate a suitable host quickly (Coulson and others 1985a). Tethered SPBs can fly up to 2.6 km and at an average speed 0.77 km/hr (Kinn 1986), and beetles marked with fluorescent powder have been recovered on the day of their release in baited traps located more than 1 km away (Gara 1967). Using concentric rings of baited traps around a central release point, Turchin and Thoeny (1993) estimated the median dispersal distance of the SPB to be 0.69 km. Based upon estimates of the frequency and distribution of lightning-struck pines, these dispersal distances, though not great, are likely adequate to allow SPBs to reach a susceptible host during any season of the year (Coulson and others 1983). Furthermore, genomic studies of SPBs collected from locations separated by dozens or hundreds of kilometers did not reveal a significant correlation between genetic and geographic distance, suggesting that free exchange of genes, and thus dispersal, may occur across substantially greater space than inferred from mark-recapture studies (Allender and others 2008, Schrey and others 2008).

The distance that individual SPBs disperse is influenced by a variety of factors, a key one being the proximity of emerging beetles to sources of attractant. Catch of marked SPBs in baited traps located 1.6 km upwind was much less if the beetle release point was adjacent to trees being mass attacked, whereas captures in unbaited traps adjacent to the release point were much greater (Gara 1967). Similarly, when brood trees in an active SPB spot were coated with fluorescent powder, proportions of marked beetles trapped at artificially induced infestations located 100, 200, and 500 m away were much greater if the spot was subjected to a cut-and-leave treatment that suppressed mass attack of new trees at the spot's head (Cronin and others 1999). These findings suggest that SPBs emerging within active spots are arrested by semiochemicals released from adjacent, newly infested trees. Consequently, they will tend to attack trees within or near the spot head rather than disperse to new locations as long as mass-attacked trees persist within the spot (Cronin and others 1999, Gara 1967). Contrariwise, the termination of spot growth and disappearance of newly infested trees from an SPB spot—either due to the artificial removal of these trees or exhaustion of suitable hosts at the location—apparently releases long-range dispersal by beetles emerging from previously infested trees within the spot (Gara 1967). Nonetheless, a significant proportion of emerging beetles do disperse from active, growing infestations (Cronin and others 1999), and these individuals may express different genes than those that remain to attack trees within their natal infestations (Florence and others 1982).

The SPB disperses predominantly during the spring and to a lesser extent in fall, whereas in summer their movements appear to be largely restricted to interiors of established spots. Median dispersal distance by SPBs emerging within concentric rings of baited traps was 1.09 km in the fall but merely 0.53 km in summer (Turchin and Thoeny 1993). Furthermore, the SPB can be captured during the spring in large numbers in traps baited with frontalin and turpentine and located hundreds of meters from the nearest spot (Billings 1988), whereas in summer such traps appear to be largely ineffective unless placed directly within an active infestation (author's personal observations). Southern pine beetles in a walking olfactometer likewise responded more strongly to an attractant mixture in the spring than in the summer (Roberts and others 1982), suggesting an overall lower responsiveness to attractant semiochemicals during periods of nondispersal. New SPB spots are established predominantly in the spring, with fewer originating in summer and fall (Thatcher and Pickard 1964), and essentially none in winter (Franklin 1970b). Fat content of emergent SPBs is greatest in the spring and fall; hence they have greater energy reserves and flight potential during their major periods of dispersal (Hedden and Billings 1977). Spots commonly stop growing in the late fall and winter, and spring dispersal may be triggered both by the return of average temperatures adequately warm for emergence and flight and the absence of trees releasing attractive semiochemicals within the overwintering spots (Gara 1967). Intense but brief flights of the SPB commonly occur during January and February on days when the temperatures exceed ~20 °C (Moser and Dell 1979a), although these flights may not generate new mass attacks (Franklin 1970b).

The southern pine beetle terminates or reduces flight activity in winds exceeding about 7 km/hr (Coster and Gara 1968, Coster and others 1978b), or when the maximum daily air temperatures are either below 7 °C or above 37 °C (Moser and Thompson 1986). A much higher air temperature is apparently required for the SPB to initiate flight (i.e., 22 °C) than to sustain it (i.e., 7 °C) (White and Franklin 1976). Solar warming of the bark may permit the SPB to initiate flight on days when the air temperature remains below 22 °C. The optimal flight temperature for the SPB is approximately 27 °C (Moser and Thompson 1986).

Tests with rotary nets indicated that most SPB flight occurs between 1.2 and 5.5 m above the ground, which roughly corresponds to the height of first and most frequent landing on mass-attacked trees during summer [i.e., 3-4 m; (Coster and others 1977a, 1997b)] (Gara and others 1965). Weather influences daily beetle flight activity (inferred from the rate of beetle catch in baited traps) to a greater extent in winter than other seasons, and during this period flight is strongly positively correlated to temperature and amount of sunlight (Geer and others 1981). Heavy rainfall can suppress beetle flight, whereas the onset of summer rainstorms and light rain can increase flight activity somewhat (Coster and others 1978b, Moser and Dell 1979a). Relative humidity greater than approximately 80 percent reduces SPB flight in both fall and winter (Geer and others 1981).

In both spring and summer, SPB flight activity is concentrated in the afternoon between 2 pm and 6 pm, with some flight occurring throughout the daylight hours (Vité and others 1964, Vité and Crozier 1968). Hopkins (1909) reported that the SPB flew also at night, but this has not been corroborated by subsequent studies (Bunt and others 1980). The SPB flies upwind in response to sources of attractive odors, and they may land at least briefly on nonbaited, vertical objects downwind from an attractive odor source while orienting upwind (Coster and Gara 1968). Following emergence, they may disperse either in the prevailing upwind or downwind direction, and season appears to influence which is more prevalent (DeMars and Hain 1979, Moore and others 1979).

3.2.2. Host Location and Selection

The SPB must kill their host trees in order to reproduce, whereas it is essentially impossible for a solitary beetle pair to kill a healthy pine. To be successful, an SPB pair must either attack synchronously with sufficient numbers of other pairs to assure capitulation of host defenses, or otherwise select hosts whose defenses have been sufficiently compromised by other agents. Thus, the optimal host location and selection strategies for individual SPB will depend upon the balance between local abundance of conspecifics and the susceptibility of available hosts.

Once SPB attacks have been initiated on an individual tree, the combination of beetle-produced aggregation pheromones and host odors becomes the principle cue used in host location and selection by SPBs that follow. Semiochemicals from these initial attacks attract other host-seeking SPBs to the tree of pheromone origin. The later-arriving beetles, in turn, initiate their own attacks and release pheromones. This self-perpetuating cycle may come to an end once the phloem resource of the host reaches its carrying capacity and no further beetles initiate attacks. However, if the concentrations of semiochemicals reach a high enough level (as occurs if beetles attack rapidly and in large numbers; see below) and suitable pines are adequately close by, arriving beetles may be induced to land on and attack these adjacent pines as well. These adjacent trees may then become new foci of attack for arriving beetles, a process called "host switching," and semiochemicals from these trees may, in turn, stimulate initial attacks on further adjacent trees. This chain reaction, in which pheromones from trees undergoing mass attack stimulate landings, initial attacks, and consequently pheromone release from adjacent trees, appears to be the underlying mechanism driving the accumulation of new infested trees in SPB spots.

Individuals that first arrive and initiate attacks on a particular tree (so-called "pioneer" beetles) face special risks, since if the tree is vigorous, their survival may depend upon their capacity to release pheromones and attract sufficient numbers of other beetles to join them in a mass attack (Pureswaran and others 2006). Within active infestations, pioneer beetles can rely to a large extent on pheromones released from currently mass-attacked trees both to guide them in selecting a new host (i.e., one adjacent to those already mass-attacked) and to insure this host's subsequent mass attack and colonization. In its strictest sense, the term "pioneer" is applied only to those beetles initiating attacks without the benefits of pheromones already being released from either the potential host or adjacent trees. Such conditions exist within the forest outside established infestations or during periods of nonoutbreak population levels. Then pioneer beetles must select a host that is adequately weakened to allow immediate colonization, or else their pheromones must be sufficient for attracting dispersed beetles to overcome host defenses. A separate understanding of host selection processes by either concentrated or dispersed populations is essential to predicting and managing SPB outbreaks, since host selection by dense SPB populations influences infestation persistence and growth rate, whereas host selection by dispersed or dispersing beetles determines when and where infestations become initiated in the first place.

Host Location/Selection within Active Infestations

Within established infestations, beetle populations are normally high enough to permit colonization of vigorous pines through mass attack. New hosts are selected for attack in response to at least four factors: 1. their proximity to recently attacked trees, 2. the density and rate of attack on such adjacent trees, 3. wind direction, and 4. appropriate visual cues from the prospective host.

Proximity to recently attacked trees

Within growing infestations, adjacent pines are typically attacked sequentially, such that the trees infested next are typically those located nearest ones currently undergoing mass attack (Vité and Crozier 1968). This effect is apparently due to the ability of semiochemicals from mass attacked trees to concentrate beetle landings in the immediate area, as suggested by the fact that both natural and artificial sources of SPB attractants (particularly the female-produced pheromone frontalin combined with host terpenes) are likewise capable of stimulating landings and attacks on all trees within a limited radius of their release point (Coster and Gara 1968, Vité 1970). In a small infestation where only one tree was being mass attacked (and thus serving as an attractant source) at any single time, Johnson and Coster (1978) determined that the probability of attack on any tree declined as the inverse square of its distance from the most recently infested tree. However, mass-attacked trees are never observed to induce new attacks more than 6-7.5 m away (Gara and Coster 1968). Consequently infestations will normally collapse (i.e., cease growing) if the distance between the most recently infested trees and uninfested pines exceeds this minimum distance (Schowalter and others 1981b), a circumstance that often occurs when the advancing heads of infestations encounter stand boundaries, power line right-of-ways, roads, sites of previous infestations, and other natural and man-made landscape discontinuities in pine abundance.

Density, age, and rate of attacks on adjacent, infested trees

The capacity of SPB-infested trees to induce attack on adjacent trees is limited to those that have been freshly infested and are still attractive to flying beetles (Johnson and Coster 1978). The attractiveness of infested trees to flying beetles (and, likewise, attractant production by attacking beetles) varies over time and is typically short-lived: approximately 99 percent of beetles are trapped on infested trees within the 7 days following attack initiation, with a distinct peak in response occurring at day 3 (Coster and others 1977a). Removal of recently infested trees from a growing SPB infestation terminated both beetle aggregation and attacks on uninfested hosts (Gara 1967). The tendency for SPB colonization to be induced on trees adjacent to an attractant source appears to be dependent on the intensity of the attractant stimulus. In an experiment conducted in an epidemic SPB area (i.e., within 1 mile of active SPB spots), the number of SPB attacks on a pine post necessary to induce mass attack on adjacent uninfested posts was approximately linearly related to the distance between the posts. In addition, such baited pine posts induced attacks on adjacent, unbaited posts only when these were located in epidemic stands, but failed to do so in stands with low populations (Gara and Coster 1968). The accumulation of fresh attacks on the baited post was much slower in the endemic stand than in the epidemic stand, and these authors speculated that the absence of spillover attacks in the former was due to the insufficient concentrations of attractants produced by the poorly synchronized attack on the baited post. Production of attractant by unpaired female SPBs occurs for only a few days (Coster and Vité 1972); hence, a host that accumulates attacks over many weeks cannot form as intense a pheromone plume as one receiving the same number of attacks synchronously. Studies conducted using synthetic attractants confirm the importance of attractant dose to the likelihood of attacks on adjacent trees: low doses of frontalin/*alpha*-pinene (0.3 mg frontalin/hour) concentrated beetle landings near the point of bait release; rates 3-10 times this induced attacks on adjacent trees, while extremely high rates (1 g frontalin/hour) caused attacks on trees up to 40 m away (Vité 1970).

Wind direction

Within infestations, the SPB tends to select host trees immediately downwind from those most recently infested, and for this reason SPB infestations tend to grow in the prevailing downwind direction (Coster and others 1978a). Flying SPBs respond to contact with an attractant odor plume by flying upwind (upwind anemotaxis), and thus they are more likely to land on objects located downwind of an attractive source than other directions (Coster and Gara 1968). Boles of uninfested trees no doubt intercept the semiochemical plumes arising from infested ones located upwind, resulting in exceptionally high concentrations of secondhand aggregation stimulants occurring at the bark surface of such downwind trees. A stream of air containing concentrated volatiles from attractive SPB-infested bolts can stimulate SPB attacks on any tree where it is directed (Gara and others 1965); hence, the wind passing through recently infested trees may produce a similar effect in trees downwind.

Visual cues from the prospective host

In the presence of high concentrations of semiochemical attractants, the SPB will tend to alight on and may attack any dark object possessing a strongly vertical silhouette similar to the bole of a standing host tree (Gara and others 1965). Within an active SPB infestation, baited pine posts were much more attractive to the SPB when placed in a vertical rather than horizontal orientation (Gara and others 1965). This presumably visually mediated preference for vertical hosts agrees well with the long-standing observation that SPB infrequently infest downed timber (Dixon and Osgood 1961; however see Moser and others 1987), and this preference may help the SPB to discriminate against nonliving hosts (Payne and Coulson 1985). In addition, this visual response appears to be only to objects with a low degree of light reflectance (i.e., dark in appearance), since multiple funnel traps are far less attractive to the SPB if painted white or yellow as opposed to black or other dark colors possessing a low average reflectance value (Strom and Goyer 2001). Furthermore, white-painted lower boles of uninfested pines received many fewer SPB landings and attacks than the unpainted portions of the same trees or adjacent, black-painted pines (Strom and others 1999).

Host selection by SPB within infestations: Other factors

Host Susceptibility. As SPB infestations expand, generally all pines above ~10 cm in diameter in the path of the moving head of the infestation are colonized and killed, resulting in an uninterrupted zone of dead pines (Dixon and Osgood 1961). However, susceptibility to bark beetle attack, as assessed by measuring resin flow and other indicators of vigor and defensive capacity, typically varies greatly among pines within stands (Cook and Hain 1987a, Martinson and others 2007). Hence the characteristic scorched earth nature of SPB infestations suggests that, within infestations at least, the SPB largely does not discriminate hosts according to their relative susceptibility (Gara and others 1965, Thatcher 1960). However, experimentally grown progeny of infrequent escape trees (pines that survive an infestation that kills all surrounding trees) produce above-average resin flow, suggesting that survival of their parents was related to an inherited capacity to resist attack or avoid selection by mass-attacking beetles (Strom and others 2002).

Host Species. At the head of an active infestation, the SPB lands on uninfested pines, as well as entirely unsuitable hardwood species, with equal frequency. In fact, the SPB can be induced to mine into hardwood trees if a stream of concentrated volatiles from logs of mass-attacked pines is directed at their bole (Gara and others 1965). Such attacks on nonhosts are ultimately abortive, but the phenomenon demonstrates that, with very high local concentrations of volatiles from mass-attacked trees, the SPB cannot distinguish host from nonhost trees prior to landing or even penetrating into the bark.

Acceptable pine host species for the SPB differ in the relative frequency of SPB-inflicted mortality, and pines with higher average levels of mortality (e.g., loblolly and shortleaf) are described as being more susceptible and/or preferred relative to those with lower mortality (e.g., longleaf and slash) (Hicks 1980, Blanche and others 1983). However, as already implied, the SPB may not discriminate pine species of differing susceptibilities when these are intermixed within active infestations. For example, SPBs are equally likely to land on, attack, and kill either loblolly or longleaf pine when these species co-occur along the front of a growing infestation (Martinson and others 2007), and other evidence suggests that SPBs may discriminate between these host species only in the absence of a pheromone plume (Friedenberg and others 2007b). However, when Virginia pine and loblolly were intermixed in a growing SPB infestation, Virginia pines received significantly higher rates of landings, attacks, and mortality than loblolly (Veysey and others 2003).

Inhibitory Pheromones. Some evidence suggests that SPB-produced olfactory repellants or attraction inhibitors may play a role in host selection. Devices releasing certain male-produced volatile compounds (e.g., verbenone and *endo*-brevicomin) can reduce SPB responses to attractant-baited traps and/or reduce landings and attacks on pines within active infestations (Payne and others 1978, Richerson and Payne 1979, Salom and others 1992). Since males are the secondarily arriving sex, these male-produced attraction inhibitors have been thought to play a role in both terminating attraction to fully colonized trees (thus serving as antiaggregation pheromones) and inducing switching in attack focus from colonized trees to adjacent, uninfested trees (Payne 1980, Renwick and Vité 1969, Smith and others 1993). However, female SPBs likewise produce compounds that can inhibit conspecific attraction to baited traps, and during attack they may actually release these compounds earlier than or simultaneously with their major attractant frontalin (Sullivan 2005, Sullivan and others 2007a). In addition, there is no *in situ* evidence that arriving males and their associated semiochemicals cause female attacks to become significantly less attractive to flying SPBs. Pine bolts and posts infested with beetle pairs are reported to be similarly attractive to conspecifics as ones infested with solitary females (Coster and Vité 1972, Franklin 1970b, Svihra 1982), and in a location with low beetle densities, standing trees infested with both sexes were more attractive than trees infested with females alone (Sullivan and others 2007b). Furthermore, the rapid loss in attractiveness of SPB-colonized trees to conspecifics (Coster and others 1977a) can be explained readily from the decline in concentration of beetle- and host-produced attractants (Vité and Crozier 1968, author's unpublished data) rather than the release of inhibitor pheromones. It is also likely that the inhibition observed to male volatiles in trapping and tree protection tests involved unnaturally high concentrations of the semiochemicals, and thus may not have reflected normal SPB behavior. Hence, the evidence is equivocal regarding whether the SPB utilize antiaggregation pheromones during host selection and colonization.

Host Location/Selection Outside of Active Infestations

Pioneer SPBs that initiate colonization of hosts located substantial distances from existing infestations cannot rely on large numbers of conspecific attacks to assist them in overcoming host defenses, and thus they must locate hosts whose defenses have been weakened prior to their arrival (Flamm and Coulson 1988). Two alternative hypotheses have been proposed for how such pioneer bark beetles locate hosts: either flying beetles orient to primary attractants arising from the uninfested host, or alternatively, they land on trees at random and evaluate the suitability of a host based on gustatory and other close-range cues (Byers 1989b, Raffa and Berryman 1979, Wood 1982b). After some unknown threshold number of beetles has become established on a host and release pheromones (perhaps as few as one), secondary attraction presumably becomes the predominant means by which subsequently arriving beetles locate the isolated host.

Host-produced odors, specifically the major resin monoterpenes, are potent synergists of the SPB's aggregation pheromones, and thereby play an important role as secondary attractants (Smith and others 1993). However, resin monoterpenes do not attract SPB to traps in the absence of pheromones (Billings 1985, Payne and others 1978). Healthy pines subjected to certain stressing treatments will become attacked by the SPB very rapidly, suggesting that host stress induces the production of attractive olfactory cues (Coulson and others 1985a, Heikkenen 1977). Lightning strikes are the single most important agent for rendering trees susceptible to the SPB in nature (Hodges and Pickard 1971, Lovelady and others 1991), and authors have speculated on the possible production of primary attractants by these trees. Two artificial procedures that duplicated the bole-length bark wound typical of a lightning strike (one employing blast cord, the other a sickle) induced SPB landing and attacks on treated pines situated far from natural sources of beetles (Coulson and others 1983, Payne 1986). Southern pine beetles responding to lightning-struck pines may be attracted by massive quantities of host volatiles released precisely within the height range of typical SPB flight, with the vertical silhouette of the tree bole providing an appropriate visual stimulus (Payne 1986). However, the aforementioned wounding/stressing experiments did not screen the trees from attacks by bark beetles; hence, it is not possible to conclude that SPB responses were due to host-produced, primary attractants alone. Under the alternative hypothesis that the SPB lands randomly on potential hosts, there is some evidence to suggest that the massive quantities of resin volatiles released by the lightning wound could mediate host selection by arresting SPB flight on the struck trees (Payne and Coulson 1985).

In the Southern United States, trees infested by the SPB are typically attacked simultaneously and/or in rapid succession by several additional bark beetle species, specifically, *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), *I. grandicollis* (Eichhoff), and the black turpentine beetle (BTB), *Dendroctonus terebrans* (Olivier) (Coulson and others 1986, Flamm and others 1993). These five species, collectively called the "southern pine bark beetle guild," each produce their own, specific attractant pheromone blends that nonetheless share many components (Smith and others 1993). Since the SPB may not be the first species to arrive at isolated, susceptible trees (Hodges and Pickard 1971, Coulson and others 1985a), it is possible that pheromones of first-arriving species may serve as host location cues (i.e., kairomones) to subsequently arriving SPBs (Svihra and others 1980). However, the SPB does not appear to be attracted to logs infested with any of the three *Ips* species or to synthetic blends of *Ips* spp. pheromones (Birch and others 1980, Smith and others 1990). On the other hand, the BTB produces frontalin, the major component of the aggregation pheromone of SPB, as well as *exo*-brevicomin, *endo*-brevicomin, and *trans*-verbenol—compounds that can synergize frontalin's attractiveness to the SPB (Payne and others 1987, Pureswaran and others 2008a, Sullivan and others 2007b). Synthetic blends that mimic the natural pheromone blend of the BTB are also significantly attractive to the SPB in field-trapping trials (Smith and others 1990). Unlike the SPB, the BTB responds strongly to identified, primary attractants released by physically wounded pines such as lightning strikes, namely, resin monoterpenes (Fatzinger 1985, Siegfried and others 1986), and this capacity may assist them in being almost invariably the first species to arrive at lightning-struck pines (Hodges and Pickard 1971). Hence the SPB may exploit the capacity of BTB to utilize primary host attractants by responding to BTB pheromones as secondary host attractants.

3.2.3. Host Attack and Colonization

Females are the sex that initiates gallery construction, and the beetles that first arrive on mass-attacked trees are predominantly females (Coster and others 1977a). Attacks are initiated near mid-bole (3-4 m height) and spread upward and downward along the bole with decreasing attack densities (Fargo and others 1978). Bunt and others (1980, data reanalyzed by Bishir and others 2004) published the only quantitative description of on-bark SPB behavior during mass attack (overview shown in Figure 3.1), and the following narrative is based on their studies unless noted otherwise. Following landing on the bark, a female searches an average of 10.2 minutes and travels 22 cm of bark surface before initiating a gallery entrance, usually within a crevice in the bark. If the female encounters an established beetle entrance, she may investigate it and afterward initiate her own entrance less than 2 cm away. Extractable chemical cues in the outer bark of preferred pine species can stimulate biting by female SPB; hence, such bark compounds may stimulate gallery initiation (Thomas and others 1981). She must chew into the bark for more than 1 hour before she is completely inside, and during this time she is highly vulnerable to predation by the clerid predator *Thanasimus dubius* (F.). She typically does not chew directly to the phloem, but rather mines the entrance at a shallow angle into the corky bark such that it penetrates the phloem tissue only gradually (Payne 1980). This behavior likely assists her in slowing the defensive response of the tree. The female uses her legs and elytra to push resin exuded by the damaged phloem tissue to the entrance where, apparently by working her back legs in the liquid, she forms it into a pitch tube of semicrystallized resin surrounding the entrance. Pitch tubes are formed only if the host is releasing resin; attacks occurring after host resistance has been reduced by previous beetle attacks or other causes may produce small or no pitch tubes (Payne 1980). If unimpeded by resin, the female then widens the tunnel where it penetrates the phloem to produce a "nuptial chamber"; this expansion provides the male adequate space to reorient his body for mating (Fronk 1947, Wagner and others 1981a). Until joined by a male, the female continues to mine in the phloem, constructing short (2-3 cm) galleries that radiate from the nuptial chamber (author's personal observations).

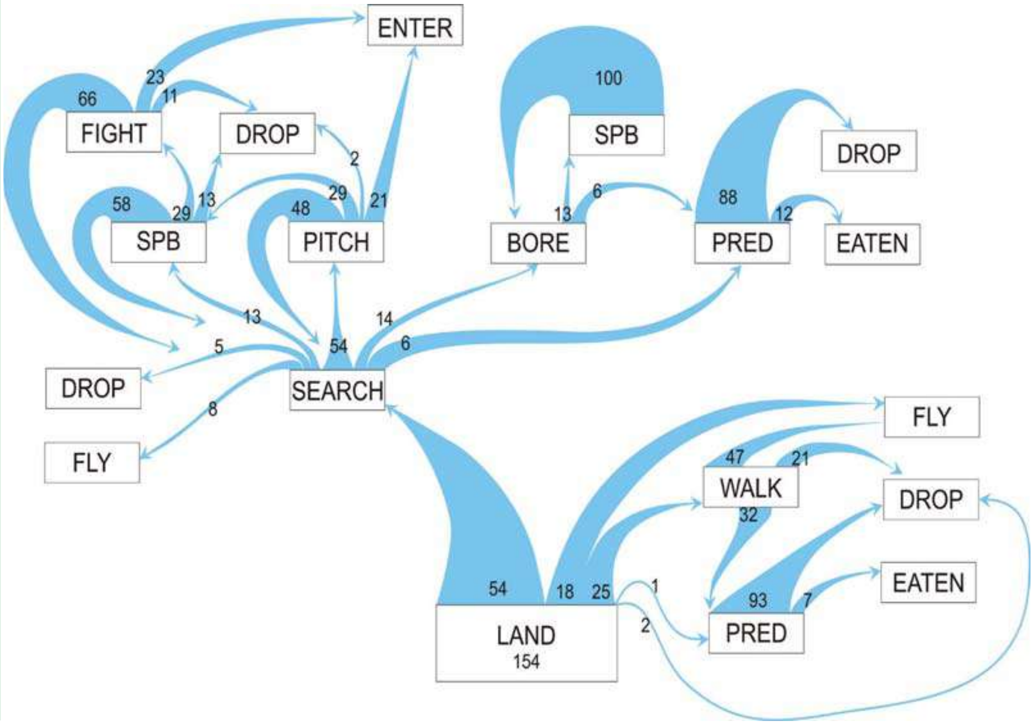


Figure 3.1—Behavioral sequences for individual SPB during mass attack on a host pine. Abbreviations of on-bark behaviors: LAND=landing; WALK=undirected walking; SEARCH=active searching of the bark surface; PITCH =investigating an entrance hole; SPB=encountering another SPB; FIGHT =fighting with another SPB; PRED=encountering a predator; EATEN= captured by a predator; FLY=flying from the tree; DROP=dropping from the tree; BORE=boring a gallery; ENTER=entering an existing gallery. Arrows are labeled with the numbers of individuals observed (out of a total of 154) to proceed from one behavior to the next. (reprinted from Bunt and others)

While forming the gallery, she occasionally stridulates, producing a series of staccato chirps (Figure 3.2A) that may signal her presence to females in adjacent galleries (Rudinsky and Michael 1973, Ryker 1988).

When the female lands on the host, her hindgut contains small amounts (tens of nanograms) of the attractant pheromone frontalin, along with approximately 100 fold greater quantities of the frontalin synergist *trans*-verbenol (Pureswaran and others 2006). Females release these compounds continuously at a slow rate while outside of a host, and they no doubt do so also while on the bark surface searching for a suitable boring site or initiating a gallery. Upon entering the bark, the female rapidly releases most of this cache of pheromone in her hindgut, presumably as a consequence of a renewal of eating and defecation. She then begins to release frontalin at a much higher rate than she did prior to entering the host (Pureswaran and others 2008b, Pureswaran and Sullivan unpublished data). Frontalin combined with either *trans*-verbenol or *alpha*-pinene from the host resin attracts SPBs of both sexes to the attacked tree, and these compounds appear to be the key stimuli for initiating and then sustaining mass attack on the host. *alpha*-Pinene and *trans*-verbenol are apparently interchangeable and redundant as attractive synergists for frontalin (Payne and others 1978); hence, *trans*-verbenol may be critical for stimulating mass attack prior to large-scale penetration of the phloem and resin release (Renwick and Vité 1969).

Both sexes search in a predominantly upward direction from their landing point (Gara and others 1965). Forty-six percent of landing beetles leave without initiating searching behavior; they either drop or fly off the bark surface. These beetles likely renew searching flight, as suggested by evidence that the SPB may land and take flight again multiple times in close proximity to an attractive source, and presumably they may even land again on the same host (Coster and Gara 1968). Encounters between either males or females, particularly when near the entrances to galleries, often result in battles in which the two insects butt heads and push against one another. If the male encounters another male in an entrance, he may attempt to dislodge the first by pushing and biting, and if larger than the first, he often succeeds. If the battle occurs within the gallery, the male may kill and dismember his rival (Yu and Tsao 1967). Whenever males encounter each other on the bark or inside a gallery, they stridulate vigorously with a rapidly pulsed "rivalry chirp" (Figure 3.2B; Ryker 1988).

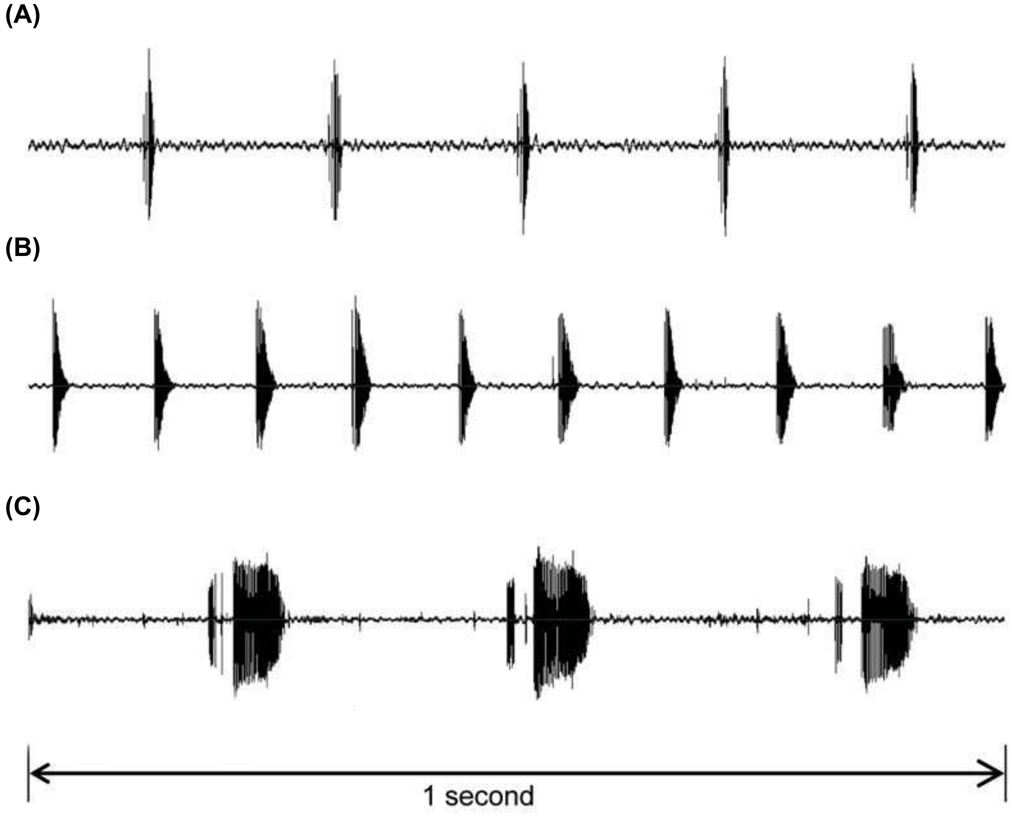


Figure 3.2—Oscillograms from sound recordings of SPBs inside a newly initiated gallery system. (A) Female chirps, (B) male "rivalry chirps", and (C) male "attractant chirps". (author's unpublished data)

Landing males search an average of 6.6 minutes and may investigate several entrances along a mean 25 cm path before stopping at one and entering. Whereas it appears that some males merely happen upon entrances at random on the bark, search by others appears more directed, possibly in response to pheromones emitted from the female entrances. This is implied by laboratory olfactometer studies in which male SPBs walked upwind to point sources of female odors (McCarty and others 1980), and their walking could be arrested by female odors emitted from artificial entrance holes (Rudinsky 1973). If the male selects a female entrance filled with liquid resin, he wades in and joins the female in clearing the gallery (Figure 3.3). Otherwise, the male first circles the entrance, digs through any frass blocking the tunnel, and then proceeds into the gallery to locate the female, who likely is extending the gallery and facing away from the entrance (Wagner and others 1981a). Upon reaching the female, he initiates courtship by jostling her elytra, while emitting a distinctive "attractant chirp" (Figure 3.2C; Yu and Tsao 1967, Ryker 1988). After possibly receiving some signal of acquiescence from the female, the male backs into the nuptial chamber or a gallery branch, reverses direction, and then backs toward the female to make end-to-end contact with her. The pair makes genital contact with the longitudinal axes of their bodies turned 90-180 degrees, and copulate for about 2 minutes (Yu and Tsao 1967). The pair mates repeatedly during gallery construction. The SPB is monogamous, and gallery systems are normally occupied solely by a single male and female. Nonetheless, if the male is removed and repeatedly replaced with another, the female will mate successively with these other males (Yu and Tsao 1967).

Figure 3.3—A pair of SPB "working" a pitch tube on a newly attacked pine.

Similar to females, males arrive with accumulations of at least two sex-specific pheromones in their hindgut: minute quantities of (+)-*endo*-brevicomin and large quantities of verbenone (Pureswaran and others 2006). The males likewise release these compounds gradually while outside the host, and then rapidly empty their hindgut during or shortly following pairing with a female. Once paired, the male begins releasing elevated levels of (+)-*endo*-brevicomin and continues to produce verbenone (Pureswaran and others 2008b, Sullivan and others 2007b). Both compounds have been shown to have complex effects on the behavior of SPB, and hypotheses concerning the biological function of both (+)-*endo*-brevicomin and verbenone for SPB are discussed elsewhere in this review.

Attacking SPB adults can survive extensive periods completely immersed in liquid resin—a remarkable feat given the demonstrated toxicity of pine resin constituents to insects including the SPB (Byers 1989b, Coyne and Lott 1976, Smith 1963). However, this capacity is not unlimited, and the beetles can be "pitched out" by an overwhelming flow of resin or "pitched in" when crystallizing resin traps them inside the gallery. The pair cannot extend their gallery or begin laying eggs until resin flow has largely ceased. Despite the risk that resin flow poses to SPB survival, SPB-attacked pine is more attractive to conspecifics if it generates a strong defensive response and produces copious resin. Resin expelled from gallery entrances releases enormous quantities of *alpha*-pinene, which at high doses has been shown to dramatically increase SPB responses to frontalin (Billings 1985), and a vigorous host response may stimulate or sustain attractant pheromone production by attacking beetles (Vité and Crozier 1968).

Following cessation of resin flow and mating, the pair proceeds to extend their gallery into the phloem with the female in front, chewing into the tissue, and the male behind, assisting the female in clearing the front portion of the gallery of frass. Initially the frass is expelled from the entrance, but once the pair has penetrated a few centimeters into the phloem, the male packs the frass tightly behind him, thereby sealing off the entrance. Thereafter, he continues to pack frass behind him while maintaining an open space of 1.5-2.5 cm at the distal end of the gallery (Fronk 1947). The pair cuts a narrow (average 3.4 mm wide), 10-35 cm long, broadly S-shaped gallery into the phloem at a rate of 2-4 cm per day at 20-25 ºC (Fronk 1947, Wagner and others 1980). They mine 1.5-2 days and extend the gallery 2.8-3.8 cm before the first egg is laid. This period of feeding presumably allows time for the enlargement of the female's reproductive organs, autolysis of flight muscles, and other physiological changes crucial to egg production. Since the first few centimeters of the gallery are more prone to be soaked with resin, the behavior may also assure greater egg survival. The length of this preliminary gallery may more than double at low temperatures, but it is unaffected by the density of attacking beetles in the surrounding bark (Wagner and others 1981a).

The female then begins to chew egg niches, semicircular pits 1-2 mm deep, into the phloem on alternating sides of the gallery (Fronk 1947). She lays a single egg into each niche after it is completed and then packs frass into the niche, covering the egg and securing it in place. The frass covering is pressed and smoothed to match the original contour of the gallery (Wood 1982a). The female lays an egg every 0.4-2.0 cm (mean 1.59 eggs/cm gallery; Foltz and others 1976). The spacing of eggs remains constant during egg laying, and is unaffected by the density of attacking beetles in the bark, but is greatest at 20-25 °C. Generally, it is reported that fewer than 3-4.5 percent of niches are left empty (Clarke and others 1979, Wagner and others 1981a), but high rates of empty niches (38 percent) have also been observed (Lashomb and Nebeker 1979). The length of this egg-bearing portion of the gallery and the total number of eggs laid per female is inversely related to density of attacking beetles in the surrounding bark, and consequently, pairs that attack relatively late will produce less egg-bearing gallery and fewer eggs than those that attack earlier. Thus mining females reduce the length of the egg gallery and the number of eggs they lay in response to greater numbers of ovipositing females around them, and this results in a final egg density within the bark that is independent of the density of attacking adults. This compensatory negative-feedback process assures a uniform amount of food is available to all larvae (Coulson and others 1976b). The females may curtail oviposition after sensing the stridulation by beetles in adjacent galleries, or they may detect chemical changes in the phloem tissue resulting from degradation and damage caused by the beetles and their associated microbes (Wagner and others 1982). These same cues may cause females to divert their galleries away from other galleries rather than cross them (Grosman and others 1992), a behavior which is responsible for much of the sinuousness typical of SPB galleries. Females mine through (i.e., cross) existing galleries frequently only when beetles are at high densities.

Throughout the gallery but predominantly in the egg-bearing portions, the pair mines "turn-arounds"—short side branches extending either a variable distance outward into the corky bark but not to the surface, or <2 mm sideways into the phloem (Wagner and others 1981a). The frequency of turn-arounds mined into the corky bark increases with temperature, and these diverticula possibly play a role in improving ventilation within the gallery.

The final 2-3 cm of the parental gallery is typically free of eggs, and its length is independent of attacking beetle density (Wagner and others 1981b). Males and females generally mine separate exit galleries into the outer bark, and the time between the initiation of these galleries and reemergence occupies from one-third to one-half of the beetles' time within the host. This prolonged period of relative inactivity may coincide with internal physiological changes required for reemergence and flight. While constructing the exit galleries, the beetles periodically return to the phloem and may construct short (≤1 cm) side galleries, presumably for nutritional reasons (Wagner and others 1981a). On average, males reemerge before females (Yu and Tsao 1967).

3.2.4. Parent Adult Reemergence

Following establishment of a brood population in one host, SPB reemerge and may attack and establish broods in two or perhaps three additional trees (Clark and Osgood 1964). Field studies have reported that 65-97 percent of attacking adults reemerge (Cooper and Stephen 1978, Coulson and others 1978). Reemergence begins as early as 4-8 days following initiation of mass attack and lasts approximately 10 days during typical summer temperatures (Coulson and others 1978, Franklin 1970b, Thatcher and Pickard 1964). At temperatures <20 °C or >30 °C, reemergence is delayed 4-17 days and lasts much longer (Gagne and others 1982). Relative to SPBs establishing an initial brood, SPBs establishing second broods produce longer egg galleries, produce more eggs, lay eggs closer together, and spend greater time in the bark before initiating an exit gallery (Wagner and others 1981b). Reattacking females are apparently capable of tunneling and laying viable eggs without a male; nonetheless, they typically pair with a male in the new host. However, when artificially deprived of males, reattacking females establish fewer galleries with egg niches, produce shorter galleries, and lay fewer eggs per day than pairs making either a first or second attack (Van Sambeek and Kile 1981).

Figure 3.4—Later-instar SPB larvae mining within feeding chambers in host phloem.

Reemergence behavior may be critical to the SPB's capacity to establish infestations from single, infested trees (Franklin 1970b). Reemerged SPBs are capable of producing aggregation pheromones (Coster 1970); hence, reemerging beetles attacking a second or possibly third adjacent tree could help maintain an attractive center at the site until brood from the original tree have completed development (Coulson and others 1978, Franklin 1970b). In addition, reemergence and reattack of adjacent trees rapidly generates overlapping generations of beetles, a condition that is key to sustaining a continuous emergence of beetles and recurrence of fresh attacks.

3.2.5. Brood Development

The eggs hatch in 4-12 days at a temperature of 30°-15 °C, but they fail to develop at temperatures ≤5 °C or ≥35 °C (Gagne 1980). After hatching, the ~ 2 mm-long larva spends its first two instars mining a threadlike gallery 3-60 mm into the cambium at approximately right angles to the parental gallery (Thatcher and Pickard 1967). This gallery may exit the cambium and disappear into the phloem tissue for the remainder of larval development, particularly in thick-barked trees (Payne 1980). Both bark beetle adults and larvae feed by cutting pieces of phloem tissue from the end of the gallery with their mandibles, and then crushing this material with their mouthparts to extract liquids. Very little solid material is ingested, and the frass consists largely of undigested phloem tissue. Nonetheless, the larvae consume their exuviae after each molt (Fronk 1947). The larva regularly pushes accumulated frass to the back of the gallery, thereby maintaining an open space of a few millimeters at the terminus. In the third instar, the larva widens the end of its mine into an ovoid or irregularly spherical feeding chamber (~3-5 mm long/wide) that gradually fills with frass as the larva develops (Figure 3.4). The total length of the final gallery is typically <2 cm. However, if the early larva encounters a zone of phloem colonized by the blue stain fungus *Ophiostoma minus*, it does not form a feeding chamber but rather extends its narrow winding gallery many centimeters through the stained tissue and may die before completing development (Franklin 1970a). In the fourth instar, the larva mines into the outer, corky bark and constructs an ovoid pupal chamber approximately 1.5-4.5 mm wide by 4-5 mm long, and there molts into a pupa (Figure 3.5; Fronk 1947). In very thin-barked trees, the pupal chamber may be formed at the interface between the corky bark and phloem. The entire larval period lasts a mean 17-45 days at constant temperatures in the laboratory (25°-15 ºC) (Fargo and others 1979). It was found to range more widely (10-62 days) in a field study in Mississippi (Mizell and Nebeker 1978). The time spent in each of the four instars is roughly equal (Goldman and Franklin 1977). Larvae held at 10 °C die before pupating (Gagne 1980). At constant temperatures, the pupal stage lasts an average of 5-17 days at 30° to 15 ºC (Payne 1980), although field studies have reported pupal development as long as 26 and as short as 3 days (Mizell and Nebeker 1978, Thatcher and Pickard 1967). Under controlled conditions, a small fraction of beetles complete pupal development in merely 1-2 days (Gagne 1980). The cuticle of the newly eclosed callow adult darkens in approximately 1 week (Figure 3.6), and then the beetle begins mining through the corky bark to produce an exit hole. The interval between eclosion of the adult and emergence lasts 6-14 days at 30° to 15 ºC (Gagne 1980).

3.2.6. Brood Emergence

During typical spring and summer temperatures in the Southeast, peak emergence occurs in the midafternoon, and this timing appears to obey an endogenously controlled rhythm rather than daily cycles in temperature, humidity, or light intensity (Kinn 1978). However, the rate of emergence increases at elevated barometric pressures (Kinn 1978). The lowest temperature at which emergence has been recorded is 12.5 °C (Gagne 1980), and since adults are rendered immobile at temperatures below 9 °C (White and Franklin 1976), the minimum temperature threshold for emergence presumably falls between these two values. During summer, brood emergence begins approximately 40 days after the initiation of mass attack (Franklin 1970b) and lasts an average of 28 days. Both sexes emerge at approximately the same time (Coulson and others 1979b).

Figure 3.5—Outer bark flakes peeled away to reveal SPB pupae within pupal chambers in the corky bark of a host.

Figure 3.6—Bark sliced perpendicularly to reveal a callow adult SPB maturing within a pupal chamber in the corky bark. Dotted lines demarcate the frass-packed gallery that the fourth instar larva mined from the phloem tissue.

3.3. OLFACTION IN SPB BEHAVIOR

The organs of olfaction in bark beetles consist of hair-like sensilla located on the antennae (Payne and others 1973). In the SPB these sensilla are located almost exclusively on the circular, laterally flattened antennal club and consist of two distinct morphological types (Figure 3.7): sensilla basiconica—cylindrical hairs that lie nearly flat against the cuticle, point distally, and are concentrated in two distinct bands that encircle the club; and sensilla trichodea II—tapering, curved hairs that protrude from the surface of the cuticle at a roughly 45-degree angle and are scattered over the more distal portions of the club (Payne and others 1973). The antennal club of both sexes has approximately 700 sensilla basiconica and 80 sensilla trichodea II. Preliminary electrophysiological studies demonstrated that both types of sensilla could respond to pheromones as well as host tree compounds (Dickens and Payne 1978b).

3.3.1. Methods of Investigating Olfaction in SPB

Olfactory sensitivities of the SPB to known or suspected semiochemicals have been studied by at least three methods: electroantennogram (EAG), coupled gas chromatography-electroantennographic detection (GC-EAD), and single sensillum recording (SSR) (Bjostad 1998, Payne 1974b). In EAG, changes in DC voltage across an antenna (in the specific case of SPB, the voltage between the antennal club and the head) are measured while individual test compounds or combinations are introduced into a stream of purified air blowing over the antenna. In GC-EAD, the effluent of a gas chromatograph (GC) is introduced into this air stream, and the antenna is exposed to compounds as they elute from the GC. GC-EAD possesses several advantages over EAG; namely, that unknown components within crude, natural extracts can be separated and assayed without prior purification steps, and test compounds can be delivered to the antenna in precisely known quantities and in greater purity than they are typically available commercially. In SSR, action potentials arising from sensory neurons within a single sensillum are recorded by electrodes measuring the voltage difference between the receptor lymph within the sensillum and the hemolymph of the antenna. Whereas EAG and GC-EAD presumably measure a summed response of many sensilla

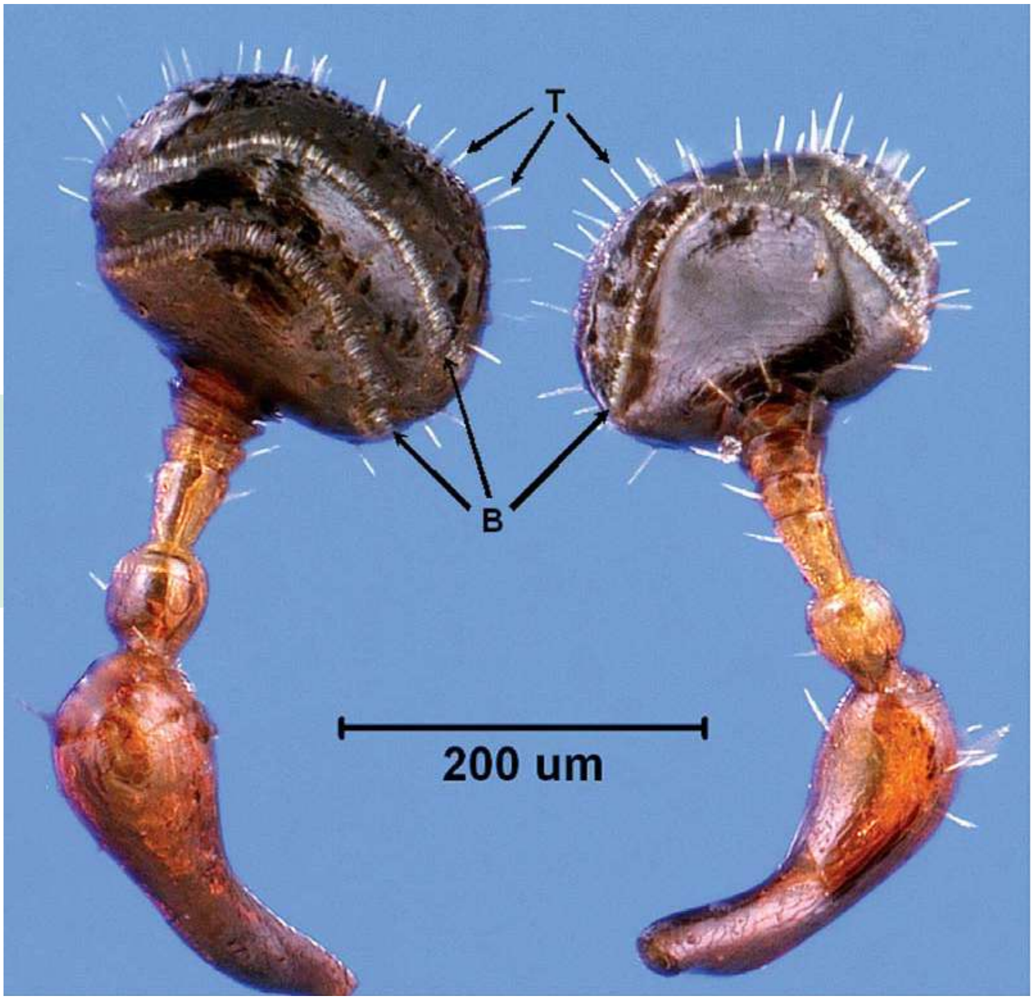


Figure 3.7—Anterior and posterior views of an SPB antenna, showing the encircling bands of sensilla basiconica (B) as well as individual sensilla trichodea (T).

at once and thus provide a picture of average responsiveness of sensilla, SSR measures responses of only the sensory neurons within the single sensillum to which the electrode is attached. Thus only SSR can identify chemical specificities of individual sensilla and olfactory neurons and precisely determine the capacity of an insect to discriminate among individual olfactory stimulants.

The most uncontroversial use of EAG and GC-EAD data is qualitative; that is, the determination of whether an insect can sense a particular airborne compound. However, at least three kinds of quantitative EAG/GC-EAD data appear to have some predictive value: 1. the response threshold; that is, the smallest concentration of an olfactory stimulant capable of eliciting a detectable voltage change in the antenna, 2. saturation voltage; that is, the maximum response amplitude that can be elicited by a single compound, and 3. the difference in concentration between threshold and saturation or the dose range of EAG response (Dickens 1979). Presumably, a relatively lower response threshold to a compound indicates greater sensitivity, a relatively higher saturation voltage indicates a greater abundance of olfactory receptors that can be stimulated by a compound, and a wider EAG response range suggests a greater capacity to distinguish concentrations of a stimulant (Dickens 1979, Dickens and Payne 1977). In addition, adaptation (desensitization to a single olfactory stimulant after prolonged exposure) can be used with EAG to estimate the capacity of antennae to discriminate among stimulants (Payne and Dickens 1976).

3.3.2. Olfactory Responses in SPB

Dozens of either insect- or host-produced compounds are capable of inducing electrophysiological responses in the antennae of the SPB (Figure 3.8; Smith and others 1993, Sullivan 2005). Southern pine beetles have a lower threshold of antennogram response and broader dose-response range for the bicyclic ketals frontalin and brevicomin than host monoterpenes (Dickens 1979, Sullivan and others 2007b, author's unpublished data). The saturation voltage produced by the female-produced attractant frontalin is greater than for any other SPB semiochemical, and a mixture of frontalin with its behavioral synergist *alpha*-pinene does not produce a greater electrophysiological response than frontalin alone (Payne 1975). Habituation of SPB antennae to frontalin blocked olfactory responses to the SPB pheromones *endo*-brevicomin, *trans*-verbenol, and verbenone, as well as to the host compounds *alpha*-pinene

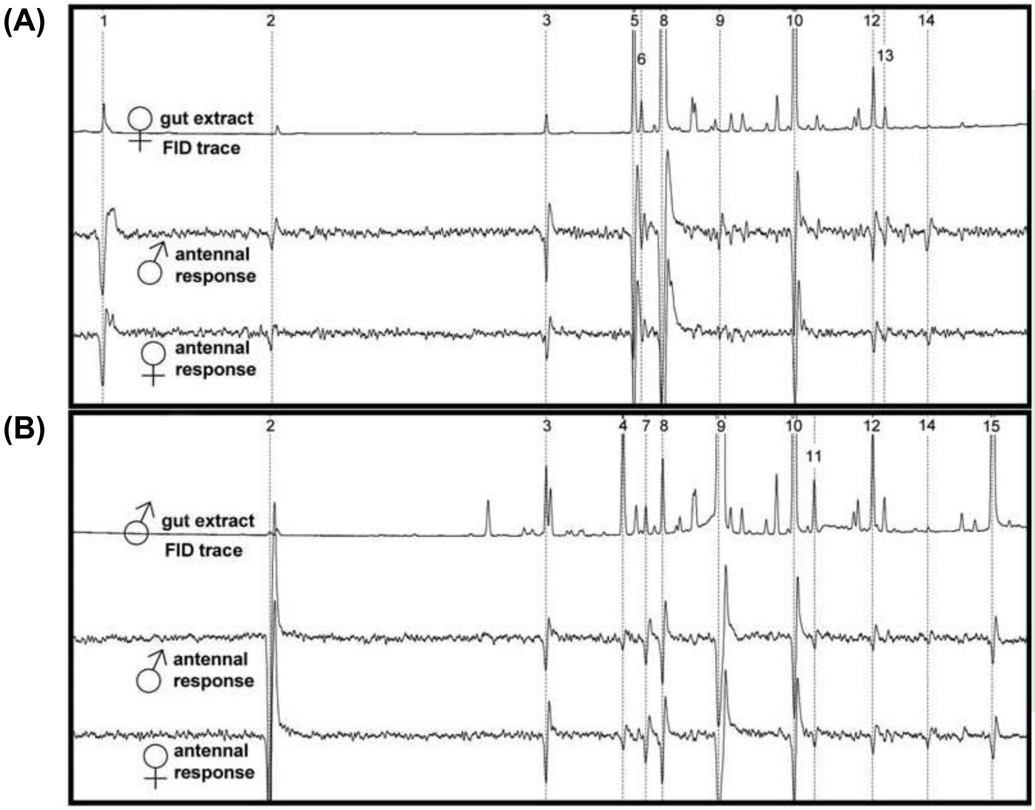


Figure 3.8—Electrophysiological responses of SPB antennae to volatile compounds extracted from the hindguts of newly emerged female (A) or male (B) adults as measured with a GC-EAD. Active compounds: (1)frontalin, (2)*endo*-brevicomin, (3)fenchyl alcohol, (4)myrtenal, (5)*cis*-verbenol, (6) *trans*-pinocarveol, (7) acetophenone, (8) *trans*-verbenol, (9) verbenone, (10) myrtenol, (11)unknown, (12)*trans*-myrtanol, (13)*cis*-myrtanol, (14)2-phenylethanol, and (15)unknown. (reprinted from Sullivan 2005)

and 3-carene. Conversely, habituation of SPB antennae to any of these latter compounds did not terminate responses to frontalin. These authors concluded that frontalin could interact with all acceptors for the other compounds but that none of these latter compounds could interact with all acceptors for frontalin. These data suggest that, in the presence of high concentrations of frontalin, all olfactory receptor neurons on the antennae may become habituated, rendering the SPB incapable of sensing or responding to semiochemicals. It is not known whether under natural conditions SPBs are exposed to concentrations of frontalin adequate to habituate all olfactory neurons simultaneously; however, if so, it may explain why SPBs land apparently indiscriminately in the presence of high concentrations of their pheromones (Gara and others 1965). Comparison of the EAG saturation voltages for these different compounds suggests that the pheromones *endo*-brevicomin, verbenone, and *trans*-verbenol interact with a higher percentage of olfactory acceptors on the antennae than the host odors *alpha*-pinene and 3-carene, and that SPB possess somewhat greater numbers of olfactory acceptors to the pheromones of the opposite sex (Dickens and Payne 1977).

During EAG recordings from SPBs with the indifferent electrode inserted into the base of the antenna, Payne (1974a) observed an alternating current signal that was superimposed on the slow voltage deflections induced by pheromone exposure, and he concluded that these were potentials arising from antennal muscle movement. The amplitude of the muscle potentials induced by frontalin were substantially reduced if antennae were exposed simultaneously to either *trans*-verbenol or verbenone (Dickens and Payne 1978a), suggesting that these two oxygenated monoterpenes may act, at least in part, by inhibiting frontalin's capacity to stimulate specific movements in the SPB.

3.3.3. Identified Semiochemicals of SPB

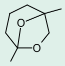
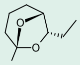
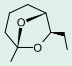
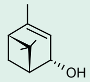
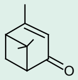
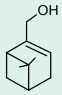
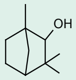
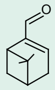
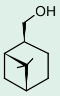
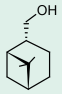
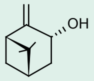
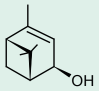
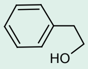
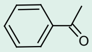
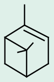
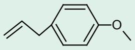
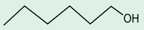
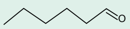
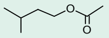
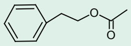
Host colonization by the SPB is mediated by airborne behavioral chemicals (semiochemicals) released by the beetles, their host trees, and also possibly their microbial and arthropod associates and nonhost tree species (Table 3.1). Due to the importance of these compounds to the SPB's capacity to initiate and sustain infestations, much effort has been invested in developing synthetic semiochemicals as management tools. The semiochemicals of aggressive bark beetles, including the SPB, are believed to function in at least four important ways (Borden 1996): 1. As aggregation pheromones—beetle-produced attractants of conspecifics that concentrate beetle arrivals on one or a few trees and insure attack densities adequate to overcome host defenses. Aggregation pheromones may also function as sex pheromones that bring the sexes together for mating. 2. As antiaggregation pheromones—beetle-produced inhibitors of conspecific responses to attractants. These compounds may be produced by beetles once they are successfully established on a host and terminate mass attack. This function presumably benefits both producing and responding beetles by preventing excessive densities of conspecifics on any single host, thereby lessening the deleterious effects of intraspecific competition (Byers 1989a). 3. As multifunctional pheromones—beetle-produced compounds that may either enhance or inhibit attraction of conspecifics depending upon their rate of release and possibly other factors. 4. As host selection kairomones—compounds produced by host trees, nonhost trees, or organisms associated with the beetle or its habitat that may be used by flying individuals to locate hosts of a suitable species and condition for colonization and to avoid unsuitable hosts. These compounds may either enhance attraction (presumably, if they indicate a suitable host) or inhibit attraction (if indicators of an unsuitable host).

SPB-Produced Compounds

Numerous volatile organic compounds have been identified from the SPB, typically by means of solvent extraction of tissues and frass followed by analyses of these extracts with gas chromatography or coupled gas chromatography-mass spectrometry. The SPB apparently resemble other bark beetles in that they lack specialized glands for the production and secretion of pheromones; rather these compounds are produced within the tissues of the alimentary canal or in the hemolymph, transferred to the lumen of the gut, accumulated in the hindgut, and released from the anus during defecation (Borden 1982).

The quantities of pheromones produced by SPBs from outbreak populations vary greatly among individuals (coefficient of variation, 60-182 percent) (Pureswaran and others 2006). Due to the large aggregation sizes and

Table 3.1—Volatile compounds known to influence movement of southern pine beetle

				Behavioral Activity[a]		
		Class[b]	Source[c]	Walking	Flight	References[d]
Frontalin		BK	F	A	A	1,2,3,4
endo-Brevicomin		BK	M	I	I,S,S/I	2,5,6,7,8,9
exo-Brevicomin		BK	M	--	I,S	5,10
trans-Verbenol			F	--	S	2,11,12
Verbenone			M	A,S/I	I,S/I	2,4,6,8,11,13
Myrtenol			F, M	S/I	I	6,14
Fenchyl Alcohol			F, M	--	I	15
Myrtenal			M	--	I	15
cis-Myrtanol			F, M	--	I	15
trans-Myrtanol			F, M	--	I	15
trans-Pinocarveol			F	--	I	15
cis-Verbenol			F	--	S	15
2-Phenylethanol		NMA	F, M, YA	I	I	14,15,16
Acetophenone		NMA	M	--	I	15
alpha-Pinene		HM	H	A	S	2,4,11,12
4-Allylanisole		PP	H	R	I	17,18
Hexanal		--	NH	--	I	19
1-Hexanol		--	NH	--	I	19
Isoamyl Acetate		--	YA	S	--	16
2-Phenylethyl Acetate		NMA	YA	S	--	16

[a] Affect on SPB movement: A = attractive; I = inhibits attraction or arrestment; S = synergizes or enhances activity of attractant; S/I = alternately synergistic or inhibitory depending upon concentration, chirality, or other factors; R = repels.

[b] Chemical Class: BK = bicyclic ketal; OM = oxygenated monoterpene; NMA = non-monoterpene aromatic; HM = hydrocarbon monoterpene; PP = phenylpropanoid

[c] Biological origin(s) of compound: F = female SPB; M = male SPB; YA = yeast associate of SPB galleries; H = host tree; NH = non-host plant species (note: The list gives the predominant source of the compound identified in the normal environment of SPB; hence, only one sex of SPB is listed if the opposite sex produces far smaller quantities.)

[d] [1]Kinzer and others 1969, [2]Payne and others 1978, [3]Payne and others 1988, [4]McCarty and others 1980, [5]Vité and Renwick 1971, [6]Rudinsky and others 1974, [7]Vité and others 1985, [8]Salom and others 1992, [9]Sullivan and others 2007a, [10]Pureswaran and others 2008a, [11]Renwick and Vité 1969, [12]Renwick and Vité 1970, [13]Rudinsky 1973, [14]Sullivan and others 2007b, [15]Sullivan 2005, [16]Brand and others 1977, [17]Hayes and others 1994, [18]Strom and others 1999, [19]Dickens and others 1992.

consequent minimal contribution of each individual to the total pheromone plume from mass-attacked trees, genotypes that produce very small amounts of pheromone may be able to persist despite the obvious fitness benefits conferred to individuals in the population by the total pheromone plume.

Southern pine beetle-produced semiochemicals fall into three chemical classes: 1. bicyclic ketals, 2. oxygenated monoterpenes, and 3. non-monoterpene aromatics. Whereas many—perhaps most—of these compounds are probably true pheromones for the SPB (i.e., compounds produced specifically for the purpose of influencing behavior of conspecifics), tests have not been performed that unequivocally prove this for any. Most studies on the behavioral activity of SPB-produced compounds have not determined whether the trial dose is one that occurs in nature, and thus, whether an active dose represents a normal or a supernormal stimulus. It is doubtful that every one of the 14 behaviorally active compounds isolated from the SPB plays a role in intraspecific communication; some may be ancestral pheromone remnants or function for the SPB primarily or solely as interspecific signals (i.e., as kairomones). Bark beetles excrete volatile metabolic waste products along with true pheromones, and some of these waste products are common to a wide range of organisms in the normal environment of the SPB (Gries and others 1990, Hunt and others 1989).

Bicyclic ketals

These compact, eight- and nine-carbon molecules occur commonly in the genus *Dendroctonus* and some other coniferophagous and hardwood-infesting species of bark beetles. They are synthesized *de novo* by means of the mevalonate pathway and, unlike many common bark beetle pheromones, are not derived from any known host-derived precursors (Seybold and Tittiger 2003). Although bicyclic ketals have been isolated from the tissues of some hardwood trees (Huber and others 1999), in the normal environment of the SPB these compounds apparently have no origins other than conspecific and occasionally heterospecific bark beetles, and thus they presumably are relatively free of signal interference from alternative background sources.

Frontalin (1,5-dimethyl-6,8-dioxybicyclo [3.2.1] octane). This eight-carbon bicyclic ketal is produced predominantly or exclusively by females, and is the only bicyclic ketal produced in significant quantities by this sex (Renwick and Vité 1968). Small quantities have sometimes been reported from males (Grosman and others 1997, Rudinsky and others 1974). Newly emerged females contain small quantities of this compound in their hindgut, which largely disappear once they begin feeding in host tissue (Coster and Vité 1972). However, aerations and combined aerations/extractions made from actively feeding or fed beetles indicate that mining into a host actually increases production and release of frontalin as much as 10 fold (Pureswaran and others 2008b). The hindguts of feeding females likely contain lower quantities than newly emerged individuals because the former are defecating (and thus emptying their hindgut of pheromones) with much greater frequency. Whereas feeding appears to enhance production of frontalin in the SPB, application of juvenile hormone (a stimulant of bicyclic ketal production in females of some *Dendroctonus* species) appears to have no effect on this compound (Bridges 1982). Female production of frontalin declines somewhat following pairing (Hofstetter and others unpublished data, Sullivan and others 2007b).

Frontalin is considered the major component of the aggregation pheromone of the SPB because it is the only semiochemical capable of attracting flying beetles in the absence of other semiochemicals, and no combination of other semiochemicals is attractive in its absence (Smith and others 1993). Nonetheless, frontalin is merely weakly attractive to flying SPBs in the absence of beetle- and host-produced synergists (Kinzer and others 1969, Payne and others 1978). Traps baited with frontalin either alone or with host odors typically catch more males than females (often two to four times more). The skewed sex ratios may be due to differential attraction of the sexes, but also may be an artifact of trapping procedures. Female SPBs do not orient as directly to sources of frontalin as do males but preferentially land some distance away (Hughes 1976), and large trapping surfaces catch the sexes in ratios that approach 50:50. Thus the sexes may be attracted by frontalin in similar numbers, but traps of a size convenient for research studies (i.e., <1 m long) may be more efficient at trapping males than females. The tendency for females to land some distance from sources of frontalin likely propels the expansion of mass attack both along the bole of each individual host (Coster and others 1977a, Fargo and others 1978) and onto adjacent trees (Hughes 1976, Vité 1970). In walking bioassays, frontalin appears to be much less attractive to females than males (McCarty and others 1980), suggesting that, for beetles walking on the bark surface, this compound may function primarily as a sex pheromone that attracts males to entrances established by solitary females.

Both newly emerged and feeding SPB produce frontalin in an enantiomeric composition of 85-95 percent (-) (Stewart and others 1977, Sullivan and others 2007b). Olfactory sensilla of both sexes of SPB are substantially more sensitive to the (-) than the (+) enantiomer of frontalin (Sullivan and others 2007b). Both the (+) and (-) enantiomers of frontalin are attractive to SPB, but the (-)-enantiomer is significantly more active, particularly with flying beetles (Payne and others 1982). The SPB is not more strongly attracted to the beetle-produced enantiomeric ratio than to a racemic mixture of the enantiomers. Modification of the structure of frontalin by either deleting or altering the position of methyl groups reduced antennal and behavioral responses by the beetles, and only one of seven such analogs (*endo*-5,7-dimethyl-6,8—dioxabicyclo [3.2.1] octane) was significantly attractive to the SPB in trapping trials (Payne and others 1988, Renwick 1970). Opening of frontalin's ring structure likewise eliminated its behavioral activity in the field (Renwick 1970).

Frontalin apparently plays a major role in mediating mass attack, since this behavior can be stimulated on uninfested trees merely by attaching frontalin baits to or near them. Frontalin appears to define the locus of mass attack more precisely than other attraction-mediating semiochemicals for the SPB, since dislocation of frontalin baits from a trap appears to effect a far greater reduction in catch than dislocation of frontalin's synergists (Sullivan and Mori 2009). However, when released at 1 g/h, frontalin stimulated a similar number of landings at poles from which it was released as unbaited poles located 10 m downwind (Vité 1970), suggesting that at high doses frontalin may release landing responses to visual (or other) cues but not stimulate orientation toward its point of origin (Hughes 1976).

***endo*-Brevicomin (*endo*-7-ethyl-5-methyl-6,8-dioxybicyclo [3.2.1] octane).** This nine-carbon molecule is produced almost exclusively by male beetles and is the major bicyclic ketal produced by this sex (Hughes 1973, Rudinsky and others 1974, Vité and Renwick 1971). In the Southeastern United States it is present in newly emerged SPBs in small amounts, but pairing with a female in a host increases the quantities isolated from males nearly 10 fold (Sullivan and others 2007b). This increase in production is apparently stimulated by pairing rather than entrance into a host, since solitary males forced to attack pine bolts do not produce *endo*-brevicomin in significantly greater quantities than newly emerged males. Exposure of callow adult males to juvenile hormone II or the juvenile hormone analog methoprene likewise resulted in increased production of *endo*-brevicomin (Bridges 1982). In contrast to populations in the Southeastern United States, newly emerged male SPB in Mexico and Central America contain relatively large quantities of *endo*-brevicomin (Vité and others 1974). Although conflicting reports exist (Grosman and others 1997, Redlich and others 1987, Sullivan and others 2007b), it appears that the SPB produces predominantly or solely the (+)-enantiomer (see Sullivan and others 2007b for detailed explanation).

GC-EAD studies suggest that the SPB antennae have a lower response threshold to *endo*-brevicomin than to any other volatile compound isolated from this species or its host (Sullivan 2005, Sullivan and others 2007b). Both sexes can sense (+)-*endo*-brevicomin at concentrations less than 1 ng/l air, or approximately one order of magnitude less than their response threshold to frontalin's more active (-)-enantiomer, and four orders of magnitude lower than to (-)-*endo*-brevicomin. In EAG habituation studies, *endo*-brevicomin ranked second to frontalin in the percentage of olfactory acceptors that could be occupied by it (approximately 75-87 percent) (Dickens and Payne 1977). The sexes do not differ in their relative sensitivity to the enantiomers.

The SPB's exceptional olfactory sensitivity to (+)-*endo*-brevicomin suggests that this compound has major ecological importance for this species. Nonetheless, despite much research, the precise behavioral activity and ecological function of *endo*-brevicomin is unclear and a subject of ongoing investigation. Releasers of racemic *endo*-brevicomin can inhibit SPB responses to attractant-baited traps (Payne and others 1978, Salom and others 1992, Vité and Renwick 1971), and it stimulates walking males to produce their rivalry chirp while inhibiting their arrestment by female odors (Rudinsky and others 1974). Consequently, *endo*-brevicomin was initially concluded to be an antiaggregation pheromone for the SPB and a short-range indicator of male presence. However, subsequent studies showed that pure (+)-*endo*-brevicomin baits can strongly (i.e., 5-45 fold) enhance SPB responses to traps baited with frontalin and host odors, while under the same conditions the (-)-enantiomer is inhibitory (Vité and others 1985, Sullivan and others 2007b). Low doses of the racemate also appeared to have some capacity to enhance responses to female-produced attractant. These data led to the hypothesis that the inhibitory activity of synthetic racemic mixtures of *endo*-brevicomin enantiomers was due to the inhibitory (-)-enantiomer overriding the synergistic activity of the (+)-enantiomer (Vité and others 1985). Since the SPB produces little or none of the (-)-enantiomer (Sullivan and others 2007b), this hypothesis also implied that *endo*-brevicomin functions as a synergistic component of the SPB aggregation pheromone.

In apparent conflict with this hypothesis, recent studies have shown that releasers of (+)-*endo*-brevicomin may nonetheless cause flying SPB responses to collocated attractant baits to be less than responses to identical attractant baits located several meters away (Sullivan and Mori 2009), a result that might be interpreted as demonstrating inhibitory activity for (+)-*endo*-brevicomin. However, this effect was shown to be due to enhanced attractiveness of the distant bait rather than reduced attractiveness of the collocated bait. Apparently (+)-*endo*-brevicomin can create a "halo of synergism" that enhances responses of flying SPBs to surrounding point-sources of female-produced attractant (in experiments, frontalin and host odors) more than to attractant sources located at the point of its release. The precise size and shape of the halo, which can be dozens of meters in diameter, appears to be influenced by the release rate of (+)-*endo*-brevicomin, as well as other variables. Presumably, one effect of SPB-produced (+)-*endo*-brevicomin in nature is to render attacks by solitary females relatively more attractive than attacks by pairs. In SPB spots, this activity might promote movement of the focus of mass attack from completely colonized trees (i.e., ones with many established pairs and thus a high density of (+)-*endo*-brevicomin-producing males) to adjacent trees being newly colonized by females. The halo of synergism produced by *endo*-brevicomin may also help define the spatial boundaries of an active SPB spot, since pioneer female attacks on uninfested trees will be more attractive, and colonization presumably more likely to be successful, if they occur within the synergistic zone associated with the (+)-*endo*-brevicomin released from previously colonized trees.

***exo*-Brevicomin (*exo*-7-ethyl-5-methyl-6,8-dioxybicyclo [3.2.1] octane).** This nine-carbon bicyclic ketal occurs in trace quantities (0.2 ng/beetle) in emerged male SPBs in Mississippi but was detected in somewhat higher concentrations (3 ng/beetle) in Arizona populations (Pureswaran and others 2008a). This compound has been reported to significantly inhibit (Vité and Renwick 1971), enhance (Pureswaran and others 2008a), or not effect SPB responses to baits composed of frontalin and host volatiles (Payne and others 1978). The reason for this variability of SPB responses is unknown. The SPB possesses a high degree of olfactory sensitivity to *exo*-brevicomin (Pureswaran and others 2008a), and *exo*-brevicomin and frontalin apparently stimulate the same olfactory receptors (Payne 1975). However, given the very small quantities produced by the SPB, it seems unlikely that this compound is itself a pheromone for the SPB. Rather, SPB behavioral responses to *exo*-brevicomin may be an accident (e.g., resulting from an incidental capacity to stimulate olfactory receptors for other semiochemicals) or may be an adaptation to sympatric, pine bark beetle species that produce *exo*-brevicomin, including *Dendroctonus brevicomis* in Arizona and *Dendroctonus terebrans* in the Southeastern United States (Payne and others 1987, Vité and Pitman 1969a). The SPB may utilize *exo*-brevicomin to identify and exploit host resources colonized by such potentially competing species.

Manipulation of host colonization behavior with bicyclic ketals

Deployment of competing, artificial sources of insect attractant has often been a successful strategy for disrupting orientation by insect pests, particularly mate-seeking moths, thereby reducing their damage significantly (Bartell 2008, Shorey 1970). In an attempt to disrupt orientation by the SPB, rice seed soaked with a mixture of frontalin and *alpha*-pinene was spread by aircraft over an active SPB infestation at a rate of 45 g and 450 g semiochemical/ha (Vité and others 1976). Although this treatment caused captures in attractant-baited traps to decrease, it simultaneously caused landings and attacks on pines already under attack in the treatment area to increase substantially, suggesting that saturation of the atmosphere with aggregation pheromone does not cause SPBs within spots to become disoriented. It is possible that the beetles oriented to synergistic aggregation semiochemicals (e.g., odors of fresh resin) released by the attacked pines but not provided by the semiochemical saturation treatment or the traps. Furthermore, visual cues may become the predominant host location cues for the SPB under conditions of aggregation pheromone saturation (Gara and others 1965).

Baits of frontalin and *alpha*-pinene deployed within the interior of active SPB infestations (i.e., attached to pines with developing brood stages and nonhost trees) can reduce aggregation on newly infested trees at the infestation's advancing head and thereby reduce or stop infestation growth (Richerson and others 1980). However, this technique appears to be ineffective when beetle densities are very high (Payne and others 1985). Attempts to manipulate SPB flight activity with point sources of attractive semiochemicals have been greatly complicated by the fact that even modest release rates can stimulate mass attacks on nearby host trees, and high release rates can stimulate attacks on trees as far as 40 m distant (Vité 1970). The tendency for synthetic SPB attractants to stimulate such spillover attacks is likely the most significant technical obstacle to using baited traps to reduce SPB populations.

Regular distribution of low-rate releasers of *exo-*/*endo*-brevicomin in an area encompassing the front edge of an advancing SPB infestation significantly reduced landing of the SPB on host trees, but did not alter the densities of beetles flying through the stand (Payne and others 1977). In a separate study, releasers of either a 50:50 or 85:15 mixture of *endo:exo* brevicomin were evenly distributed over the bole of trees located within the path of an advancing SPB infestation. Although this treatment reduced SPB landings and prevented SPB mass attack of the treated trees, it failed to prevent their ultimate mortality, possibly due to greatly increased attacks by the associate *Ips avulsus* (Richerson and Payne 1979). While brevicomin failed as a protectant for individual trees, brevicomin-induced competitive displacement of the SPB by *I. avulsus* was proposed by these authors as a possible tool for inducing spot collapse (Payne and Richerson 1985).

Oxygenated monoterpenes

In common with other coniferophagous bark beetles, the SPB produce a diversity of cyclic ten-carbon unsaturated alcohols, aldehydes, and ketones. These generally share the same carbon backbone as one of the major resin monoterpenes of the host pines, and beetles derive them at least in part from the oxidative detoxification of resin compounds through the action of cytochrome P-450 enzymes (Seybold and others 2006). Exposure of the SPB to high atmospheric concentrations of host volatiles results in accumulation of elevated quantities of oxygenated monoterpenes in the hindgut (Hughes 1973, Renwick and others 1973). Individually these compounds may possess little potential message specificity as semiochemicals, since they have numerous alternative sources in the environment of the SPB. The capacity to oxidize hydrocarbon monoterpenes enzymatically is possessed by a diversity of microorganisms including symbionts of the SPB and other bark beetles (Bhattacharyya and others 1960, Brand and others 1975, Dhavilikar and others 1974, Leufven 1991). Many of the oxygenated monoterpenes produced by the SPB are likewise produced by sympatric species of *Ips* and *Dendroctonus* bark beetles (Skillen and others 1997), or can be generated spontaneously during the exposure of resin monoterpenes to air (Hunt and others 1989).

The hindguts of newly emerged and reemerged SPBs contain very large quantities of oxygenated monoterpenes; they may compose more than 1 percent of beetle body weight and are visible as oil droplets within the dissected tissue (Vité and Crozier 1968, author's unpublished data). Adult emerged beetles apparently emit these compounds continuously, and enclosures containing large numbers of SPBs possess a strong odor of two major hindgut constituents, verbenol and verbenone (author's personal observations). The beetles' hindguts are largely depleted of oxygenated monoterpenes within a day after they enter a host, suggesting that these compounds are released rapidly while attacking beetles are either still on the bark surface or are initiating galleries (Coster and Vité 1972; Pureswaran and others 2006, 2008b; Sullivan 2005). The SPB continues to generate and release oxygenated monoterpenes once they enter a host and begin feeding; however, the extent of this likely depends upon the concentrations of host monoterpenes to which the beetles are exposed while mining.

***trans*-Verbenol (*trans*-4,6,6-trimethylbicyclo [3.1.1]hept-3-en-2-ol).** *trans*-Verbenol is present in very large quantities in the hindguts of newly emerged female SPBs (approximately 2-10 µg), but it occurs in 1-2 orders of magnitude smaller quantities in males (Grosman and others 1997; Pitman and others 1968, 1969; Pureswaran and others 2006; Renwick 1967). This monoterpene alcohol shares the same carbon backbone as *alpha*-pinene, the predominant resin monoterpene of the major host pines for the SPB (Coyne and Keith 1972). The southern pine beetle presumably can generate this compound by direct oxidation of *alpha*-pinene derived from its host, since exposure of females to high atmospheric concentrations of *alpha*-pinene results in elevated concentrations of *trans*-verbenol in the hindgut (Hughes 1975, Renwick and Hughes 1975, Renwick and others 1973). The mean enantiomeric composition produced by the SPB has been reported to be 60:40 (+)/(-) (Plummer and others 1976) and 25:75 (+)/(-) (Grosman and others 1997); however, these differences could have resulted from examination of beetles reared on species or populations of pines with differing enantiomeric ratios of the *alpha*-pinene precursor (Byers 1983).

Dickens and Payne (1977) reported that *trans*-verbenol occupied a larger percentage of antennal acceptors in males than females. However, dose-response studies indicated a similar threshold of olfactory response to both enantiomers by both sexes of the SPB (author's unpublished data).

trans-Verbenol is an attractive synergist of frontalin for flying SPBs (Renwick and Vité 1970). It appears to be interchangeable with *alpha*-pinene in this function, since *trans*-verbenol is ineffective as a synergist when concentrations of *alpha*-pinene are also present (Payne and others 1978, Renwick and Vité 1969). Pioneer females initially arriving on a host may release *trans*-verbenol to synergize conspecific attraction to frontalin before they have penetrated the phloem and triggered release of *alpha*-pinene from the host. Turpentine rich in *alpha*-pinene, as well as purified *alpha*-pinene, is generally much less expensive than synthetic *trans*-verbenol; thus, the former have been used rather than the latter as synergists for frontalin in bait formulations for the SPB (Billings 1988). *trans*-Verbenol may also play some role during courtship and in close-range communication by beetles on the bark surface (Rudinsky 1973, Rudinsky and others 1974). It is not known whether the enantiomeric ratio of *trans*-verbenol influences SPB behavioral responses.

Verbenone (4,6,6-trimethylbicyclo [3.1.1] hept-3-en-2-one). Verbenone is present in very large quantities in hindguts of male beetles that are either newly emerged or newly arriving on a host (approximately 0.5-10 µg/insect) but in much smaller quantities in females (5-100 ng/insect; Grosman and others 1997, Pitman and others 1969, Pureswaran and others 2006). Entrance into host tissue reduces these quantities considerably in males but has minimal effect on females (Pureswaran and others 2008b, Sullivan and others 2007b). Verbenone, like verbenol, has the carbon backbone of *alpha*-pinene, and it can be derived from verbenol by a further oxidation of the hydroxyl group (Renwick 1970). As with *trans*-verbenol, the SPB apparently can generate verbenone also through the oxidation of *alpha*-pinene derived from the host (Hughes 1975). Verbenone may also arise through conversion of beetle-produced *trans*-verbenol by the action of SPB-associated microbes (Brand and others 1976) or spontaneously by contact of either *alpha*-pinene or verbenol with the air (Hunt and others 1989). Males newly emerged from loblolly pine contain the two enantiomers in a mean ratio of 36:64 (+):(-), whereas females may contain nearly the reciprocal ratio (Grosman and others 1997).

Verbenone can influence behavior of the SPB in a variety of ways. In trapping trials, verbenone at high doses (>5 mg/h) reliably reduces response of flying male beetles to combinations of frontalin and host odors, but inhibition in flying females has proven less consistent (Payne and others 1978). As a consequence of the typically greater inhibition of males, verbenone tends to shift the sex ratio of responding beetles toward females (Renwick and Vité 1969). In the laboratory, verbenone also inhibited upwind anemotaxis by walking male and female SPBs to triplicate (a 1:1:12 mixture of frontalin, *trans*-verbenol, and *alpha*-pinene) when concentrations exceeded the concentration of attractant, but at 1/100 the attractant dose, it significantly increased frequency of female responses (McCarty and others 1980). At very low concentrations, verbenone is reported to increase the frequency with which walking males are arrested and produce an attractant chirp at a release point of female attractant, whereas concentrations 100 times the arresting dose caused males to pass the attractive source and emit a rivalry chirp (Rudinsky 1973). Verbenone has been called a multifunctional pheromone based upon its dose-dependent, alternatively attractive/inhibitory activity with walking SPBs (McCarty and others 1980, Rudinsky 1973); however, there is minimal evidence suggesting that verbenone enhances attraction of flying SPBs at any dose (however, see Salom and others 1992, Test 2).

Salom and others (1992) examined the effect of verbenone chirality on its capacity to inhibit attraction of flying SPBs in the field. In a test in which a low dose of host odors (2 mg/hr *alpha*-pinene) was used as synergist with frontalin, (+)-enriched verbenone was more effective at inhibiting male beetles than (-)-enriched verbenone. However, in tests where a high dose of host volatiles (3600 mg/hr turpentine) was used as a synergist for frontalin and in which SPB responses to attractant-only control traps were generally 10 fold greater, (+)-enriched verbenone was equally or less inhibitory than racemic verbenone or a 34 percent(+):66 percent(-) mixture.

Verbenone's capacity to inhibit SPB attraction has inspired efforts to use this semiochemical to stop SPB mass attacks within infestations. Devices releasing a total of 80 mg verbenone/day/tree were attached at 2 m intervals along the bole of uninfested pines located in the trajectory of a growing SPB spot, but this failed to reduce SPB landing and attack density or prevent mortality of the treated trees. Multiple studies have shown that verbenone releasers placed on freshly infested and uninfested trees located along the advancing head of an SPB spot can slow or stop spot growth (addressed in detail in chapter 26). However, treatment of the spot head with verbenone does not alter the abundance or distribution of flying beetles within the spot (Johnson and Coster 1980, Salom and others 1995); hence, the treatment apparently neither prevents beetles emerging within the spot from locating and aggregating at the spot head nor causes beetle dispersal from the spot. Since verbenone also apparently does not significantly reduce SPB landing rates on or near treated trees (Richerson and Payne 1979, Salom and others 1995), the mechanism by which verbenone treatment causes infestation collapse remains a matter of speculation.

Myrtenol (4,6,6-trimethylbicyclo [3.1.1] hept-3-en-10-ol). Myrtenol is present in large quantities (0.4-2 µg/insect) in emergent and in lesser quantities (3-50 ng/insect) in attacking male and female SPB (Pureswaran and others 2006, Renwick and others 1973, Sullivan and others 2007b). Like verbenone and *trans*-verbenol, the SPB generates myrtenol in greater quantities after exposure to the host monoterpene *alpha*-pinene (Hughes 1973, Renwick and others 1973). Both the attractant chirp and arrestment were elicited more frequently from walking male SPBs when low concentrations of myrtenol were added to an attractive blend (frontalin, *alpha*-pinene, and *trans*-verbenol), whereas at high concentrations myrtenol inhibited these responses (Rudinsky and others 1974). This led the authors to conclude that myrtenol, like verbenone, was a multifunctional pheromone for the SPB. At a release rate of 1.5-3 mg/d, myrtenol significantly reduced response of SPBs to traps baited with *alpha*-pinene and frontalin within active SPB infestations (Sullivan and others 2007a).

Other oxygenated monoterpenes. Several additional oxygenated monoterpenes have been identified from newly emerged or pine resin-exposed SPBs, including fenchyl alcohol, 6-hydroxycamphene, myrtenal, *cis*-myrtanol, *trans*-myrtanol, *cis*-3-pinen-2-ol, *trans*-pinocarveol, pinocarvone, and *cis*-verbenol (Hughes 1973; Renwick and Hughes 1975; Renwick and others 1973, 1976; Rudinsky and others 1974; Sullivan 2005; Vité and others 1974). They generally have been detected in both sexes, but with significant quantitative dimorphisms with respect to *cis*-verbenol and *trans*-pinocarveol (predominantly females) and myrtenal and pinocarvone (predominantly males) (Grosman and others 1997, Renwick and others 1973, Sullivan 2005). Antennae of both male and female SPBs are sensitive to fenchyl alcohol, myrtenal, *cis*-myrtanol, *trans*-myrtanol, *trans*-pinocarveol, and *cis*-verbenol, and all six of these compounds were found to modify SPB responses to traps baited with a combination of frontalin and *alpha*-pinene. Fenchyl alcohol, *cis*-myrtanol, and *trans*-pinocarveol significantly reduced responses of one or both sexes when released at 3-50 mg/day, whereas myrtenal and *trans*-myrtanol were inhibitory at 27 and 66 mg/day, respectively, but not at lower doses. *cis*-Verbenol baits releasing 59 mg/day but not lower doses significantly increased SPB responses to frontalin and *alpha*-pinene, but significant levels of *trans*-verbenol contamination in these baits may explain this result (Sullivan 2005). None of these oxygenated monoterpenes altered the sex ratio of SPBs responding to the standard attractant.

Non-monoterpene aromatics. 2-phenylethanol is produced in small quantities (<30 ng per insect) by both newly emerged and attacking SPBs of both sexes, although it is detected in greatest quantities in solitary, feeding females (Sullivan 2005). It likely arises as a waste product from beetle metabolism of the amino acid phenylalanine (Gries and others 1990). It is also produced by yeasts and filamentous fungal associates of SPB galleries (Brand and others 1976, Sullivan 1997). 2-Pheylethanol reduced the frequency of upwind anemotaxis by walking SPBs to a source of attractant (Brand and others 1977), and devices releasing 3-80 mg/day significantly reduced catch of SPBs in traps baited with frontalin and *alpha*-pinene (Sullivan 2005, Sullivan and others 2007a).

Acetophenone is produced in small quantities (<40 ng/insect) by both sexes and in relatively greater amounts by newly emerged males (Sullivan 2005). Devices releasing 0.5-27 mg/day significantly reduced responses of males or both sexes to traps baited with frontalin and *alpha*-pinene, and relatively higher release rates shifted the responding sex ratio significantly toward females.

Regional variation in pheromone production and response

Both production of and response to pheromones appears to vary regionally for the SPB. Grosman and others (1997) compared semiochemical content of SPBs from populations in three States and found significant differences in the quantities and enantiomeric ratios of several constituents. In addition, SPBs in a walking olfactometer appeared to prefer volatiles produced by host-attacking beetles from their own region over those produced by beetles from distant States (Berisford and others 1990).

Compounds Produced by Host and Nonhost Trees

Although evidence suggests that the SPB may utilize host-produced olfactory cues to locate uninfested, susceptible trees (Payne and Coulson 1985), to date no host-produced compound or blend has been identified that is attractive to flying SPBs in the absence of the pheromone frontalin. Nonetheless, host-produced volatiles are potent synergists for SPB aggregation pheromone components, and evidently play an important role in mediating mass attack. Raw pine resin and the monoterpene fraction distilled from resin (i.e., turpentine) synergize response by both sexes to frontalin-baited traps (Billings 1985, Kinzer and others 1969, Payne and others 1978). When monoterpene components of the resin of *Pinus taeda* were tested separately for their capacity to enhance attractiveness of a blend of frontalin and *trans*-verbenol, *alpha*-pinene had a stronger effect than *beta*-pinene, 3-carene, camphene, limonene, myrcene, terpinolene, or 4-allylanisole (Renwick and Vité 1969). Although unattractive to flying SPBs, *alpha*-pinene by itself is somewhat attractive to walking beetles (McCarty and others 1980). *alpha*-Pinene is the predominant monoterpene constituent of resin of the major host species for the SPB (Coyne and Keith 1972, Mirov 1961), and is likewise the dominant monoterpene constituent of turpentines derived from these trees. Rapid release of loblolly pine turpentine (1.8-3.6 g/day) increases catch of SPBs in traps baited with frontalure (frontalin and *alpha*-pinene in a 1:2 formulation at 50mg/day) by 15-28 times (Billings 1985).

4-Allylanisole, a minor component of the constitutive resin of SPB host pines (Mirov 1961, Drew and Pylant 1966), is the only host-produced compound reported to reduce response of the SPB to sources of attractant. Devices releasing approximately 160-1,200 mg/day significantly reduced beetle responses to traps baited with frontalure, and walking adult beetles were repelled from locations where 4-allylanisole had been painted on the substrate (Hayes and others 1994, Strom and others 1999). When released from pine boles either with a string of release devices or with a microencapsulated form sprayed onto the bark, 4-allyanisole significantly reduced SPB attack density on pines rendered susceptible by treatment with N-methyldithiocarbamate (Strom and others 2004).

Various small organic molecules, particularly six-carbon alcohols and aldehydes, are associated with angiosperms and other nonhosts for coniferophagous bark beetles, and they appear to be used by foraging bark beetles during selection of suitable host habitat and individual hosts (Zhang and Schlyter 2004). Two such compounds, hexanal and 1-hexanol, either separately or in combination, have been shown to significantly reduce SPB responses to traps baited with frontalin and turpentine (Dickens and others 1992). In addition, a blend of four nonhost volatiles (1-hexanol, hexanal, *cis*-3-hexen-1-ol, and nonanal) significantly reduced responses by the SPB to traps baited with frontalin and *alpha*-pinene in one of two trials (Sullivan and others 2007a).

Compounds Produced by Competing Bark Beetle Species

Pines infested by the SPB are usually also infested by other bark beetles in the southern pine bark beetle guild. The SPB and the other members of the guild compete with one another for the phloem resource, but reduce this competition to some extent by each colonizing separate portions of the tree bole (Flamm and others 1987b, Flamm and others 1993). Bark beetles are commonly inhibited but sometimes attracted by pheromones of competing species (Byers 1989b), and evidence suggests such interactions occur among members of the southern pine bark beetle guild (Birch and others 1980, Svihra and others 1980). Cross-attraction is believed to enhance host-finding by secondarily arriving species, whereas cross-inhibition likely reduces direct competition by promoting spatial partitioning of host resources among species (Byers 1989a). Logs infested with males of either one or two species of *Ips* belonging to the guild failed to attract SPBs, whereas male attacks by *I. grandicollis* reduced SPB responses to bolts infested with female SPBs (Birch and others 1980, Svihra and others 1980). Synthetic blends of *Ips* spp. pheromones likewise failed to attract SPBs (Billings 1985), whereas a pheromone blend characteristic of BTB attracted them in small numbers (Smith and others 1990).

Compounds Produced by SPB-Associated Microbes

A rich flora of microorganisms has adapted to life within the galleries and bodies of the SPB, and several of these associates produce SPB semiochemicals. Cultures of three SPB-associated yeasts, *Hansenula holstii* Wickerham, *Pichia pinus* (Holst) Phaff, and *P. bovis* van Uden et do Carmo-Sousa, produce at least three compounds (2-phenylethanol, isoamyl acetate, and 2-phenylethyl acetate) that alter responses by SPB to an attractant mixture in walking bioassays (Brand and others 1977). In addition, cultures of one of the fungal symbionts carried in the mycangium of female SPBs can convert the SPB-produced semiochemicals *cis-* and *trans*-verbenol into another SPB semiochemical, verbenone (Brand and others 1976). However, studies have not yet determined whether these microbes produce semiochemicals under natural conditions or whether this production significantly impacts SPB behavior.

3.4. SPB BEHAVIORS MEDIATED BY VISUAL CUES

Vision appears to play a crucial role in host identification for flying SPBs. The SPB has a presumably visually mediated preference for landing on objects with a vertical rather than a horizontally oriented profile. Pine posts baited with freshly infested log sections attracted few or no SPB attacks when suspended horizontally, but received many attacks when erected vertically (Gara and others 1965). However, black-colored barrier traps with a broadly rectangular profile were equally efficient at trapping SPBs as black multiple-funnel traps possessing a strong vertical profile and a similar trapping surface area (McCravy and others 2000). Traps consisting of plastic panels were more attractive to the SPB when colored black than when transparent, but clear panels were more attractive than white, suggesting that black surfaces are attractive and white ones repellant to the SPB (Strom and others 1999). When pines in the path of a growing SPB infestation were painted with either black or white paint to a height of 4.5 m, white-painted trees received many fewer landings and attacks within the painted portions of the bole than black-painted trees (Strom and others 1999). Fontalure-baited multiple-funnel traps painted either white or yellow caught significantly fewer SPBs than traps painted black, blue, brown, green, or red, whereas these latter five colors did not differ in attractiveness (Strom and Goyer 2001). Surface hue (dominant wavelength) appeared to be much less important to beetle responsiveness than overall reflectance across the visual spectrum, with high reflectance values being the least attractive (Strom and others 1999). Visual responses of host-seeking beetles in the field appear to be substantially different from those of beetles emerging within enclosures, as the latter are strongly attracted to sources of light (Tsao 1965).

3.5. SPB BEHAVIORS MEDIATED BY ACOUSTIC CUES

As with all other species of *Dendroctonus* so far examined, the SPB appears to utilize acoustic signals for short-distance intraspecific communication (Ryker 1988). No tympana or similar organs specialized for the sensing of airborne sound have been identified in the SPB or other bark beetles, and it has been speculated that they may only be able to sense vibrations received through the substrate or from direct contact with other insects (Lewis and Cane 1992). Both sexes of the SPB stridulate (produce sound or vibrations by rubbing body parts against one another) using cuticular structures on the abdomen and/or the elytra. Males stridulate by moving the tip of the abdomen up and down, causing a pair of sclerotized processes on the posterior margin of the seventh abdominal tergite (the plectrum) to scrape a row of parallel, transverse ridges on the ventral surface of the elytra (the file) (Michael and Rudinsky 1972). The file of SPB males includes an average of 66 teeth spaced 2.8-4.6 µm apart. Female SPBs lack this elytral file; rather, they have a file with 16-18 teeth spaced 3.1-4.1 µm apart located on the posterior margin of the last abdominal sternite. The tip of the final abdominal tergite (the pygidium) acts as the plectrum in females (Rudinsky and Michael 1973). The chirps produced by SPB stridulation are only faintly detectable by the unaided human ear.

Male SPB entering the gallery of a solitary female produce a distinctive attractant chirp that presumably serves as a courtship signal for inducing mating receptivity in the female (Figure 3.2C). Male SPBs likewise produce this sound when encountering female frass or blends of female semiochemicals at artificial entrances (Rudinsky 1973). Male-male encounters elicit a rivalry chirp that is significantly shorter in duration and has a faster rate of toothstrikes than the attractant chirp (Figure 3.2B). The rivalry chirp is likewise produced by males either encountering a blend of male- and female-produced semiochemicals or when confined with other males within an enclosure (Rudinsky and Michael 1974, Rudinsky and others 1974). Males also stridulate vigorously when handled, producing distinctive stress chirps (Ryker 1988). Gallery-initiating females stridulate as an apparent courtship signal to a male that enters her gallery (Figure 3.2A); in addition, female stridulation may mediate spacing of female attacks and galleries within the bark (Rudinsky and Michael 1973, Grosman and others 1992).

3.6. CONCLUSIONS

The past 50 years have generated much information on the basic biology and behavior of the SPB, particularly regarding the processes of host selection and colonization during outbreaks. Most studies have examined beetles within active spots, whereas much less research has been performed on dispersed or dispersing populations. The reason for this bias is obvious: the bulk of SPB-inflicted tree mortality occurs within spots, and spot suppression remains the core technique used for managing outbreaks. In addition, research within spots typically involves many fewer practical obstacles than studies of dispersed populations. Spots are relatively easy to locate in the forest and typically persist at a single location for many months. However, development of management techniques for preventing SPB outbreaks will likely require major improvements in our understanding of behaviors that allow the SPB to persist in the landscape at suboutbreak population levels.

4

Southern Pine Beetle Population Dynamics in Trees

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Abstract

Successful mass attack of a pine tree by the southern pine beetle (SPB) results in the tree's death and provides opportunity for colonization of the new phloem resource and reproduction by a new generation of SPBs plus hundreds of associated species of insects, mites, fungi, and nematodes. The within-tree portions of the SPB life history can be divided into component processes of colonization (including attack, mating, gallery construction, and oviposition), parent adult reemergence, brood development and survival, and emergence of a new generation of adults. Variables considered in relation to the attack process are threshold density needed to overcome tree resistance, spatial distribution of attacks on trees, rate of attack through time, attack density, and tree resistance to attack. Southern pine beetle females that successfully colonize pine phloem select a single mate, construct galleries in phloem, and oviposit eggs along the margins of those galleries. After oviposition, a variable, and frequently high, proportion of parent adults reemerge and are then available to colonize additional hosts. The reemergence process is strongly influenced by temperature but weakly by parent adult density. Within-tree development of the new SPB brood proceeds in the phloem from egg hatch through four larval stages, the last being completed in a cell in the outer bark in which pupation occurs. Pupae become callow (teneral) adults, then brood adults that subsequently emerge to colonize new hosts. Within-tree development is strongly influenced by temperature, season of the year, SPB density, fungi (both beneficial and antagonistic), and mortality from a variety of predaceous and parasitic species. The effects of temperature on development, and to a lesser extent mortality, have been described. Estimation of the amount of mortality to within-tree populations is difficult to accurately measure, and it is even more challenging to identify and quantify causes of stage-specific mortality.

Keywords

bark beetles
competitors
parasitoids
population dynamics
predators
Scolytidae

4.1. INTRODUCTION

The purpose of this chapter is to briefly synopsize the life history of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) from the period of time at which attacking adults successfully overcome tree defenses, become parents, and initiate reproduction, until emergence of the new brood adults. Researchers have been fascinated for more than 100 years with the biology of this insect, its sudden appearance and population outbreaks, and then its equally rapid collapse and disappearance from forests (Hopkins 1909, MacAndrews 1926). The beetles' natural history within their host trees has been the subject of much investigation (Coulson 1979, Thatcher 1960, Thatcher and others 1980). This summary will focus on SPB arrival at trees, their mating and construction of galleries for egg deposition, reemergence of parents following oviposition, and development and survival of larvae until they pupate and emerge as brood adults.

As southern pines are attacked and successfully colonized by the SPB, there is simultaneously initiated an ecological succession event during which hundreds of species of insects, mites, fungi, and nematodes arrive and use the newly available pine resource (Blackman and Stage 1924, Camors and Payne 1973, Dixon and Payne 1979b, Stephen and others 1993). Other chapters in this encyclopedia document the biology and role of some of these species, but for most of them, detailed knowledge of their population dynamics and impact on the SPB remains obscure.

4.1.1. Southern Pine Beetle (SPB)

The SPB is classified as among the most aggressive of bark beetles. As a primary bark beetle species, it can at high population densities attack and kill any of the southern pines in its range (Coulson 1979, Paine and others 1984). Life history and behavior of the SPB is also discussed in chapters 2 and 3. The attack process is initiated when one or more pioneering SPB adults land on pines and begin to chew through the outer bark of tree bole, encountering the resin defenses of the tree (Payne 1980). If not "pitched-out", or encapsulated by tree resin, these adults release pheromones in concert with tree-produced compounds. If a sufficient population of SPB adults is in proximity to detect these semiochemicals, mass aggregation by additional male and female SPBs results, and the tree bole may be colonized from about 1 m aboveground up the bole to a height that may be well into the live crown (branches are not colonized). The process of SPB host selection and mass aggregation is described in detail (see chapter 3).

The within-tree portions of SPB life history can be divided into the component processes of colonization (including attack, mating, gallery construction, and oviposition), reemergence, brood development and survival, and emergence (Coulson 1980). Discussions in literature vary in the way authors distinguish between types of adults, making it useful to categorize adults as attacking, parents, reemerging, and brood (or emerging). Mature adult beetles (attacking adults, reemerged adults, and brood or emerging adults) are, for the most part, physically indistinguishable from each other and are the collective life stage that occurs outside of host trees. Within the phloem and outer bark of trees are found parent adults, eggs, four larval stages, pupae, and brood (callow or teneral) adults (Figure 4.1).

4.2. ATTACKING ADULTS

Attacking adults are those that aggregate at and attack new host trees, overcoming preformed and induced tree resistance (Nebeker and others 1993). Once tree resistance has ceased and attacking adults are tunneling in host phloem, they are then considered parent adults. It is these parent adults that create galleries and oviposit the eggs that form the new brood population that develops in and emerges from that tree. The attack process has been well studied, and in addition to requiring favorable climatic conditions, variables that are important to this process include: 1. threshold density needed to overcome tree resistance, 2. spatial distribution of attack on trees, 3. rate of attack, and 4. attack density.

Research to investigate attacking populations of beetles has been conducted using a series of approaches designed to measure different components of the attack process. Bunt and others (1980) observed the behavior of individual arriving and attacking beetles on the bark surface of trees. Sticky traps or windowpane traps were used to intercept beetles at the bark surface (Coster and others 1977a, Dixon and Payne 1980, Hynum 1980). Counting numbers of attacking beetles within defined sample units, both through sample dissection or radiographs, is an important technique (Coulson and others 1975b, Pulley and others 1977). Collecting bark samples and measuring evidence of attack sites on bark surface or within phloem tissues avoids problems with timing of sample collections (Linit and Stephen 1978) and is also used as an attack density estimation technique (McClelland and others 1979, Reeve and others 1998). All of these adult estimation procedures have been used to gather the information discussed below.

Thalenhorst (1958) first proposed the idea of a threshold density of attacks that must be exceeded if bark beetles are to kill a tree, and this concept has been examined and reemphasized by other researchers (Berryman 1978; Hodges and others 1979, 1985; Mulock and Christiansen 1986; Raffa and Berryman 1983; Paine and others 1984). Hodges and others (1979) proposed 100 attacks/m^2 as a tentative mass attack density threshold needed to overcome the average loblolly or shortleaf pine. Their estimate is roughly supported by data from Linit and Stephen (1982), who noted two pines in the middle of a large infestation in which all other neighboring trees were successfully attacked, with attack densities at mid-bole of 71 and 51/m^2, that successfully resisted mass attack. The variables and interactions that determine the threshold density at which a tree is successfully mass attacked and killed by the SPB are dynamic, complex, and not fully understood. Clearly this threshold is not only a function of the total number of attacks, but also of the rate at which the challenge occurs. A tree may be able to resist attacks from 500 beetles if they occur over several weeks, but if the same number of beetles arrive and attack within a day, the tree's chance of survival is greatly reduced. The abundance of the adult bark beetle population that can detect pheromones emanating from a newly attacked tree must be a critical factor in providing the adults that respond to the pheromone source and challenge the defenses of the potential host tree. Estimates of SPB adult dispersal distances suggest that beetles may disperse about 500 m in summer and up to 1 km in fall (spring estimates were not made) (Turchin and Thoeny 1993). The size of the geographic area in which beetles can detect the pheromone must be a function of many variables. Proximate weather conditions to a potential host tree are important. Within a forest stand a multitude of interacting factors, such as temperature, relative humidity, wind, rain, barometric pressure, and canopy cover, all influence the dispersal of and effective response distance to pheromones produced by the initial beetles attacking a potential host tree (Fares and others 1980).

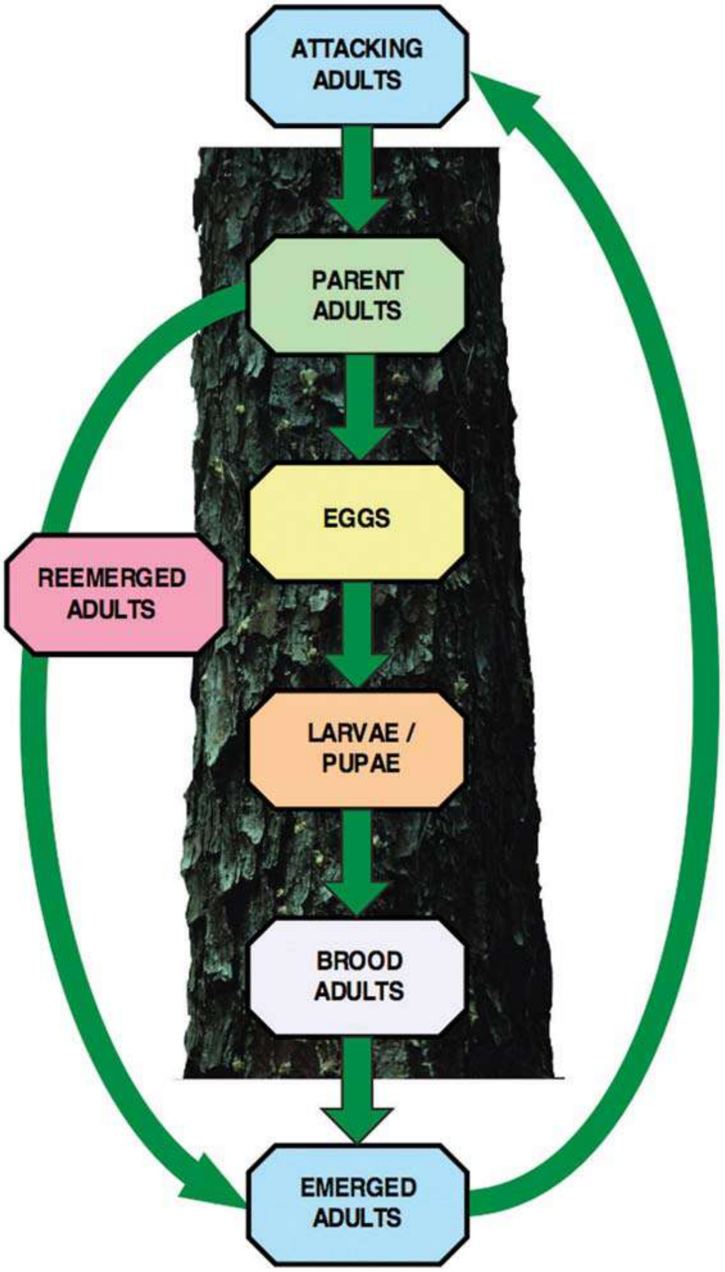


Figure 4.1—A diagram of the SPB life cycle illustrating measurable components of reproductive and developmental stages external to and within host trees. Adults attack trees and if successful, become parent adults, oviposit their eggs, and may then reemerge from that tree. Eggs within phloem develop through four instars, pupate, become callow (brood) adults, and emerge to attack new trees.

Those species of insects that are able to detect trees being attacked and use as kairomones some aspect of the insect- or tree-produced semiochemicals may also influence the threshold attack density. Primary among these species is *Thanasimus dubius* (F.), the adults of which arrive during SPB mass attack and may affect the bark beetles' mass-attack effort by killing significant numbers of attacking SPB on the bark before they enter the tree (Reeve 1997). The pine engraver bark beetle complex, *Ips* species, probably arrives after the threshold density is exceeded and mass attack successful. Although pine sawyers (*Monochamus* species) have been reported to arrive at trees under attack and their oviposition sites may be filled with tree resin (Dodds and Stephen 2000), it seems unlikely that they exert significant influence on the success of bark beetle mass attack (however see chapter 12 for discussion of their impact as competitors). Additional relationships that affect thresholds may be the microorganism complement (e.g., blue stain fungi) associated with colonizing beetles that may be complicated partners that aid in overcoming tree defenses but later become antagonistic to bark beetle reproduction (Klepzig and others 2001a).

Tree defense, as indicated by its ability to defend itself through the preformed and induced responses of the resin system (Nebeker and others 1993), is a central and key factor as to whether the tree lives or dies. Physical and chemical properties of the tree's resin are linked to its susceptibility to SPB attack (Hodges and others 1979). Because the SPB is a primary bark beetle, it is frequently noted that when beetle populations are sufficiently high, the resistance threshold of all trees of any vigor level can be conquered (Paine and others 1997). However, in most situations beetle populations are endemic (low), and a more complex interaction of multiple factors determines whether or not a tree will be successfully killed. Through years of elegant experimentation and investigation, Peter Lorio developed and explained the tradeoffs that exist between a tree's cellular growth, or differentiation, and how that may influence success of bark beetle attack (Lorio 1986). The growth-differentiation balance hypothesis is predicated on the idea that pines early in the spring put their energy into growth, and later in the summer, when moderate water stress begins to switch cellular metabolism toward latewood production, the tree produces maximal amounts of resin that result in more effective defense against beetle and fungal invasion. Seasonal changes in trees' induced responses have been documented (Stephen and Paine 1985), and field observations support the idea that SPB populations tend to grow at faster rates in such times as spring when there is a likely lower resistance threshold.

The rate of attack varies in ways that are not fully understood. In studies of successfully mass-attacked trees, the majority of attacking adults arrive on the second day (Bunt and others 1980) or third day (Coster and others 1977a) of mass attack, and nearly all (97 percent) attacking adults arrive within a nine-day period (Dixon and Payne 1979b). Beetles are trapped at trees under attack from morning through late afternoon; however, the greatest numbers are caught at about 5 pm. (Coster and others 1977a). Although the sex ratio of attacking adult SPB is close to 1:1, it has been reported to vary during mass attack with slightly more females being trapped initially and the ratio later favoring males as attacks progress (Coster and others 1977a, Hynum 1980). Females after landing on the tree begin searching for a suitable crack or crevice in which to begin tunneling (Bunt and others 1980). Males, in attempting to locate female entrance holes, often interact and fight with other males prior to successful entrance (Bunt and others 1980). As soon as the male enters the female-initiated gallery he releases verbenone and *endo*-brevicomin, which, as the density of attacks increases, begins to reduce the attractiveness of the tree to both males and females (Payne 1980). The sex ratio of this monogamous species essentially is 1:1 during emergence (Coulson and others 1976b).

The spatial and temporal distribution of SPBs attacking host trees has been well studied (Coster and others 1977a, Coulson and others 1976b; Fargo and others 1979; Mayyasi and others 1976b). Intensive field sampling of trees resulted in the development of a model illustrating the spatial and temporal patterns of SPB attack (Figure 4.2). Attacks are concentrated in the first 3 days, then decline rapidly. Initial attacks occur at about 3.5 m on the tree bole and spread rapidly up and down from that region (Coster and others 1977a, Fargo and others 1979) with the highest attack densities just below the central portion of the infested bole (Coulson and others 1976b, Fargo and others 1979). Arrival of attacking adults usually occurs 1 or 2 days prior to their successful entry into the tree (Coulson 1980).

Many different methods have been used to estimate density of attacking adults, including counting numbers of pitch tubes on the bark surface, removing bark with attached sapwood containing attacking adults and dissecting to count attacking beetles (Coulson and others 1976c), making radiographs (x-rays) of bark with attached sapwood to estimate density of attacking beetles in samples (Pulley and others 1977), and removing bark after completion of attack (and sometimes after reemergence of parents) to search for evidence of attack sites (Linit and Stephen 1978, Stephen and Taha 1976).

Attacking adult density, when measured on large numbers of bark samples, can be expressed as frequency of counts (Figure 4.3). Usually these density figures are presented as numbers per some unit of bark surface area; e.g., 1 dm^2 (=100 cm^2) or per square feet. Some authors present numbers of attacking beetles, and some present numbers of attacks (which is equivalent to numbers of attacking beetles divided by two). The earliest attack density estimates are from MacAndrews (1926), who counted SPB attacks on felled trees and reported much variation, but an average of 4.1 attacks/dm^2. Three studies supported by substantial data sets (Fargo and others 1979, Reeve and others 1998, Stephen and Taha 1979a, 1979b,) all show a central tendency and similar range of attack densities (Figure 4.3). Coulson and others (1976b), using a three-parameter nonlinear model, estimated an average attack density of 4.6/dm^2 at the mid-bole region for 50 trees sampled in East Texas. Attacking adult density was estimated at four times during the year by Stephen and Taha (1979a), and they report mean density varying from 6.8 to 5.2 attacks/dm^2, which is within a

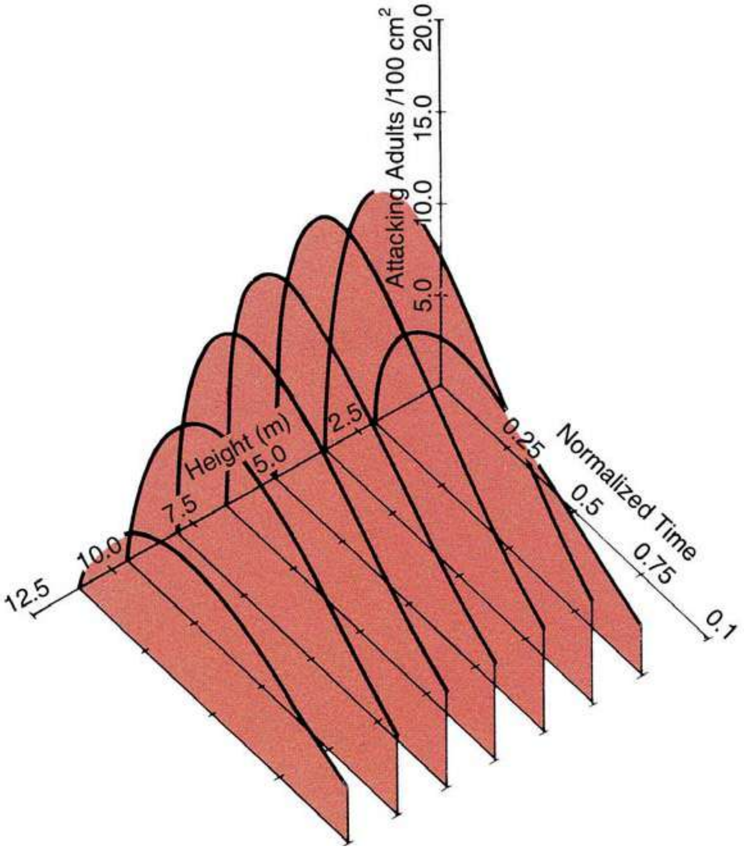


Figure 4.2—Summary of model projections representing the spatial and temporal patterns of SPB attack on an average host pine tree. Y axis = adult density, X axis = height on infested bole and Z axis = normalized time. Time is normalized from zero to one, with one representing 14 days. (illustration from Fargo and others 1979, Coulson 1980)

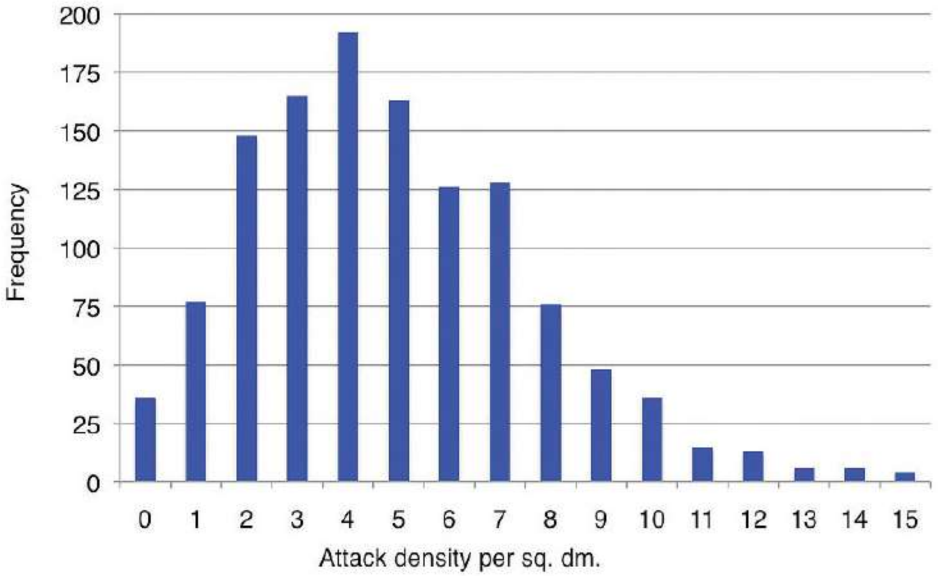


Figure 4.3—Distribution of numbers of successful SPB attacks per 1 dm^2 bark sample unit (= 100 cm^2). Mean attack density is 4.92 ± 0.27 (SE) and the mode is 4. Each attack is equivalent to a density of two beetles (one male and one female per attack). Data summaries from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977 with about 1,240 attack samples used in this analysis. (illustration from Stephen and Taha 1976, 1979a, 1979b)

range reported by other authors (Reeve and others 1998). The amount of observed variation in SPB attack density (Figure 4.3) is significant and is potentially linked to successful brood production if intraspecific competition occurs at high densities. Coulson (1979) reports that intraspecific competition is minimized because as density of gallery increases, females reduce the number of eggs laid; however, other researchers suggest that at higher attack densities, intraspecific competition can result in significant reduction in brood survival (Reeve and others 1998). In addition to competition with members of its own species, the SPB must compete with a complex of three *Ips* bark beetles for phloem in which to reproduce (chapter 12).

Maximum attack density occurs at 3.5 m and gradually decreases toward the extremes of the infested bole (Coulson and others 1976b). Normally near the base of infested trees, SPB attacks are not found much below a height of 1 m; however, there is great variation in the height of attacks near the top of infestation (Thatcher and Pickard 1964). There does not appear to be a simple correlation of height of infestation and height of the tree (MacAndrews 1926). For trees sampled at a particular time of year, however, within a given infestation, height at the top of infestation appears correlated with increasing tree diameter (Stephen and Taha 1979b). The factors that do influence height at the top of infestation are not fully understood but three factors—available population of attacking adults, season of the year, and abundance of *Ips* competitors—all appear to be important variables. The most complete use of phloem in infested trees appears to occur in spring when SPB populations are high and few *Ips* species present. Later in the year, during periods when SPB populations are very high and infestations are growing rapidly, particularly in midsummer, trees may be mass-attacked in a very short period of time. For unexplained reasons the height to which colonization of the SPB extends may not exceed 6 or 8 m, despite sufficient adults available to colonize the higher parts of these trees (Figure 4.4). This clearly has implications for availability of phloem for competing *Ips* species (chapter 12), and the varying pattern of seasonal change in height at the top of infestation is an interesting, unstudied aspect of the SPB biology.

Mortality to attacking adults is highly variable, poorly quantified, and believed to primarily involve two sources: predation from natural enemies (Figure 4.5) and resin defenses of trees (Figure 4.6). It is important to emphasize how much variability exists in the effectiveness of these mortality factors and how difficult it is to measure such mortality over the full spectrum of conditions likely to occur.

Predation of attacking adults on the surface of trees has long been attributed to adult checkered beetles (Figure 4.5), *Thanasimus*

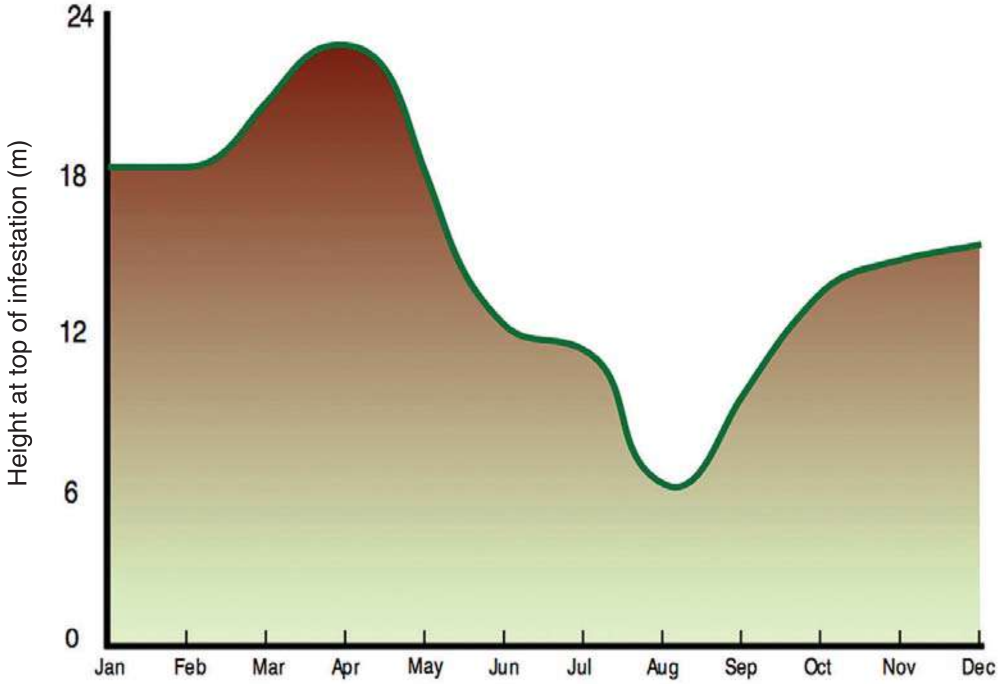


Figure 4.4 —Adaptation of data presented in Figure 2 of Thatcher and Pickard (1964) illustrating changes in height of attack and colonization of infested bole as a function of season. During cooler seasons the height at top of infestation is greater, and during hotter summer periods it may be much lower.

dubius (F.) (Hopkins 1899). Irregularities and crevices in pine bark, coupled with the extent to which adults are able to conceal themselves, render field experiments to estimate predation on SPB adults difficult. In laboratory situations Turnbow and others (1978) reported that *T. dubius* adults consumed about 1.3 adult SPBs per day (except ovipositing females consumed about 2.5 per day), and Thatcher and Pickard (1966) reported that *T. dubius* killed an average of 2.2 adults per day. Reeve (1997) also working in the laboratory concluded that *T. dubius* adults can reduce populations of SPB attacking adults by about 40 percent, and when the ratio of *T. dubius* adults to SPB was high, per capita consumption of the SPB increased to about six beetles per day. Reeve also emphasizes that a long-term survey in Louisiana indicates *T. dubius* exhibits a numerical response to SPB population density changes and suggests that this correlation is supported from SPB trapping and monitoring data used to predict wide area trends in SPB population increase (Billings 1988). Predator populations may vary as a function of infestation size and trajectory (i.e., whether populations are increasing or decreasing and how long the infestation has existed). Stephen and others (1989) reported that as region-wide SPB infestations increased, peaked, and then dramatically declined, within-tree density of predator populations significantly increased during the peak and post-peak decline periods.

Resin defenses are considered the primary means whereby pines resist attack and invasion by insect and fungal attack (Paine and others 1997). The importance of resin as a defense is unquestioned, yet few studies have quantified variation in attacking adult mortality that is attributable to resin. This likely is due to the difficulty in accurately measuring numbers of attacks that are unsuccessful, particularly if the trees do not succumb to mass attack, and the fact that so many genetic and environmental factors affect resin production and flow (Nebeker and others 1992). The pitch tubes associated with SPB attacks differ as a function of tree resistance, resin flow, attack density, and probably other variables. Reddish pitch that is still flowing suggests a tree that is under attack and still resisting (Figure 4.6). Beetles

Figure 4.5—Adult checkered beetles, *Thanasimus dubius* (F.), mating on pine bark. (photograph by Ron Billings)

Figure 4.6—Reddish pitch tubes as evidence of SPB attacks and pine resin defense. (photograph by Erich G. Vallery. USDA Forest Service, SRS-4552, www.forestryimages.org)

attacking vigorous pines can be entombed in resin formed at the site of their attack (Figure 4.7). Drier pitch, and pitch plus reddish beetle excrement (frass), indicates a tree that has been successfully colonized (Figure 4.8). A data-rich model showing that seasonal patterns of tree growth and moisture availability greatly affect resin production was developed by Lorio (1986), and site quality, tree stress, and seasonal variation in inducible tree resistance does occur (Paine and Stephen 1987a, Stephen and Paine 1985). In loblolly pine, successful and unsuccessful attack densities in control trees and trees that had been subjected to severe short-term stress varied seasonally and with moisture stress but showed a range of attacking adult mortality from 6.4 to 47.4 percent (Lorio and others 1995, Stephen and others 1988).

The other pine tree resistance mechanism, an induced hypersensitive response (Berryman 1972), initiates cellular and biochemical changes at the site of beetle attack resulting in cell death, new impermeable cell layers, and synthesis of monoterpene and phenolic compounds (Paine and others 1997). The induced hypersensitive response may serve not only to contain growth of fungi inoculated during mass attack, but also negatively affect bark beetle reproduction (Paine and Stephen 1988). The two tree defense mechanisms, preformed resin system and induced hypersensitive response, are inseparably linked, and their potential impact on within-tree beetle survival is key to the tree's life or death. An induced hypersensitive response lesion can be triggered both by fungal inoculation and attacking SPBs (Figure 4.10).

4.3. PARENT ADULTS

From a functional perspective, parent adults are simply attacking adults that are successful. As resistance of trees is depleted and adult beetles enter phloem tissue (Figure 4.9), they mate and then are considered parent adults (Figure 4.1), and it is they who will create galleries in which eggs are laid and the new generation initiated. The SPB is a monogamous bark beetle, meaning that for the purpose of mating, gallery construction, and oviposition, each attacking female is associated with one male (Coulson and others 1976b, Osgood and Clark 1963). Chapter 3 discusses the behavioral aspects of mating and gallery construction.

The sequence of mass attack is such that the midsection of the tree bole is normally attacked first, and colonization above and below that area lags in a somewhat predictable manner, resulting in a nonuniform beetle population age structure in infested trees (Coulson 1980, Fargo and others 1979). The abundance of available attacking adults (e.g., infestation size and age structure), coupled with seasonal effects (e.g., temperature) can greatly influence the rate of mass attack within individual trees (Coster and others 1977a). It is not uncommon to find attacking adults in the lower and upper margins of the infested bole at the same time that parent adults, eggs, and sometimes larvae are found near mid-bole. This complicates within-tree sampling and estimation of within-tree SPB populations. A hypothetical model (Figure 4.11) was proposed that illustrates the actual proportion of different SPB life stages contained in an infested tree based on what observers noted as the predominant beetle life stage found at breast height (Hines and others 1980). Samples of different size, number, or timespecific to life stage sampled may be required to enable accurate estimation of different SPB life stage densities, thus requiring multiple visits through time to acquire the samples needed for all life stages (Coulson and others 1975b, 1979a; Stephen and Taha 1976).

High density of attacking adults is often necessary to overcome tree resistance; however, high density of parent adults can result in competition among the brood they produce. Mechanisms to avoid this have evolved (Coulson and others 1976b), and include limiting amount of egg-bearing gallery produced by parents, the number of eggs produced per female, and the length of time parent females remain in the tree (Wagner and others 1981a). The length of time that parent adult beetles are in the tree is also a function of temperature. Density of the attacking population has a weak influence on length of time beetles remain in trees, as lower density situations result in beetles being in trees for a longer period (Wagner and others 1982).

Parent adult beetles reemerge following gallery construction and oviposition (see section 4.5 below – Reemerging Adults); thus, it is only when dead parent adults are found in galleries that their mortality can be assessed. Dead adults at the beginning of galleries are often associated with crystallized resin and then classified as attacking adult mortality. Mortality to parent adults is usually considered as minimal, but it is safe to say that it is poorly studied and not well understood. Owing to the obvious difficulties of tracking beetles in the field, no such studies have been done that monitor brood production of parents of known ages. In pine bolts colonized and held in a laboratory, however, about 95 percent of females reemerged after producing their first brood, but only 73-84 percent of females reemerged following production of their second brood (Wagner and others 1981b).

Fecundity of parent adults ideally would be determined by examining entire, individual female galleries in naturally infested trees. SPB gallery structure is sinuate, and galleries frequently cross over each other, even at normal attack densities (chapter 12). Thus gallery structure coupled with sample sizes that are normally 1 dm^2 makes it impossible to follow individual galleries from field samples. In the laboratory, using bolts with forced infestations of SPB adults, Clarke and others (1979) isolated individual galleries and found average female fecundity, measured as number of egg niches per gallery, was 159 (SE of 12.6). They also reported that counting egg niches is a suitable measure of egg production in the laboratory and suggest it is probably accurate in the

Figure 4.7—Fresh resin on pine bark with SPB adults encased in the pitch tube. (photograph by Erich G. Vallery. USDA Forest Service, SRS-4552, www.forestryimages.org)

Figure 4.8—Knife blade pointing to reddish frass collecting in bark crevices, evidence of successful SPB attacks. (photograph by F.M. Stephen)

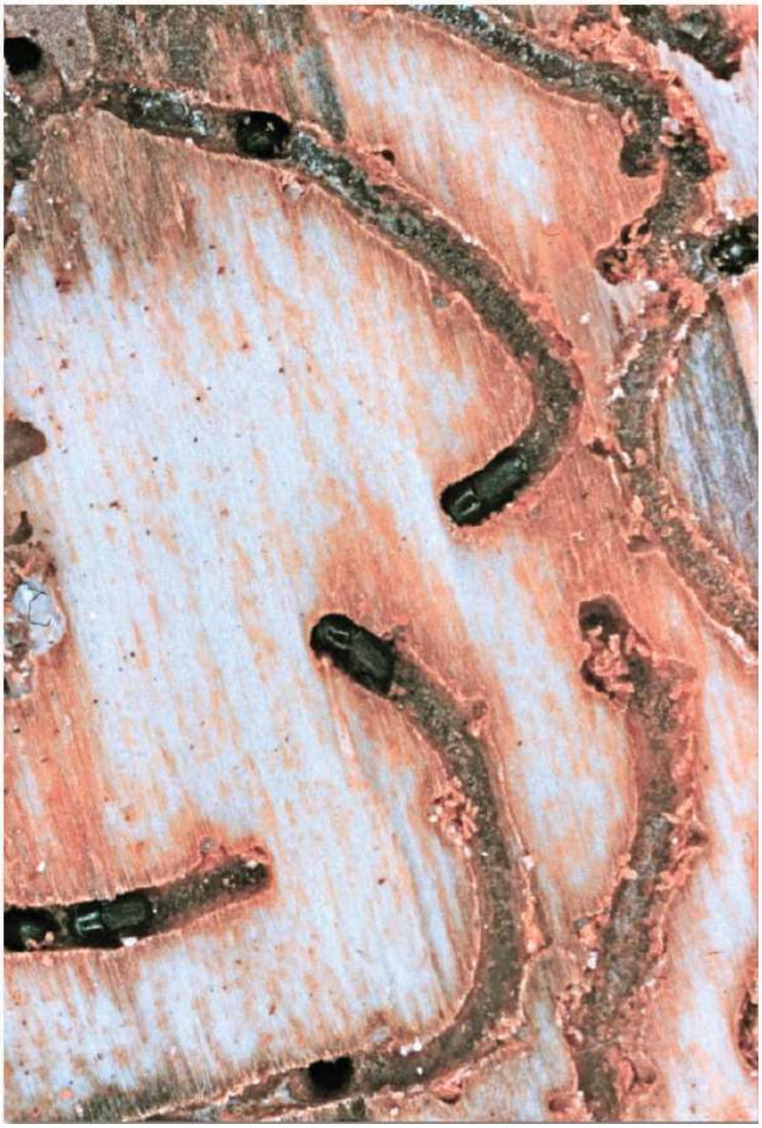


Figure 4.9—SPB adults creating egg galleries in fresh phloem. Note that galleries are free of packed frass and that egg niches and eggs are visible along margins of the galleries. (photograph by F.M. Stephen)

field. The method normally used to estimate fecundity from trees in the forest is to cut bark samples and remove them from the tree, including outer bark, phloem, and the attached sapwood facing (Coulson and others 1976c). In the lab it is possible then to measure attack densities and amount of gallery produced per sample unit and calculate gallery length and egg density per female as an average for the sample (Coulson and others 1976c, Pulley and others 1977, Stephen and Taha 1976). Using these techniques, parent adult fecundity was determined for bark samples collected from 125 infested pines in an outbreak of the SPB that was increasing in magnitude in southwest Arkansas from June through October 1976. The average eggs per attack (i.e., eggs/female/dm^2) remained quite consistent, ranging from 26.2 to 28.4 during that period (Stephen and Taha 1979a).

During laboratory colonization studies Wagner and others (1981b) reported that parent adults were more fecund, producing more gallery and eggs during their second brood than their first. They also demonstrated the complex interactions among temperature, adult density, female size, and month of adult emergence in terms of their effects on gallery construction and fecundity (Wagner and others 1981a).

4.3.1. Gallery Construction

Southern pine beetle females initiate attack, and one male joins each female. The female creates a nuptial chamber in the phloem where mating occurs. Galleries are then initiated in which the female will oviposit her eggs (Figure 4.9). Gallery construction proceeds rapidly, and by the second day following initiation of mass attack (and prior to maximum attack density) rate of gallery construction is at its peak (Fargo and others 1979). That study predicted average expected gallery length of 80 cm/dm^2 of bark area. Foltz and others (1976) developed a model based on field data collected from SPB-infested pines in East Texas, and created probability density functions based on sample height as a function of infested bole height. That model (Figure 4.3 in Foltz and others 1976) and the parameters they derived results in predicted gallery lengths ranging from about 68 to 97 cm of gallery/dm^2. Both of the above estimates coincide extremely well with the frequency distribution data of Stephen and Taha (1979b), with a mean based on Monte Carlo sampling of 85.0 cm gallery/dm^2 with standard error of the mean of 7.74 (or, using frequency counts a mean value of 73.7 and a mode of 75) (Figure 4.12). Examination of the raw data presented by Nebeker and others (1978b) reveals much variation among samples at all tree heights, but somewhat generally lower mean values than the above studies. Most field investigations of adult galleries have been based on bark samples removed from infested trees, and the limited area of the samples meant that individual female galleries could rarely be discerned in their entirety. In laboratory studies (Wagner and others 1981a, Wagner and others 1982) individual pairs of beetles produced averages of 23-27 cm of gallery when allowed to colonize unattacked phloem. Clarke and others (1979),

Figure 4.10—Cut-away bark revealing phloem tissue and the two components of pine defense against colonizing bark beetles and their fungi. Resin exuded from severed ducts is visible, and two induced lesions can be seen. The circular lesion in the lower center was initiated in response to blue stain fungal spores experimentally placed against the phloem of a healthy pine. The pine was also attacked by the SPB, and the induced lesion at the right of the image surrounds the gallery made by an attacking adult. Note the similarity in the induced response to both invasions. (photograph by F.M. Stephen)

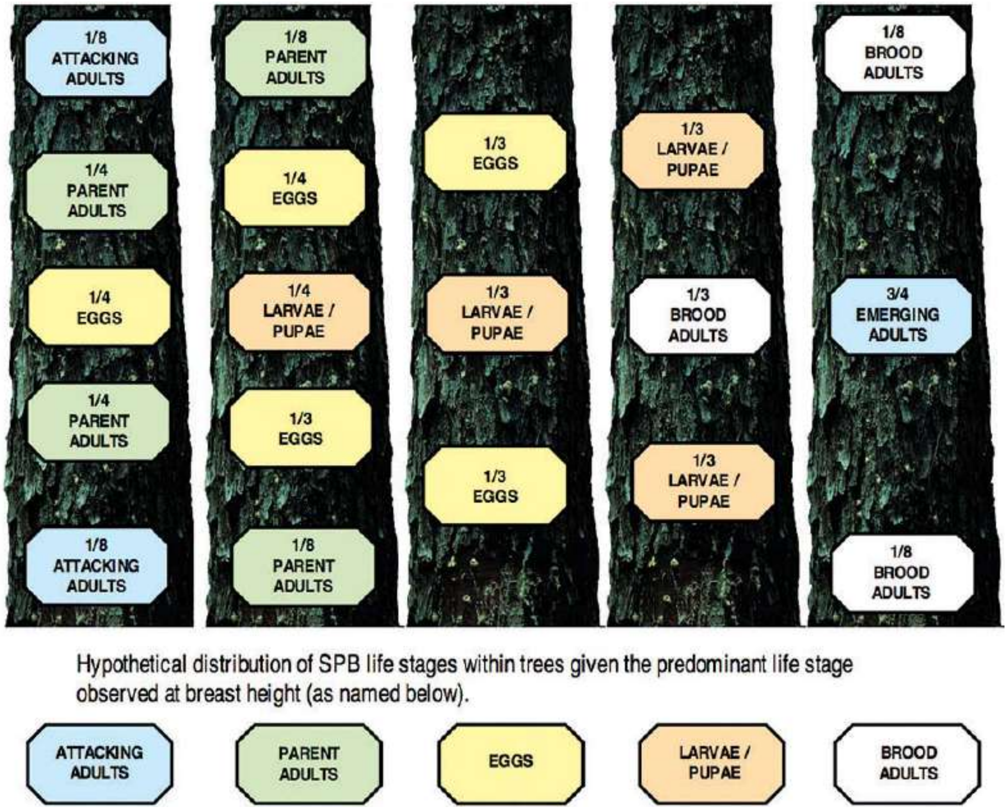


Figure 4.11—Figure adapted from data presented by Hines and others (1980), who proposed a hypothetical model of the actual proportions of different beetle life stages within infested trees given what observers report when the bark is cut away at breast height and the life stage present there is noted. The figure shows five hypothetical trees, and beneath each is a colored box that represents a different SPB life stage. Within each tree is a series of colored boxes that represent the proportion of the SPB life stages that are actually in the tree. For example, for tree one, attacking adults are seen at breast height, but in that tree are 25 percent attacking adults, 50 percent parent adults, and 25 percent SPB eggs. Based on a sample of 200 infested trees

using bolts in which infestations of SPB adults were forced, isolated individual galleries and found a mean per female gallery length of 67 cm (SE of 48 cm). It is unclear as to the causes of these large differences in gallery per female between these studies.

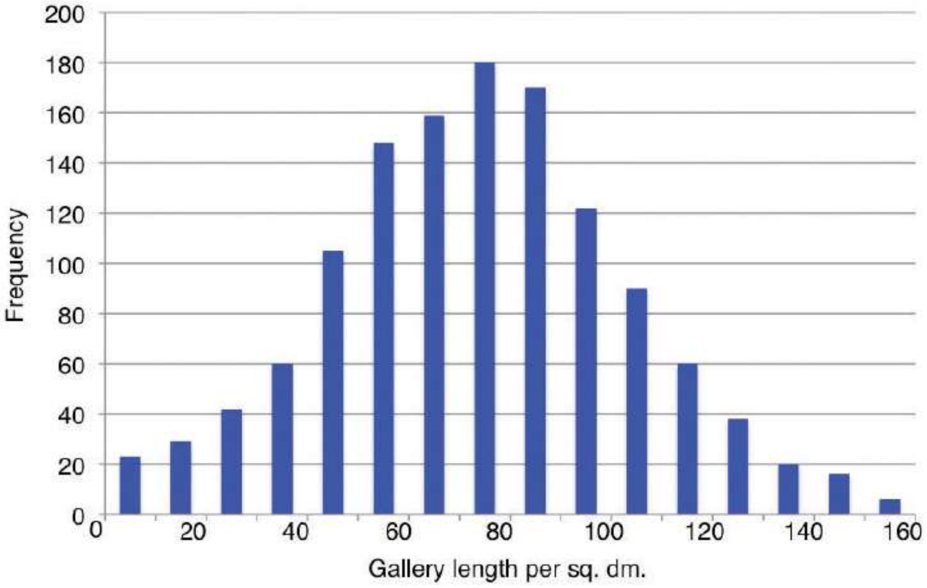
The relationship between density of attacking adults and the amount of gallery each female produces has been a focus of research because of the potential implications for intraspecific competition at high attack densities. Coulson and others (1976b) reported that density of gallery (and density of eggs) per dm^2 was independent of attacking adult density. These results differ from the findings of Reeve and others (1998), whose data suggested that as density of attacks increased, density of gallery produced per dm^2 also increased. However, both groups report that gallery/attack (and eggs/attack) decrease exponentially with increasing attack density, meaning that individual females decrease the amount of gallery produced and eggs laid as attack density increases. Coulson and others (1976b) postulated that this mechanism of resource utilization is important in minimizing competition among SPB immatures; however, Reeve and others (1998) suggest that at attack densities common in field situations, intraspecific competition does occur and results in significant decrease in brood survival.

Wagner and others (1981a) found that gallery construction and oviposition varied as a function of temperature, with greatest amounts of gallery produced at 15 °C and the least amount at 30 °C, while the fewest eggs were laid at the coldest temperature tested (10 °C). In addition to effects of temperature, it was established that whether or not beetles were producing their first or second brood was important to gallery construction and oviposition. Interestingly in laboratory situations, over all temperatures tested, females produced more gallery and oviposited greater numbers of eggs during their second attack cycle rather than their first, a finding that confirms the importance of reemerging beetles to SPB population dynamics (Wagner and others 1981b). Of further significance is that in late winter and early spring female beetles are larger than their counterparts who emerge in summer, and they consequently produce more gallery and eggs than the smaller beetles emerging later in the year (Wagner and others 1981a).

4.4. EGGS

Adult females chew niches in the sides of the egg galleries and oviposit eggs individually into these niches. The eggs are held in the niches by fine, packed boring dust (Thatcher 1960). Wagner and others (1981a) described egg galleries with regions at the beginning and end of the galleries that are free of eggs, and a section between those egg-free regions in which oviposition occurs. They note that resin associated with sites of initial attack may cause egg mortality and speculate that the egg-free region at the beginning of galleries is a means to avoid that mortality. Clarke and others (1979) reported about 4.3 cm of egg-

Figure 4.12—Distribution of total SPB gallery length recorded per 1 dm^2 bark sample unit. Mean gallery length is 85.01 ± 7.74 (SE). The gallery length density counts appear normally distributed with about 85 percent of counts ranging from 35 to 115 cm of gallery per dm^2. Data from 1268 samples on 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977. (illustration from Stephen and Taha 1976, 1979a, 1979b).



free gallery at the beginning of a gallery. Near the initiation of beetle attack sites, pines often produce induced hypersensitive response tissue (Figure 4.10), and this defensive reaction has been shown to reduce both the amount of egg gallery produced by individual beetles and the number of eggs/cm oviposited in those sections of gallery (Paine and Stephen 1988).

The regularity and spacing of eggs within galleries has been the subject of considerable research, probably because the dissection of galleries to estimate egg numbers is tedious, and measuring only gallery length could serve as a valuable index to estimate egg density. An important paper by Foltz and others (1976) concluded that the number of eggs/cm of gallery was constant, yielding a value of 1.59 eggs/cm; however, their model did not account for the egg-free region at the beginning of galleries. Clark and others (1979) in lab studies working with introduced beetles in bolts estimated 2.42 egg niches/cm egg gallery, a number significantly higher than that reported by Foltz and others (1976). Wagner and others (1981a), also in a lab setting, found variation in numbers of eggs/cm gallery related to temperature, with 1.39 eggs/cm at 10 °C increasing to 2.04 eggs/cm at 20 °C and then decreasing as temperature increased to 1.75 at 30 °C. They discovered that at 15 °C, SPBs produced more gallery per mating pair than at other temperatures, and at 30 °C the least gallery per pair was constructed (Wagner and others 1981a). These authors also reported that as gallery density increased, parent adults turned more frequently, thus creating a greater serpentine pattern of gallery structure, and they hypothesized that this could be an adaptation to minimize interaction or competition with other beetles. More than 97 percent of all egg niches that were examined contained eggs (Wagner and others 1981a), a result confirmed through numerous dissections of field-collected bark samples (F. M. Stephen, unpublished data). Within individual egg galleries, Wagner and others (1981a) found that the number of eggs per unit of gallery was relatively constant, supporting the observations of Foltz and others (1976), but they did not concur with the constant value of 1.59 eggs/cm. In fact the variation in eggs per cm associated with individual galleries ranges from about 1.2 to 2.7 eggs/cm of gallery, and thus suggests the need to dissect egg galleries to more accurately estimate reproduction.

Egg density per sample unit of bark area (phloem) is a statistic calculated by many authors. Foltz and others (1976) modeled the results of field data collected from SPB-infested pines in East Texas, and created probability density functions that considered sample height as a function of infested bole height. That model (Figure 3 in Foltz and others 1976) and the parameters they derived resulted in predicted estimates of egg density of 155 to 117 eggs/dm^2. Their estimates coincide well with a larger data set reported by Stephen and Taha (1979b) and are summarized here. The estimates of egg density per dm^2 (Figure 4.13) (not obtained through a model, but by dissection of individual galleries) are 135.66 ± 5.85 (SE). Interestingly, if the above two mean values for gallery length (85.0 cm/dm^2) and egg density are used to estimate average number of eggs per cm of gallery, the resulting mean value is 1.596, which is nearly identical to the eggs/cm gallery constant originally proposed by Foltz and others (1976). It is the factors influencing variation around that mean that may be of great significance in influencing how populations of the SPB are changing.

Potential mortality agents of SPB eggs include abiotic factors such as resin (toxicity and crystallization), heat, cold, and variation in phloem moisture. Oleoresin is likely to affect eggs, but little data exist that show the amount of egg mortality attributable to resin. The egg stage was reported to be most resistant to cold temperatures, with eggs exposed to -20 ^{o}C not being adversely affected (Beal 1933). A study designed to evaluate mortality in relation to phloem moisture found an average of 15.5 percent egg mortality (Wagner and others 1979), but that study, along with that of Webb and Franklin (1978), could not link egg mortality to phloem moisture. Analysis of SPB within-tree populations over a 3-year period showed large variation, but on average about 40 percent survival from egg to 3rd instar (Gagne and others 1980). Although causes could not be established, these authors suggested host factors, not predator and parasitoids, were the cause of mortality. Numerous predators have been suggested or confirmed as egg mortality agents, and include both insects (Dixon and Payne 1979b) and mites (Moser 1975), but the amount of mortality to eggs from natural enemies in field situation remains uncertain. Evidence for parasitoids of the SPB eggs has not been conclusive.

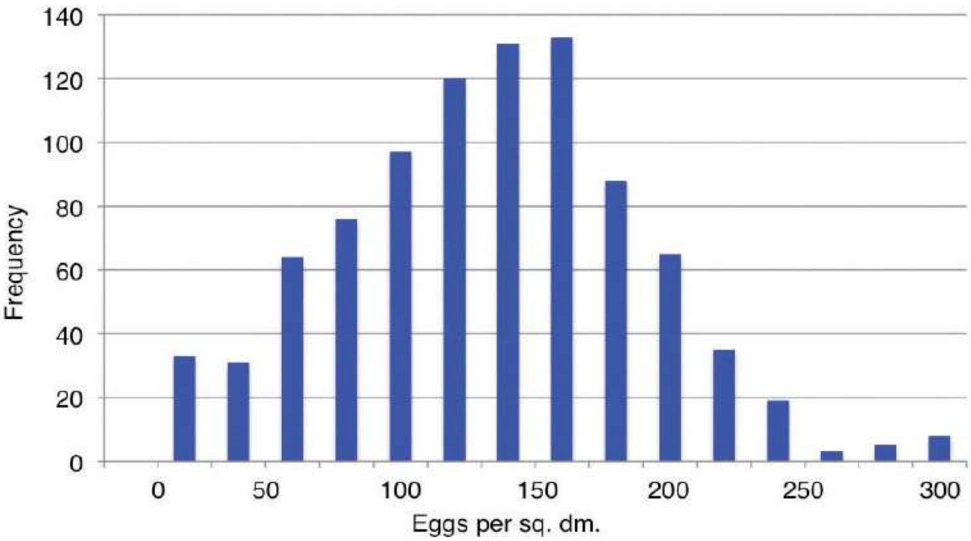


Figure 4.13—Distribution of total SPB egg density, determined by gallery dissection, per 1 dm^2 bark sample unit. Mean egg density is 135.66 ± 5.85 (SE). The egg density counts are slightly skewed to the right with a mode of 160, with about 85 percent of counts falling between 60 and 200 eggs/dm^2. Data from 908 samples from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977. (illustration from Stephen and Taha 1976, 1979a, 1979b)

4.5. REEMERGING ADULTS

Southern pine beetle parent adults normally exit their host tree after they have mated, constructed galleries, and oviposited eggs (MacAndrews 1926, Thatcher 1960). Holes initiated in egg galleries that exit directly to the bark surface were first described in detail by Hopkins (1899) and later termed ventilation holes (MacAndrews 1926), but Wagner and others (1981a) report that they are holes through which parent adults reemerge. Reemerging parent adults (termed "sister broods" in the European literature) are described for many bark beetle species, and their importance in SPB population dynamics has long been recognized (Coulson and others 1978, Franklin 1970b, Thatcher and Pickard 1964). These beetles may greatly increase the available attacking beetle population and, as they are capable of both producing pheromones (Coster 1970) and responding to pheromones (Coulson and others 1978), they can thus create continual attraction sources within infestations (Franklin 1970b).

Coulson and others (1978) reported that the percentage of parent adult beetles reemerging varied from about 90-99 percent. They found the highest percentages of reemergence occurred in the mid-bole region (2.0 – 8.0 m). Their modeling of the reemergence process revealed a normal (bell-shaped) distribution in regard to the timing, with peak reemergence occurring about 5 days from its initiation, although this rapid reemergence time was not substantiated in subsequent studies (Gagne and others 1982) that reported about a minimum 10-day residence time. Other research has reported different proportions of the adult population reemerging. Cooper and Stephen (1978) examined SPB populations that were not in the central epidemic areas of East Texas but on a more northern fringe population in Arkansas, and found on average lower reemergence (mean of 65 percent, ranging seasonally from 9.3 percent to 83 percent) over an 8-month period. Their lowest estimate was in late winter/early spring populations, and the highest in the fall.

Temperature plays an important role in determining the amount of time that adults spend in the tree creating galleries and ovipositing. Under experimental conditions in the laboratory, parent adult residence time as a function of temperature follows a typical backwards J-shaped curve (Gagne and others 1982). They noted that the lowest temperature at which reemergence occurred was 12.5 °C, and the shortest residence time for adults from attack to reemergence, about 10 days, was at the optimum temperature of 27 °C, a time that corresponds well with data from other field observations (Franklin 1970b, MacAndrews 1926, Thatcher and Pickard 1964). Males often initiate exit galleries and on average reemerge about 1.5 days before females at temperatures below 30 °C, but at or above 30 °C the opposite was found (Gagne and others 1982, Wagner and others 1981a). Gagne and others (1982) developed a model of the reemergence process that incorporates both temperature and physiological time to enable accurate prediction of the distribution of remerging beetles over calendar time. The entire process of reemergence from a single tree has been estimated to take about 14 days (Coulson and others 1978).

Attack density was examined as a possible influence on the rate of parent adult reemergence (Wagner and others 1981a) but was found to have only a weak effect on the time that parents spend in trees, with adults at higher densities reemerging slightly faster than those at low density.

It has been noted that after females have mated, they can produce viable eggs in second brood, even without mating again (Wagner and others 1981b). The number of times that females are capable of reemerging and producing new brood is not known, but it has been confirmed that they can (Clark and Osgood 1964, Yu and Tsao 1967, Wagner and others 1981b). This fact may have important implications for population dynamics as Wagner and others (1981b) reported that egg production in second broods is as great or greater than in the initial brood.

4.6. LARVAE AND PUPAE

4.6.1. Development

Following eclosion from eggs, 1st stage larvae begin feeding in phloem. They complete four larval instars (Fronk 1947, Goldman and Franklin 1977, Mizell and Nebeker 1979) and then pupate in the outer bark when it is of sufficient thickness. Successful larval development is intimately tied to presence or absence of fungal symbionts vectored by attacking adults or their mite associates (Barras 1973, Bridges and Perry 1985, Goldhammer and others 1990, Hofstetter 2010, Klepzig and others 2001a). When larvae are in tissue in which blue stain fungi dominate, their galleries are long and winding, and their development is hindered. This image (Figure 4.14) is of a 1 dm^2 bark sample, on which blue stain fungi have colonized the middle portion from top to bottom. The SPB galleries at the left of this sample, associated with nonstaining mycangial fungi, are of normal density and show larval feeding cells that are close to the niches from which the eggs hatched and larvae developed. The SPB galleries in the central portion of the sample are characterized by long, winding larval mines and an apparent lack of complete larval development at the time this sample was collected. Owing to movement of 4th stage larvae, prior to pupation, from the phloem-sapwood interface toward the outer bark, larvae are often not visible on the inner face of bark samples. SPB galleries on phloem, colonized also with mycangial fungi, exhibit short larval mines of only a few millimeter leading to the broad feeding cells in which pupation occurs (Figure 4.15). The inability to count actual numbers of larvae present on/in a sample also leads to difficulties in accurately estimating larval densities or the mortality factors acting on those larvae.

The speed of SPB development within trees and its astounding rate of population increase is a function of its ability to grow rapidly at warm temperatures. MacAndrews (1926) noted that within trees the length of time required for development from egg to adult ranged from 39 to 49 days, depending upon the time of year, and Thatcher and Pickard (1967) reported that along the southern gulf coastal plain in East

Figure 4.14—A photograph of the inner bark surface (phloem) of a 100 cm^2 bark sample. Normal SPB egg galleries, with short larval mines and broad feeding cells in which pupation occurs, are seen at the left side of the image. This is indicative of SPB development when mycangial (nonstaining) fungi are present. In the center of the sample the dark area exhibits colonization by blue stain fungi. There are few larval mines in this portion of the sample, and those that exist are long and winding with little evidence of complete larval development. (photograph by F.M. Stephen)

Figure 4.15—A photograph of the inner bark surface (phloem) showing normal SPB egg galleries with short larval mines culminating in broad feeding cells where pupation occurs. Because the pupae have moved from the phloem toward the outer bark, no SPB life stages can be seen on the sample. (photograph by F.M. Stephen)

Texas, under favorable conditions seven to eight generations could be completed in a single year. Field investigations have attempted to characterize larval development as a function of temperature, with estimates of development time from 10 to 63 days (Fronk 1947, Mizell and Nebeker 1978, Thatcher and Pickard 1967). Despite difficulties in rearing larvae, detailed laboratory studies in which beetles were held at a series of constant temperatures (Wagner and others 1984a) enabled construction of models that can accurately predict larval development as a function of temperature. Predicted larval development ranged from 61 days at a low temperature of 12.5 ºC to the fastest time of approximately 14.3 days at approximately 27 ºC, with a significant slowing of development at hotter temperatures, while the maximum temperature at which larval development can proceed was 33.6 ºC. In the laboratory, larvae failed to pupate at constant low temperatures of 10 ºC and at temperatures of 33 ºC and above (Wagner and others 1984a).

4.6.2. Density

Density of SPB larvae and pupae has been estimated for within-tree populations in multiple studies (Gagne and others 1981, Stephen and Taha 1979b). Frequency distributions of several hundred 1 dm^2 samples provide a good estimate of the variability in density found in 1st stage (Figure 4.16) and late stage SPB immatures (Figure 4.17). The data presented in these figures are from 181 trees sampled in 17 infestations at six geographically separated locations in southeast Arkansas between 1975 and 1977. During 1975 area-wide populations were increasing, with an outbreak peak in 1976 and populations severely declining in 1977, thus providing examples of densities from diverse populations. The distribution of 1st stage larvae (Figure 4.16) is near normal, with a mean of approximately 130 larvae/dm^2 sample. Confidence intervals of 95 percent around this

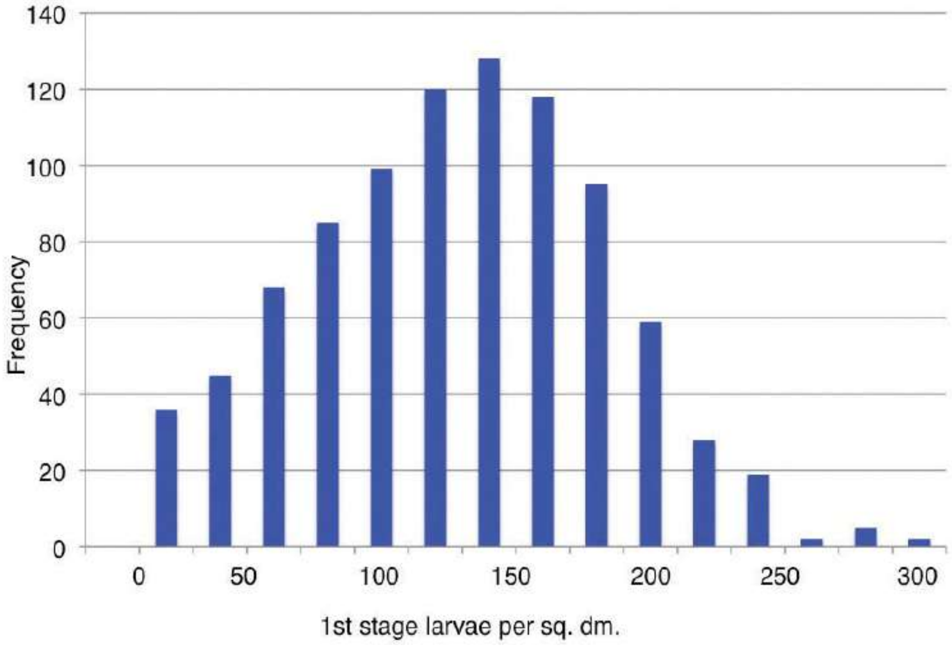


Figure 4.16—Distribution of SPB 1st instar larvae, determined by gallery dissection, per dm^2 bark sample unit. Mean 1st instar larval density is 129.88 ± 5.55 (SE). Data from 909 samples from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977. (illustration from Stephen and Taha 1976, 1979a, 1979b)

mean enclose values from approximately 119 to 141/dm^2. Late stage immatures (Figure 4.17) include 3rd and 4th stage larvae and also pupae, as separation of these life stages within bark/phloem samples is difficult. The frequency distribution of late stage immatures deviates more from a normal curve than does the distribution of 1st stage immatures, possibly as a result of differential mortality to populations at higher densities. The mean value of late stage immatures is approximately 34/dm^2, with confidence interval estimates ranging from approximately 31 to 37/dm^2.

4.6.3. Mortality Factors

One of the greatest challenges facing researchers investigating SPB population dynamics is accurate estimation of the different factors that kill beetle life stages in the cryptic environment beneath the bark. Mortality agents to stages of SPB occurring within trees are known to include abiotic factors such as oleoresin (e.g., toxicity, flow rate, and crystallization), heat, cold, and moisture. The effects of these factors can be modified by the host tree and by climate or weather acting upon that tree. Biotic mortality agents are insect predators, parasitoids, and competitors, plus mites, nematodes, fungi, and birds.

Multiple authors have listed natural enemy species that are confirmed or believed to be predaceous or parasitic on immature SPB (Berisford 1980, Dahlsten 1982, Dixon and Payne 1979b, Franklin 1969, Fronk 1947, Massey 1974, Moser 1975, Moser and others 1971, Overgaard 1968, Thatcher 1960, Stephen and others 1989, 1993), and many other publications list natural enemies that are found with *Ips* species and probably also attack the SPB. The difficulty is not in creating lists of natural enemies (although in many cases we are uncertain of the host specificity of these species), but rather in being able to assign accurate quantitative estimates of mortality to these individual species. Life tables (Southwood and Henderson 2000) remain an excellent way in which to characterize the amount of mortality occurring at different life stages and also to identify causal agents and the variation in that mortality that may occur through time and in different forest stands or geographic locations. No complete life tables have been created for SPB populations, and stage-specific mortality estimates that quantify variability in mortality, seasonal changes in mortality agents, or variation in mortality associated with different trend trajectories, such as increasing and decreasing regional population levels, do not exist.

Although their most valuable attributes arise when multiple life tables are created to illustrate changing stage-specific mortality, average or summary life tables do allow a general examination as to where mortality does occur throughout an organism's life span. A very general summary life table, derived from estimates of mean density for the SPB (Table 4.1), shows average density and mortality to eggs, 1st stage larvae, larvae/pupae, and emerging adults based upon the data presented by Stephen and Taha (1979b). Apparent mortality, that mortality within a stage that

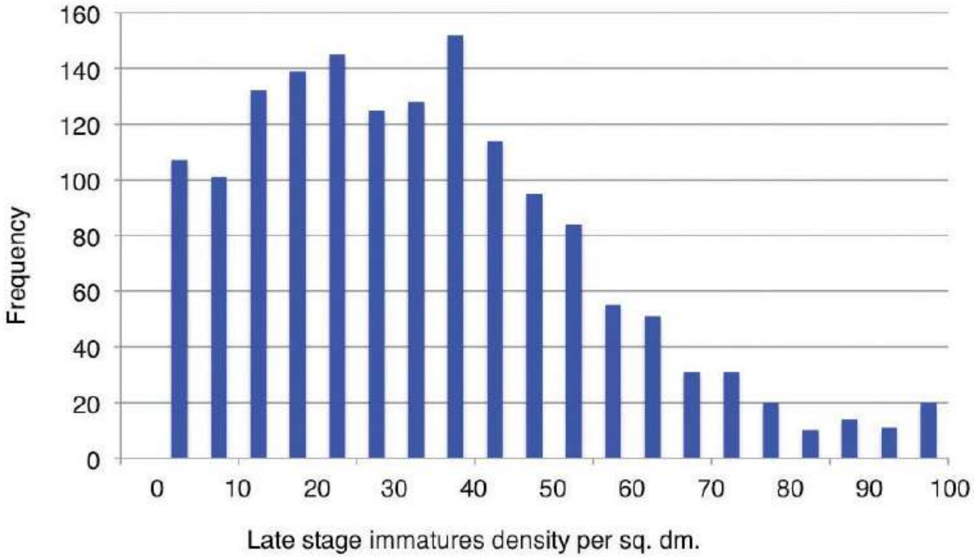


Figure 4.17—Distribution of SPB late stage immatures (larvae and pupae), determined by radiograph examination and bark sample dissection, per 1 dm^2 bark sample unit. Mean late stage immature density is 34.06 ± 1.25 (SE), and the data are skewed to the right. Data from 1,565 samples from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977. (illustration from Stephen and Taha 1976, 1979a, 1979b)

Table 4.1—Average mortality table for within tree SPB based on data from Stephen and Taha (1979a). Average density (per dm^2) and mortality are presented for SPB eggs, 1st stage larvae, late stage larvae/pupae, and emerging adults. Also shown are calculated apparent and real mortality for these stages and generation mortality. (see text for further explanation)

SPB life stage	No./dm^2 entering life stage	No./dm^2 dying during life stage	% apparent mortality	% real mortality
Eggs	135.7	5.8	4.30%	4.30%
1st stage larvae	129.9	95.8	73.70%	70.60%
Last stage larvae/pupae	34.1	14.5	42.50%	10.70%
Emerging adults	19.6			
Generation mortality				85.60%

is based upon the number entering the stage, helps to visualize those life stages in which greater or lesser amounts of mortality occur. Real mortality, based upon the initial number of individuals (eggs) at the start of life, is additive and when summed provides a measure of total, or generation mortality. The generation mortality calculated (85.6 percent) (Table 4.1) is low and may reflect a very rapidly growing bark beetle population, or high mortality to adults moving between trees, or a combination of both.

Challenge of Estimating the Amount and Causes of Mortality

As alluded to above it is a difficult challenge to accurately estimate the density of SPB immatures in the cryptic environment they inhabit beneath the bark, and numerous authors have published techniques to enable proper sampling of these insects (Coulson and others 1975b, 1979a; Hain and others 1978; Linit and Stephen 1978; McClelland and others 1978; 1979; Nebeker and others 1978a; Pulley and others 1977; Stephen and Taha 1976, 1979a). It is safe to state that it is considerably more difficult to accurately estimate densities of natural enemies of bark beetles than it is the beetles themselves. Even sampling to estimate different life stages of the SPB is challenging as dispersion of attacks, eggs, and emerging adults can all differ, and more samples are required to measure emerging beetles than to measure attacking beetles (Stephen and Taha 1976). Because natural enemies can be highly aggregated in relation to their bark beetle hosts, the number of samples and/or size of the sample area must often be greater to assess natural enemies than it is required for bark beetles (Stephen and Taha 1976).

A further problem in determining mortality to bark beetles within trees is the fact that the process of predator and parasitoid arrival and colonization of bark beetle-infested trees is dynamic (Dixon and Payne 1979b, Stephen and Dahlsten 1976). This means that bark samples removed from trees to measure bark beetle immatures may not yet reflect the mortality from agents that colonize these trees later in the development cycle. Also, the distribution of bark beetle life stages within trees is not uniform from base to top of infestation, and bark samples taken to estimate beetle larvae and pupae (plus predators and parasitoids) at mid-bole may be entirely too early to provide similar estimates above and below the mid-bole region (Figure 4.11). In a similar manner, sampling for brood adults might be appropriate at lower and upper regions of the bole, but if samples are taken at mid-bole the SPB may have emerged, and estimates of its natural enemies will also be erroneous (Figure 4.11). Suffice it to say that timing of sample collection, as well as number and size of samples used to estimate within-tree SPB populations and their natural mortality agents, is an extremely complicated task, and this explains, in part, why so little quantitative information is available on amounts and causes of stage-specific SPB mortality.

In addition to challenges of aggregation patterns changing during the beetles' life history and the dynamic colonization process occurring along the infested tree bole, a further obstacle to measuring beetle numbers and mortality is the difficulty of accurately seeing numbers of some life stages on the inner-bark face of the samples that are removed from infested trees (Figure 4.15). Examination of this figure reveals adult galleries, some larval mines, and some pupal cells, but no SPB larvae or pupae can be seen. Dissection of bark samples can locate some life stages but is not completely accurate and is destructive to the samples. A preferred technique involves radiography of the infested bark (Berryman and Stark 1962, DeMars 1963, Nebeker 1981). A partial bark sample radiograph, also termed x-ray (Figure 4.18), provides a good example of the diversity of SPB life stages and the natural enemies that prey on them. In this magnified image, dark parent adult egg galleries can be seen, and SPB pupae and brood adults are visible in their pupal chambers. Also evident are empty pupal cells (possibly from predation), parasitoid immatures in pupal cells (which have consumed their host bark beetle), and dead SPB in various stages of decomposition. A dipteran predator (not in a pupal cell) is visible in the left central section of the image.

Predators

The composition of predator species that attack bark beetles in the genus *Dendroctonus* is fairly constant among the different bark beetle species (Stephen and others 1993). The primary insect orders that contain species predaceous on SPB are Coleoptera, Hemiptera, and Diptera. Multiple authors have published lists categorizing these bark beetle predators (Berisford 1980, Linit and Stephen 1983, Moser and others 1971, Overgaard 1968, Stephen and others 1989, Thatcher 1960).

Predators normally cause greater mortality to within-tree immature populations of the SPB than do parasitoids (Linit and Stephen 1983). The extent of predation by individual species is generally unknown; however, through exclusion, Linit and Stephen (1983) estimated an average density of 4.4 predators/dm^2, and further estimated that each predator destroyed approximately three prey. In another study predator-caused mortality was reported to be 15 percent of the SPB population (Moore 1972). There are predator species that, by most authors, are considered of primary importance because of their abundance, their feeding habits, their ability to respond to SPB or *Ips* pheromones or to host odors, or because of their synchrony with SPB life cycle. Chapter 10 provides an in-depth discussion of predation and its role in SPB population dynamics.

Thanasimus dubius (Fabricius) (Coleoptera: Cleridae) is often considered to be the most significant predator of the SPB (Mignot and Anderson 1969, Nebeker and Mizell 1980, Reeve 1997, Thatcher and Pickard 1966).

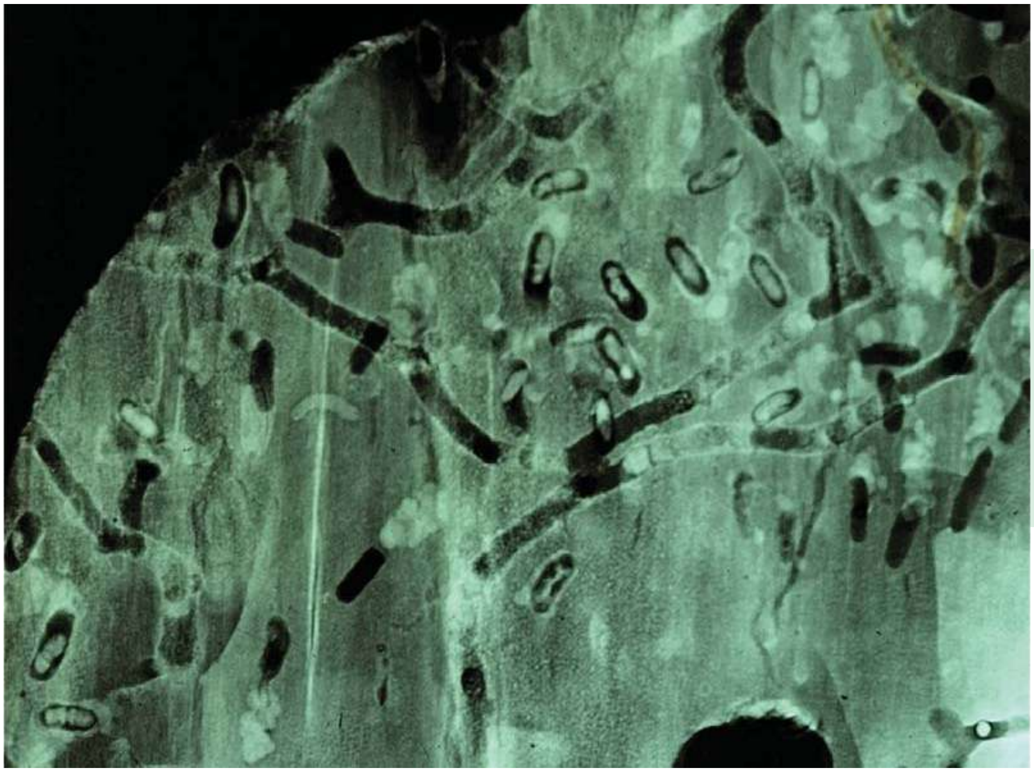


Figure 4.18—Radiograph (x-ray) of a partial bark sample containing late stage immature *D. frontalis*, parasitoids, and predators, plus dead beetles and empty pupal cells. (photograph by F.M. Stephen)

Owing to the ability of *T. dubius* adults to detect and respond to SPB pheromones, the adult clerid beetles arrive and prey on adult SPB adults during mass attack (Dixon and Payne 1979a , Thatcher and Pickard 1966, Vité and Williamson 1970). The clerid adults also oviposit on infested trees, and their developing larvae prey on SPB and other immature insects beneath the bark. One estimate suggests that *T. dubius* predation results in approximately 13 percent mortality to SPB populations (Moore 1972).

Other coleopterans that are listed as common predators of SPB include *Nudobius cephalus* Say (Staphylinidae), *Temnochila virescens* (F.) and *Tenebroides* spp. (Trogositidae), *Cylistix* spp. and *Platysoma parallelum* LeC. and *Plegaderus* spp. (Histeridae), plus *Aulonium* spp. and *Lasconotus* spp. (Colydiidae), and *Corticeus* spp. (Tenebrionidae) are included as facultative predators (Berisford 1980, Linit and Stephen 1983, Moser and others 1971). Common predators often found in abundance with SPB include true bugs, the sucking insects *Lyctocoris elongatus* (Reuter) and *Scoloposcelis mississippensis* (Drake and Harris) (Hemiptera: Anthocoridae) (Linit and Stephen 1983, Moser and others 1971). Another predator that is reported as one of the most abundant collected, yet whose contributions to mortality are poorly understood, is the long-legged fly *Medetera bistriata* Parent (Diptera: Dolichopodidae) (Linit and Stephen 1983, Moser and others 1971).

Mites are common and abundant associates of SPB (Moser and Roton 1971) and clearly play an important role in its population dynamics (Klepzig and others 2001a, Lombardero and others 2000c). Moser (1975) tested 51 candidate mite species and determined that 31 of these species are predators of SPB. Most predation favored 1st instars, followed by eggs, late instars, and pupae. Adult SPBs were not attacked. Many of the extensive complex of mite associates of SPB are not predaceous and have little or no effect on the beetle; however, as more is learned about the complex of mites and fungi that are found with the SPB it seems clear that linked interactions exist that may be important in driving the population fluctuations characteristic of this species (Hofstetter and others 2006a).

Invertebrates are not the only predators that potentially influence within-tree populations of SPB. Woodpeckers have long been recognized as important mortality agents to beetles developing within trees (Hopkins 1899). The main species that are predators of SPB are downy woodpecker *Picoides pubescens*, hairy woodpecker *Picoides villosus*, and pileated woodpecker *Dryocopus pileatus* (Kroll and Fleet 1979, Kroll and others 1980). Woodpeckers flake bark from SPB-infested trees to expose the beetle immatures. Late-stage larvae, pupae, and brood adults are likely preferred life stages, and in terms of percent mortality to SPB, woodpeckers are second only to clerid beetles in the amount recorded (Moore 1972). Woodpeckers also forage on other bark beetle associates, with preference for Cerambycidae such as the southern pine sawyer, *Monochamus titillator* (F.) (Drumtra 1997).

Parasitoids

A complex of hymenopteran parasitoid species is found attacking late stage SPB immatures within infested trees. Bark beetle parasitoids often attack more than one species and even different genera of bark beetle hosts, for example *Ips* and *Dendroctonus* (Berisford 1974b, Stephen and others 1993). Multiple authors have compiled lists of bark beetle parasitoids that have been reared from SPB-infested bark (Berisford 1980, Franklin 1969, Goyer and Finger 1980, Linit and Stephen 1983, Moser and others 1971, Overgaard 1968, Stephen and others 1993), and most report six to eight species as being most commonly found. Within-tree samples taken from 72 separate infestations over a 17-year span beginning in 1975 showed that eight parasitoid species were nearly always present, being collected from 63 to 94 percent of all of these infestations (Stephen and others 1997). The most common and abundant parasitoids collected from bark samples containing the SPB were Hymenoptera in the family Braconidae *Coeloides pissodis* (Ashmead), *Dendrosoter sulcatus* Muesbeck, *Spathius pallidus* Ashmead, *Meteorus* spp. prob. *hypophloei* Cushman, and in the superfamily Chalcidoidea family Torymidae *Roptrocerus xylophagorum* Ratzeburg, family Pteromalidae *Dinotiscus dendroctoni* (Ashmead), and *Heydenia unica* Cook and Davis, and family Eurytomidae *Eurytoma* species (possibly a hyperparasitoid). More information on each of these species and additional parasitoids is found in chapter 8.

Despite the abundance of collections of these species, little has been published that indicates parasitoids are able to regulate SPB populations. An estimate of 1.9 parasitoids/dm^2 was reported for Louisiana (Goyer and Finger 1980). Through natural enemy exclusion and subsequent within-tree sampling, Linit and Stephen (1983) estimated that on average 2.1-4.6 parasitoids/dm^2 were found in studies in Arkansas and Georgia. During studies of SPB populations that were expanding, epidemic, and returning to low endemic levels, the respective density of parasitoids in those populations was reported at 3.5, 5.4, and 8.6/dm^2 (Stephen and others 1989). Few studies have monitored either parasitoid density or the mortality attributable to those parasitoids. An exception is a 2-year study conducted in East Texas from February 1991 to May 1992 in which an infestation was followed over time and infested bark periodically collected and analyzed to estimate SPB and parasitoid densities within the sampled trees (Stephen and others 1997). They suggest that although parasitoid numbers tracked the increases and decreases in SPB numbers over time, percent parasitism did not, and averaged 5-6 percent, never exceeding 10 percent. A hypothesis has been developed as to why parasitoids may not be responding effectively to changes in host density, and the argument made that with sufficient nutrition for adult female parasitoids, longevity and fecundity can be increased, and biological control of the SPB may be achieved (Stephen 1995, Stephen and others 1997).

Competitors

The biology and impact of competitors, those scolytids and cerambycids that compete for the phloem that becomes available when a tree is killed by the SPB, is discussed in chapter 12. Successful SPB mass attack means that phloem of the newly colonized tree becomes immediately available to a complex of bark beetles and long-horned beetles, all of which compete for the new resource. In addition to the SPB, bark beetles in the genus *Ips*, *I. avulsus, I. grandicollis*, and *I. calligraphus*, as well as the black turpentine beetle, *D. terebrans,* may be colonizers and competitors. In addition to these scolytid beetles, long-horned (cerambycid) beetles of several species, the most important being the pine sawyers (*Monochamus* spp.), also compete for their larval feeding sites in this temporarily available community. Because aggregation pheromones are signals used by most of the bark beetles to locate and exploit the limited food source comprised by this newly found tree, it is likely that both intra- and interspecific competition among those arriving individuals will develop (Raffa 2001). As competition can negatively affect the fitness of all individuals, mechanisms to avoid or minimize competition will evolve. For the bark beetles these mechanisms include their systems of chemical communication expressed through differences in timing and rate of arrival, variation in body size and ability to use thicker and thinner phloem, and gallery structure, oviposition, and larval feeding habits. When bark beetle and *Monochamus* larvae compete, the competition is highly asymmetric, meaning that *Monochamus* is not affected by the presence of the bark beetles, which can be greatly disadvantaged by the feeding of the much larger cerambycid larvae (chapter 12). In addition to consuming phloem, *Monochamus* larvae have been documented killing and eating SPB larvae when they encounter them (Dodds and others 2001). This provides additional nitrogen for the developing *Monochamus* and may hasten their larval development. Despite considerable research to document the existence of competition throughout the processes of attack, reemergence, oviposition and larval development, the larger question of how competition influences SPB population dynamics remains uncertain.

Fungi

Three species of fungi are intimately associated with the SPB and have significant impact on its within-tree development and reproduction (Ayres and others 2000, Barras 1973, Bridges 1983, Goldhammer and others 1990, Klepzig and others 2001a). *Entomocorticium* sp. A (an undescribed basidiomycete, formerly referred to as isolate SJB122) and *Ceratocystiopsis ranaculosus* Perry and Bridges, are fungal species carried and nurtured in specialized chambers (mycangia) in the pronotal areas of female SPBs (Klepzig and others 2001b) that are inoculated into phloem during gallery construction, and as these fungi grow, they are fed upon by developing larvae and are beneficial to bark beetle growth and reproduction (Ayres and others 2000, Goldhammer and others 1990). *Ophiostoma minus* (Hedgc.) H. and P. Sydow, is an ascomycetous fungus carried on the exoskeleton of the beetle and by phoretic mites (Bridges and Moser 1983). This fungus is highly visible, causing "blue stain" in infected wood, and is antagonistic to developing SPB larvae (Barras 1970). Comparison of larval growth and development in regions of phloem with mycangial fungi vs. phloem colonized by blue stain fungi (Figure 4.14) graphically illustrates the effect of these different fungi on beetle development. Sorting out the complexity of interrelationships among coexisting fungi, mites, and SPB is an exciting area of research that has been the focus of much recent interest (see chapters 9 and 11).

Heat and Cold

Cold temperatures have long been implicated as important in SPB population dynamics (Hopkins 1899), and low temperatures can be a significant mortality factor to within-tree populations of SPB immatures and adults (Beal 1933). McClelland and Hain (1979) found differential survival of larvae during winters that were relatively mild or severe in North Carolina. Nearly 100 percent brood mortality occurred during a severe winter during which low temperatures ranged from -7 ^{o}C to -19 ^{o}C.

Interaction of moisture and temperature affects larval survival, as larvae in phloem were killed upon exposure to -12 ^{o}C for short periods of time, whereas at the same temperature, larvae in the outer bark with lower moisture survived (Beal 1933). More recent studies established a supercooling point at which larval mortality occurred at about -13 ^{o}C in October and November, and about -9 ^{o}C in March (Lombardero and others 2000a). However, research with 4th instars (prepupae) in the outer bark (Tran and others 2007) found a lower supercooling point, averaging -14.6 ^{o}C, and extending to as low as -19.9 ^{o}C, perhaps supporting Beal's (1933) observations.

Models of SPB development as a function of temperature have been developed (Wagner and others 1979). For larvae, shortest development time was at 30 ^{o}C, at which development was completed in approximately 12.8 days. The range of constant temperatures at which larval development could be completed extended from 10 ^{o}C to 33.6 ^{o}C. From their model, Wagner and others (1979) concluded that the shortest time for pupal development was approximately 4.4 days at 30 ^{o}C.

Changes in phloem moisture may influence successful larval development. In loblolly pine, phloem moisture on average decreases immediately following attack but increases about 30 days post-attack and may be a mortality factor to late-stage larvae (Webb and Franklin 1978). Wagner and others (1979) found that phloem moisture began to decrease after attack and continued to decrease until the pupal and callow adult stage, at which time rehydration began to occur. The primary effect of moisture was seen as delaying larval development during the 2nd and 3rd stages when moisture was too high or too low. Development of 4th stage larvae and pupae was slower in trees that exhibited high bark moisture during those stages (Wagner and others 1979).

4.7. EMERGING BROOD ADULTS

Estimates of SPB emerging brood adult densities vary greatly (Gagne and others 1981, Stephen and Taha 1979b). Among the earliest estimates are those of MacAndrews (1926), who reported an average beetle emergence density of about 300 per square feet (equivalent to 32.3/dm^2) from pines near Asheville, NC. In later studies between 1975 and 1977 from three populations in North Carolina described as low-level, estimates of brood emergence density varied from 5.2 to 8.6 adults/dm^2 (Hain and McClelland 1979). They also reported that in 1978 when regional beetle populations had begun to expand, comparing expanding vs. nonexpanding infestation spots yielded estimates of 11.6 adults/dm^2 vs. 8.3 adults/dm^2 respectively (Hain and McClelland 1979). In a model of emerging adult density in Texas, as a function of normalized height on infested trees, maximum average emergence density was reported as about 12 adults/dm^2 (Mayyasi and others 1976a). A different modeling approach (Reeve and others 1998) resulted in estimates of from about 23 to 46 emerging adults/dm^2 at optimal attack densities (4-5 attacks/dm^2).

Data collected from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977 yielded a frequency distribution of emerging adults (Figure 4.19) that shows the increasing deviation from the rather normally distributed egg density estimates (Figure 4.13) of the same data set (Stephen and Taha 1979b). The mean value of emerging adults (22.8 adult/dm^2) is generally lower than reported by MacAndrews (1926) or that predicted from the higher estimates of Reeve and colleagues (1998), but higher than values reported by Hain and McClelland (1979) or Mayyasi and others (1976a). The skewed distribution in Figure 4.19 does show the great variation in emergence, and that many samples collected from the Arkansas infestations are equivalent to the values reported from the other studies.

Evaluation of the sex ratio of emerging brood confirms a 1:1 ratio of males to females (Coulson and others 1979b). The process of brood emergence is similar in pattern to that of attack and reemergence, with highest density of emerging beetles per day (approximately five) occurring at about 3.5 m up the infested bole (Coulson and others 1979b). The process of attack and colonization is not uniform in time (Fargo and others 1979) (Figure 4.2), resulting in brood emergence frequently beginning in the mid-bole region of the tree while brood adults (or earlier life stages) remain above and below (Figure 4.11). The temperature-dependent process of emergence extends over a rather long period of time, estimated at 28 days by Coulson and others (1979b).

4.8. CONCLUSIONS

Literally hundreds of published studies document aspects of biology of the SPB within trees. From the astute observations of Hopkins (1899) 110 years ago to the present, scientists remain fascinated by the processes of mass attack, gallery construction and oviposition, adult reemergence, eclosion, and development of larvae, pupae, and brood adults in the cryptic environment beneath the bark of infested pines. Although researchers have learned a remarkable amount about all aspects of the life of this beetle within trees, there remains even more that is still elusive. We know that the threshold density of beetles needed to overcome the resistance of a tree is dynamic. It must be a property of the tree and its intrinsic health and resistance, plus the population of bark beetles that is able to gather for mass attack. We suspect that mortality to the attacking adult population, for example by *T. dubius* predation, is important, but we don't know if that can keep a tree from being successfully mass-attacked. We know that pine tree resistance to beetle and fungal invasion involves both a preformed resin system and induced hypersensitive response, but the impact of these resistance mechanisms on actual life stages of beetles within trees remains undefined. We know that when pines are successfully attacked, SPBs and associates vector a fungal complement that is critical to the rate of increase of the beetle population that will develop in that tree. Much new information is emerging about these symbiotic and antagonistic relationships; however, much is still unknown.

Researchers have shown that attacking SPBs colonize the mid-bole portions of the tree first and then spread up and down from there, and that this dynamic process results in different beetle life stages being found at the same time at different heights within trees. Remarkably complex chemical communication coupled with behavior enables SPB adults to regulate their attack density as trees are colonized. Intensive sampling yields an average of slightly less than 5 attacks/dm^2, but this average is variable. The amount of gallery length and oviposition is also influenced by the beetles' own density, and variation in gallery length and egg density is considerable. Following

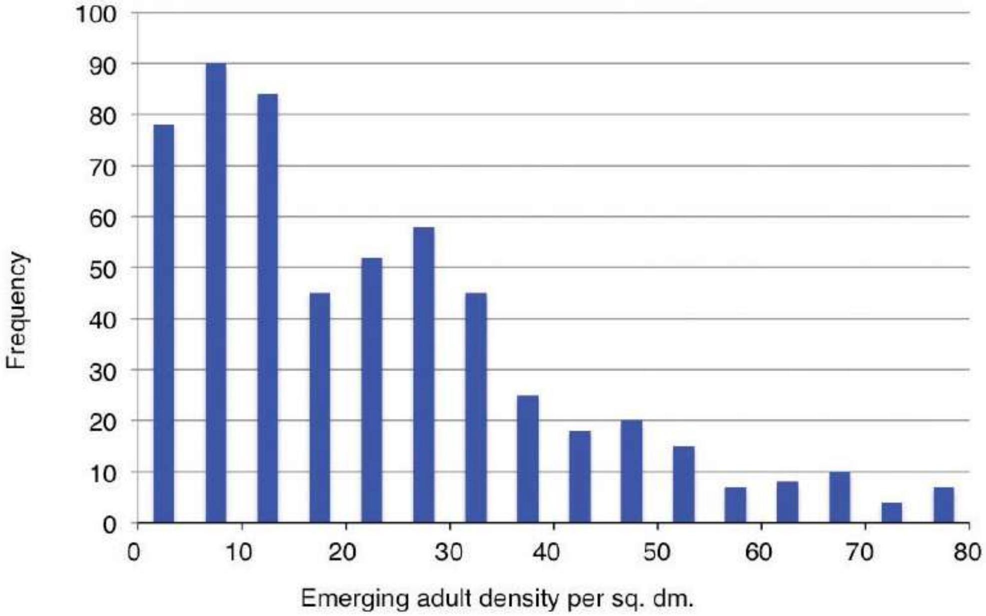


Figure 4.19—Distribution of emerging SPB adults, determined by collection of on-tree emergence traps, per 1 dm^2 bark sample unit. Mean emerging adult density is 22.82 ± 1.59 (SE) and count data are skewed to the right. Data from 566 samples from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977. (illustration from Stephen and Taha 1976, 1979a, 1979b)

oviposition a high proportion of parent adults reemerge and are capable of responding to and producing pheromones, and it is known that reemerged adults can be equally or more fecund than newly emerging brood. Female oviposition along the margins of their galleries has yielded estimates of eggs per cm of gallery, but those relationships appear more dynamic than originally believed. Most egg niches contain eggs, and egg mortality is usually fairly low. Temperature drives the processes of gallery construction, oviposition, reemergence, and brood development, and careful research has enabled description of these relationships. Development of young larvae is negatively affected by blue stain fungi, but positively influenced by presence of mycangial fungi, which enhance acquisition of nitrogen required for larval development.

We have mapped the sequence of arrival of SPB and also its predators, parasitoids, and competitors to newly infested trees. Detailed lists of SPB associates and their putative roles have been published. We now know that predators, parasitoids, and competitors are much more than background noise, and are in fact a primary reason why infestations grow or decline. However, the impact and role of individual species is very poorly understood, and the biology and population dynamics of most remain a mystery. Sampling within-tree populations of larvae and pupae and accurately assessing their density plus the factors that cause mortality remains a challenge, but one that has been addressed. No complete life table studies have been created for SPB, but average densities at key points in the life history have been estimated and average mortality determined. Bark beetle predators and parasitoids are generally not species-specific in their feeding preferences, but a predictable complex of predators, parasitoids, and competitors is known. Less is known about their role during different trajectories of SPB population change.

Exhaustive research published from the early 1970s into the 1980s involved intensive field sampling of populations of SPB within trees. Much of this research was supported under the auspices of the Expanded Southern Pine Beetle Research and Application Program (ESPBRAP). Many of these studies were predicated on the idea that climbing standing trees and sampling these insects *in situ* was essential. The data sets collected during this period are unique and could prove remarkably valuable to future examination of within-tree SPB populations. Efforts to preserve these data must be made, because whether it is a problem of labor or expense, or the danger of tree climbing is considered too great, studies published in the last 20 years rarely involve intensive field sampling that is conducted high on the bole of infested trees. The legal questions associated with graduate students and technicians climbing 25 m into the crown of infested pines may preclude large quantities of such data ever again being collected. Perhaps the largest of these within-tree data sets were collected under the leadership of F. M. Stephen at the University of Arkansas (approximately 6,000 samples collected from 643 trees, from 35 infestations in five States over 12 years) and R. N. Coulson at Texas A&M University, with a comparable data set collected from 1971 to 1984 in East Texas. Other researchers collected SPB within-tree population information by climbing standing trees, including F. P. Hain at North Carolina State University, who conducted such investigations from 1975 until 1978, and T. E. Nebeker at Mississippi State University, who also sampled from the mid-1970s to about 1980. It would be of great benefit if these data sets could be accessible to future generations of scientists who are exploring the life history and biology of SPB within trees.

5

Southern Pine Beetle Ecology: Populations within Stands

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Abstract

Populations of southern pine beetle (SPB) are typically substructured into local aggregations, each with tens of thousands of individual beetles. These aggregations, known as "spots" because of their appearance during aerial surveys, are the basic unit for the monitoring and management of SPB populations in forested regions. They typically have a maximum lifespan of 1 year, being born in the spring when dispersing SPB aggregate at points in the forest. Spots that survive to the following spring produce the dispersing beetles that form a new population of spots. SPB epidemics rise and fall with interannual variation in the number of spots within a region. Many spots, especially those that begin small, die an early death by midsummer. Others may grow throughout the summer and into the winter via a self-propagating progression of tree attacks that is critically structured by semiochemicals. Forces that influence the growth of populations within spots strongly influence the dynamic fluctuations in SPB impacts on regional forests. These forces include pine species composition, habitat edges, age and basal area of pine stands, tree defenses, the predator *Thanasimus dubius*, interactions with phoretic mites and fungi, climate, and movement of beetles into and out of spots.

5.1. THE SOUTHERN PINE BEETLE AS A POPULATION OF SPOTS

The demographic structure of southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) populations is hierarchical (Coulson 1979). As with any population, the direction and rate of change in abundance is determined by the birth rate and death rate of individuals. However, for most of the year SPB populations tend to be substructured into local, semiautonomous aggregations that can be recognized from an airplane as "spots" in the forest where trees are dying and the crowns are changing color (Billings and Ward 1984). In the Southeastern United States, where they have been most studied, these spots tend to have an annual life cycle, typically being "born" in the spring when dispersing beetles aggregate to form local infestations and generally surviving no longer than spring of the next year (≈ 3–5 generations) when beetles disperse and new aggregations can be formed. Thus, some essential properties of SPB populations can be characterized in terms of the birth rate and death rate of spots. SPB abundance in a landscape grows when there are more spots in one year than the previous year. Most simply this can be understood as the population of spots producing more dispersing beetles in one spring than was required to initiate them the previous spring. The Southern Pine Beetle Information System of the USDA Forest Service (SPBIS) monitors populations via systematic aerial surveys for spots followed by inspection on the ground. Management decisions (e.g., cut-and-remove suppression tactic vs. monitoring) are typically applied on a spot-by-spot basis within a forest. Hence, there are both theoretical and practical reasons for understanding the demographics of beetle spots. Accordingly, there have been scores of technical scientific papers that address the factors influencing the biology of SPB spots. What determines the number and location of spots that are formed in the spring? What determines the growth of beetle populations within spots and therefore the number of trees that are eventually killed by any particular aggregation if left untreated? Finally, what determines whether any particular spot will sustain beetle reproduction throughout the upcoming year to produce dispersing beetles the following the spring?

5.2. HOW BEETLES TURN INTO SPOTS

Local aggregations of beetles, or spots, are usually started during spring when beetles disperse out of last year's spots and employ pheromones to aggregate in mass attacks of host trees at new points within the forest. Spring dispersal flights in the Southeastern United States are thought to peak at about the time as dogwood (*Cornus florida*) flowers (March to April). Not surprisingly, there is a positive relationship between the abundance of dispersing beetles in spring, as measured by pheromone-baited traps, and the number of beetle spots that subsequently appear in the summer (Billings 1988, Billings and Upton 2002). However, the average number of spots formed increases more than linearly with the abundance of dispersing beetles, presumably because aggregation efficacy increases more than linearly with abundance (Martinson 2007). This is an example of positive demographic feedback ("Allee effect" or positive density-dependence; Berryman 2003, Turchin 2003), which is intrinsically destabilizing to population dynamics (promotes outbreaks and crashes), so the effect of disperser abundance on spot formation presumably contributes to forest pestilence from SPB. The location of new spots within forests is partly nonrandom, but also appears to have a large component of stochasticity. In forests with a mix of loblolly and longleaf pine, spots are 3-18 times more likely to form in loblolly pine than in an equal area of longleaf stands, and the frequency of spots/km^2 of loblolly forest is disproportionately high in stands that are about 25-35 years of age, and are more frequent in some soil types than others (Friedenberg and others 2007b, Lorio and Sommers 1985, Zarnoch and others 1984). However, it is not presently possible to accurately predict which particular pine stands will develop SPB spots in a particular year, and probably never will be (the stochastic component). It is common for spots to form around a pine tree that has recently been hit by lightning (Coulson and others 1983, 1986; Ku and others 1980b; Rykiel and others 1988). Of 1,904 spots that were systematically ground checked in the Kisatchie National Forest, 51 percent contained a lightning-struck tree near where the spot began (Mason and others 1985). The conventional wisdom is that dispersing SPB initially orient towards volatiles released as a result of the lightning strike, and that the pheromones produced by the first-arriving beetles synergize the attractiveness for additional beetles that produce more aggregation pheromones, fueling a positive feedback that can attract thousands or tens of thousands more beetles over the next days to weeks (Blanche and others 1985, Hodges and Pickard 1971). Lightning strikes can be very numerous in these forests, and it may be largely chance which ones happen to trigger a cascade of attacking SPB (Coulson and others 1999b, Lovelady and others 1991). It is not known what causes the initiation of the many other spots that are not associated with a lightning-struck tree, but it apparently requires very little to trigger the process of spot formation during spring in a forest with abundant SPB. Captures of dispersing SPB during the spring are quite uniform in space at the scale of a National Forest Ranger District and in forests with high SPB abundance.The deployment of even small amounts of SPB pheromone in the spring can trigger the formation of spots that quickly become self-propagating almost anywhere there are pine trees (Friedenberg and others 2007b).

5.3. THE EARLY LIFE OF SPB SPOTS

Because spots are nearly impossible to detect until the first-attacked trees die and their crowns turn red, there have been almost no direct observations of SPB biology during the first 6-8 weeks in the life of a spot. Thus our knowledge of the early life of spots is largely based on what can be inferred beginning about 2 months after the spots were initiated. The SPBIS includes records of the number of beetle-infested trees with red or green crowns at the time of ground inspection (Clarke and Billings 2003, Petty 2005). When the aerial surveys are regular and the ground inspections are conducted shortly after aerial detection, the number of red trees recorded in the SPBIS database can be taken as an estimate of the number of trees attacked by the SPB adults that immigrated into the spot as it was forming. From an analysis of about 26,000 such spots from national forests in 11 States of the Southeastern United States, the median initial size of the spots (red trees at time of detection) was 14, with 90 percent of spots falling within the range of 4 to 50 trees (Friedenberg and others 2007a). With attack densities in the mid-bole of about 10 beetles per dm^2, a tree that is 60 feet tall with 10-inch diameter represents 2,000-3,000 attacking adults (Coulson 1980), so a typical spot might represent the aggregation of 25,000-50,000 SPB adults, and large spots in stands with large trees must begin with aggregations of > 100,000 SPB.

Many spots, especially if they begin small, die an early natural death and therefore fail to contribute dispersing beetles to the population the following spring. Hedden and Billings (1979) reported natural local extinction in 100 percent of SPB spots in East Texas that began with fewer than 10 trees. Analyses of about 26,000 spots in the SPBIS database (encompassing national forests in 11 States over 20 years) indicated that about 35 percent of the smallest spots (4-5 red trees at detection) were already inactive (no new trees under attack) at the time that they were ground checked. Such spots very seldom become active again. In the same database, spots that began with about 25 trees were only inactive in 10 percent of the cases, and spots that began with 50 or more trees were inactive in <5 percent of the cases (Friedenberg and others 2007a). The effect of initial spot size on the probability of spot extinction is another source of destabilizing positive feedback in SPB population dynamics (larger initial population size promotes higher per capita growth rate of the population).

The susceptibility of small spots to extinction is presumably influenced by predation from the specialist predator *Thanasimus dubius* (Reeve 1997) and by the difficulty that small populations of attacking beetles have in overwhelming tree defenses (Berryman and others 1985). However, the strongest force may arise from small populations being more likely to experience a break in the continuity of new attacks. Spot growth is dependent on the successful attack of new trees at the periphery of previously attacked trees. The progeny of the first wave of attacking beetles join in the attack of new trees by detecting pheromone plumes released from those trees by attacking adult beetles that entered the tree within the last 7-10 days (Gara and others 1965, Pureswaran and others 2006). If the wave of attacks that initiated the spot was the product of relatively few beetles, it is more likely that there will be a break in the progression of new attacks; in which case there is no pheromone plume to organize the attack behavior of SPB adults that subsequently emerge, and their searching behavior is more likely to take them out of the immediate area of the spot to an uncertain fate elsewhere (Gara and Coster 1968, Gara and others 1965, Franklin 1970b). In support of this model, experimental removal of trees currently under attack—and therefore removal of the associated pheromone plume—can cause the local extinction of spots via undirected emigration of subsequently emerging SPB (Gara 1967). Further evidence for the generality of this mechanism comes from the observations of researchers and forest health personnel who report that spots that have become inactive—and subsequently remain inactive—frequently contain trees that are still producing thousands of newly developed SPB adults. Models of the progression of age distribution in local SPB populations show that temporal gaps in the abundance of adults are expected under realistic demographic scenarios, especially when the initial spot size is small and/or the waves of attacks that initiated the spot were quite synchronous (Friedenberg and others 2007a). This requirement of SPB spots for an uninterrupted progression of new attacks is the theoretical basis for the suppression tactic known as cut-and-leave (USDA 1987), which is essentially an operational version of the experiments reported by Gara (1967).

5.4. SPB SPOTS DURING MID- TO LATE SUMMER

5.4.1. Population Structure

If not suppressed (Clarke and Billings 2003), SPB spots that are still active in midsummer (green trees coming under attack) have a relatively high probability of continuing to grow in size during the remainder of the year and surviving to be a source of dispersing beetles the following spring. By this time the beetles that originated the attack in spring are dead, and subsequent growth of the spot reflects the pattern of new trees coming under attack, oviposition by attacking adults within those trees, and the development of new progeny that subsequently emerge as adults and join in further attacks (Coulson 1980; Coulson and others 1989; Feldman and others 1981a, 1981b; Lih and Stephen 1989; Lih and Stephen 1996). Although there may be some immigration of beetles from nearby spots (Cronin and others 1999), local demographics are thought to dominate population dynamics within spots for several more generations until the following spring (Coulson and others 1989; Fargo and others 1982, 1985; Martinson 2007; Thatcher and Pickard 1967; Ungerer and others 1999). The importance of local demographics was evident in studies by Martinson (2007) that revealed temporal waves of dominant cohorts progressing as predicted by physiological models from ovipositing adults to eggs, larvae, pupae, callow adults, and newly emerged adults (Fargo and others 1982; Wagner and others 1981a, 1984a, 1984b). The stage structure of populations within two spots in the Oakmulgee Ranger District tended to converge by late summer on a stable stage structure of approximately 48: 34: 6: 4: 8 for eggs: larvae: pupae: callow adults: and ovipositing adults (with total populations in each of ≈ 50,000 SPB). The population of adults that are attacking trees at any time is a mix of individuals that are attacking their first tree and those that have reemerged from attacks within at least one previous tree (Cooper and Stephen 1978, Coulson and others 1978, Franklin 1970b, Gagne and others 1982, Wagner and others 1981a, 1981b,1982). Based on dissection of the spermathecae, which permitted separation of virgin females attacking their first tree from previously mated females, Martinson (2007) estimated that 47-77 percent (depending on spot and the date) of female adults joining the attack of trees were previously mated, and therefore had previously entered at least one other tree.

5.4.2. Spatial Pattern of Spot Growth

By midsummer, the attack of new trees within active SPB spots typically becomes concentrated in one area along the periphery of previously attacked trees and acquires a head that begins to snake slowly through the pine forest (Coster and others 1977a, Franklin 1970b, Payne 1980, St. George and Beal 1929). Figures 5.1-5.3 contain visualizations of actual spot growth in three spots in which SPB landings on trees were monitored at 3-day intervals during mid- to late summer. SPB are remarkable in their ability to aggregate attacks on particular trees (Coster and Johnson 1979b). Landing rates on individual trees frequently exceeded 200 SPB adults $\cdot$ 600 cm^{-2} $\cdot$ 3 d^{-1}, which on these pulp-sized trees scaled up to ≈ 5000 landing SPB/day. (Note that these values greatly overestimate the number of flying SPB in the population because ≈ 60 percent of landing beetles quickly drop or fly from the tree, presumably to land somewhere else again; Bishir and others 2004) At the same time, most trees further than a few meters distant had zero landing beetles. The next tree to come under attack was almost always immediately adjacent to one or more trees that were already under attack (Gara and Coster 1968, Johnson and Coster 1978). During 48 days of observation, we observed 41 new trees come under attack —an average of 2.5 new trees per 3 days. In almost all cases, initial landings on a tree were quickly followed by mass attack involving tens of thousands of SPB landings over the next 10-14 days, followed soon thereafter by the death of the tree. During this continuing process, SPB adults are recruited into the pool of attacking adults as they emerge from the source tree in which they developed, which is generally within ≈ 50 m of the head of the spot (Pope and others 1980, Schowalter and others 1981b). Examination of a transect running from the head of the spot to the source trees typically reveals a spatial pattern matching the developmental progression, in which the resident SPB tend to be dominated by landing adults, then ovipositing adults and eggs, then young larvae, then late larvae and pupae, and finally callow adults and emerging adults (Coulson and others 1979b, 1980b; Fargo and others 1978). The pattern of spot growth gives little indication of favoring pine trees that are more or less suitable for SPB reproduction. Rather it appears that the next trees to get attacked were just those that happened to be in the wrong place. However, there is evidently some level of discrimination because the progeny of trees that appeared to escape attack have strikingly higher resin flow than the progeny of randomly selected mother trees, implying that the SPB sometimes avoid trees with a genetic tendency for high resin flow (Strom and others 2002).

The patterns of spot growth are structured by plumes of tree volatiles plus SPB pheromones that emanate from trees under active attack (Gara and others 1965, Payne 1980). Our appreciation for the complexity of this chemical and behavioral system has grown from the initial identification of frontalin as an aggregation pheromone (Renwick and Vité 1970), to the description of antiaggregation pheromones that can reduce attack rates on individual trees (Payne and others 1978), to our present recognition that SPB produce at least five different pheromones (Pureswaran and others 2008b), whose effects on SPB behavior depend upon total amounts, relative amounts, chirality, and possibly even relative spatial position (Sullivan and others 2007b). There has been a longstanding interest in the possibility that manipulation of pheromone signals could provide a means for controlling SPB damage by disrupting the normal patterns of tree attacks and spot growth, and some results have been promising, but no semiochemical-based tactics have yet been developed into generally practical operational techniques (Clarke and others 1999, Dickens and others 1992, Gara and others 1965, Payne and Billings 1989, Payne and others 1992, Salom and others 1995, Strom and others 2004, Sullivan and others 2007a, Watterson and others 1982).

5.4.3. Factors that Influence Population Growth Within Spots

Habitat Edges

SPB spots commonly die when the growing head encounters the edge of a pine stand, or even a fire lane or modest gap within the pine stand. This is presumably because the growth of the spot depends upon there being additional suitable host trees within a few meters of trees that are already under attack, perhaps because new attacks are a consequence of one or a few SPB making a mistake by initiating attacks and beginning to release aggregation pheromones on a tree that is close enough to fall within the pheromone plume of a tree under attack. It has been hypothesized that new attacks are initiated by "pioneer" beetles that have a behavioral predisposition for being the first to attack a tree. However, individual-based natural selection should discourage such behavior because early attacking beetles have low fitness relative to those that join attacks that have already begun, presumably because they typically encounter robust resin flow from healthy trees (Pureswaran and others 2006). Not surprisingly, there does not appear to be any group prescience in the direction of spot growth. That is, local populations do not appear to steer away from upcoming barriers to continued spot growth, such as the edge of a hardwood stand. A simple and perhaps satisfactory model for the orientation of spot growth is that the spot head begins to grow in a compass direction that is effectively random, perhaps influenced by stochastic patterns of air movement within the subcanopy that influence the shape and direction of pheromone plumes (Thistle and others 2004).

Basal Area of Host Trees

There is a strong pattern of SPB spots tending to grow more within stands that have a high basal area of host trees (Belanger 1980; Cameron and Billings 1988; Hedden 1978; Hedden and Lorio 1985; Hicks and others 1981; Ku and others 1980b; Kushmaul and others 1979;

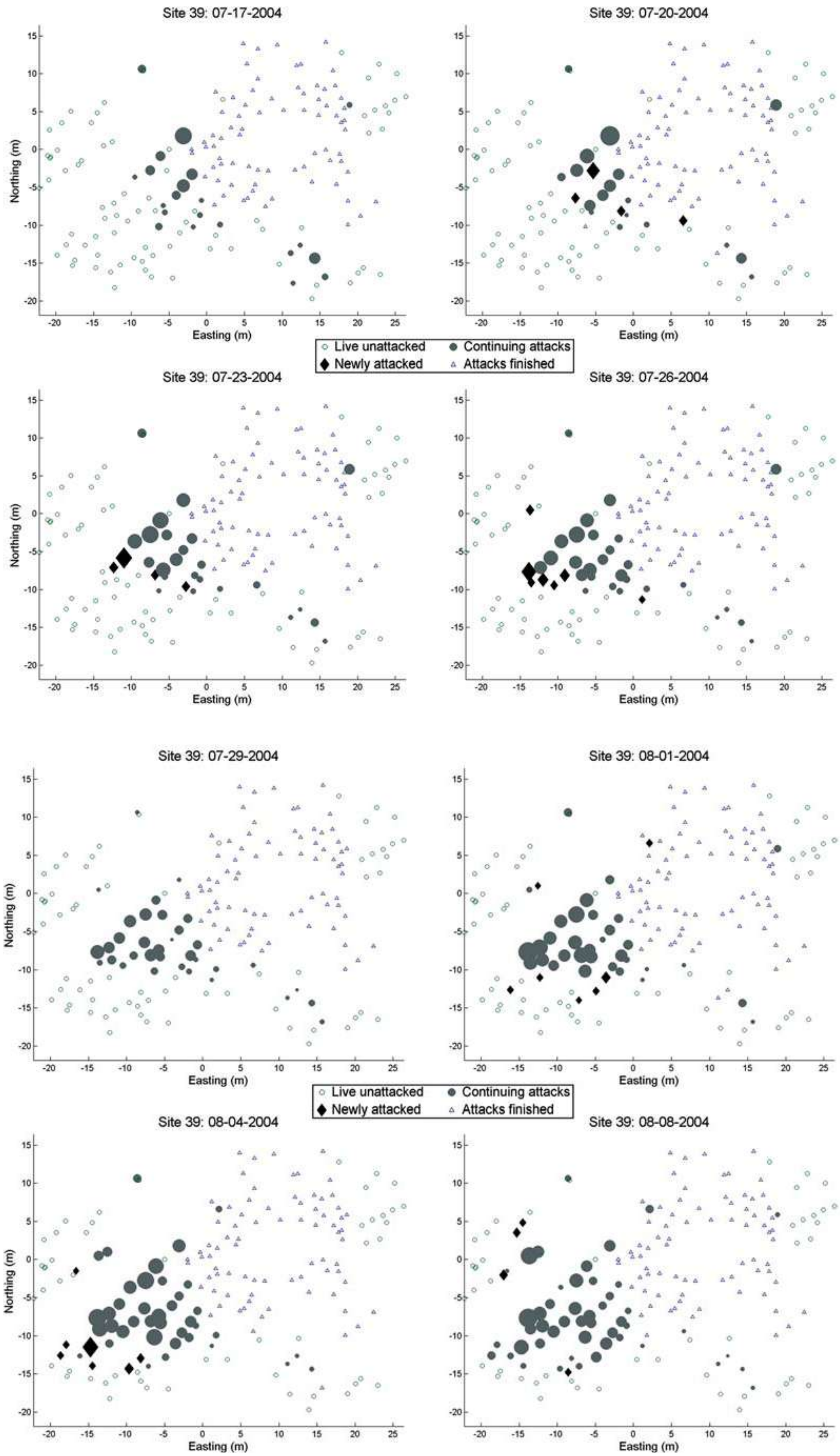

Figure 5.1—The progression of tree attacks within a fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #39 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 348-23): 22 years old, 13 ha (32 acres), diameter at breast height (± SD) = 19 ± 4 cm (6-9 inches), height = 20 ± 3 m (56-72 feet), percent live crown = 29 ± 10, basal area = 36 ± 7 m^3 / ha (125-186 ft^2 / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand. (continued on next page)

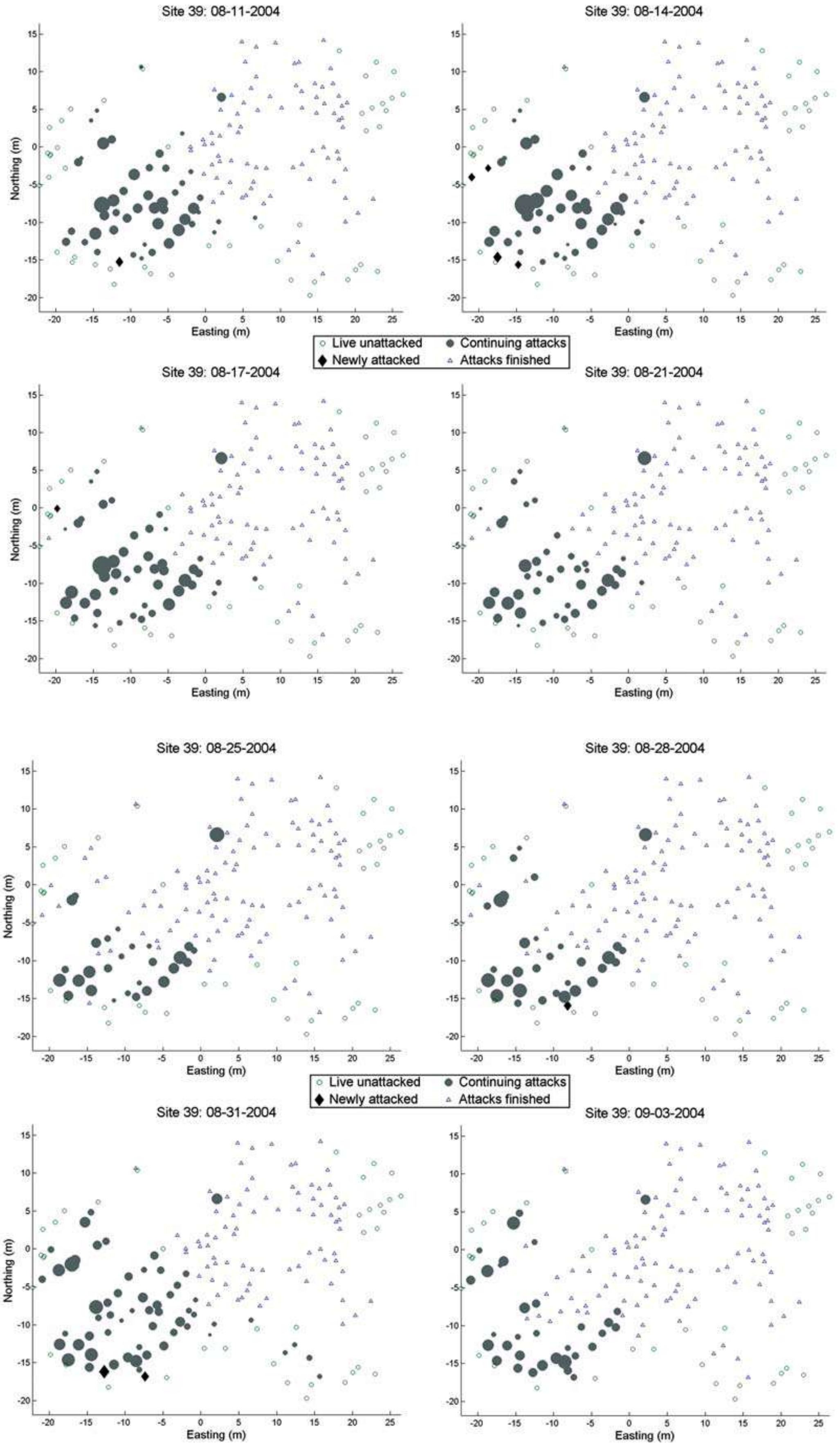

Figure 5.1 (continued)— The progression of tree attacks within a fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #39 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 348-23): 22 years old, 13 ha (32 acres), diameter at breast height (± SD) = 19 ± 4 cm (6-9 inches), height = 20 ± 3 m (56-72 feet), percent live crown = 29 ± 10, basal area = 36 ± 7 m^3 / ha (125-186 ft^2 / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand.

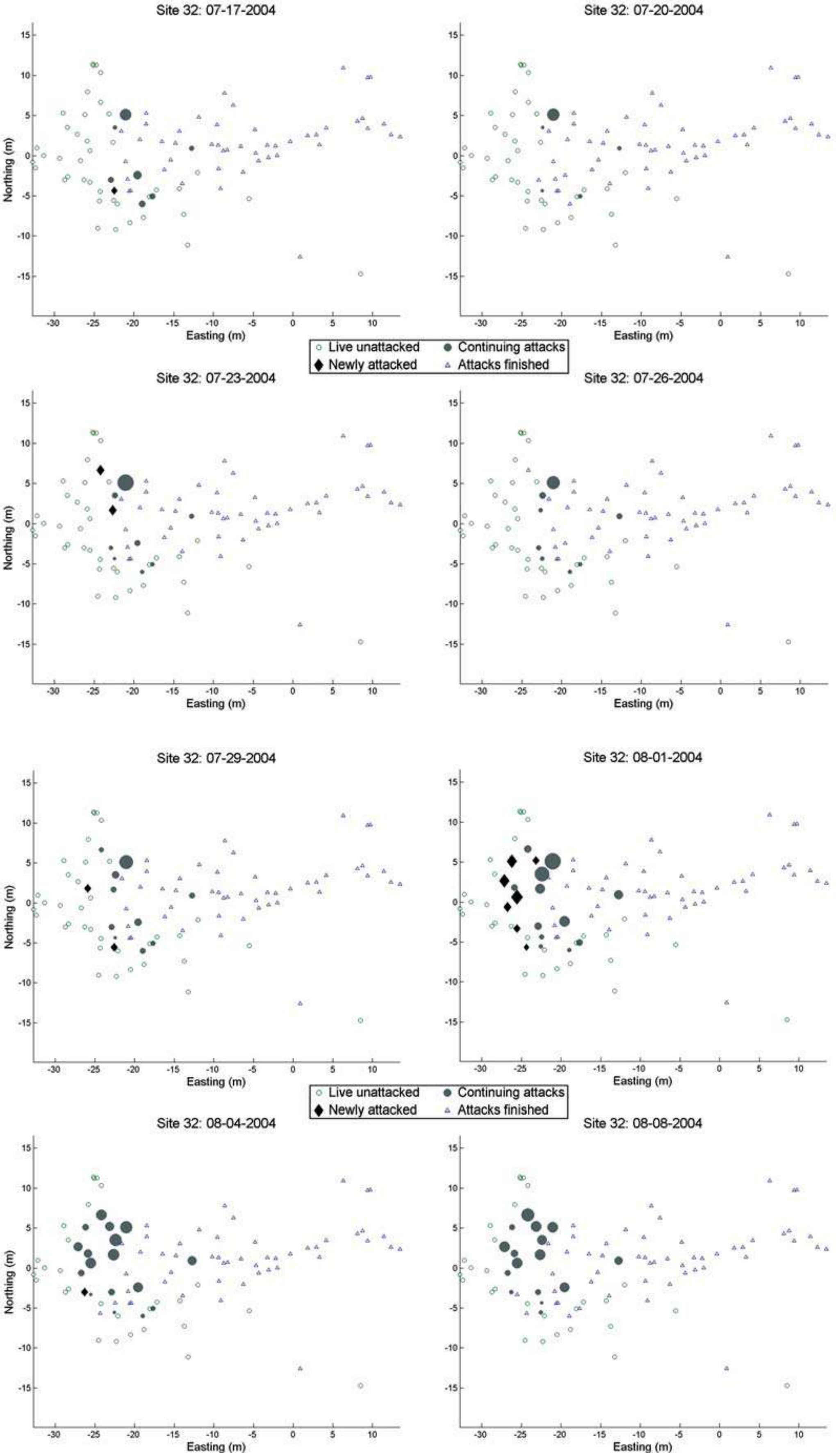

Figure 5.2 — The progression of tree attacks within a moderately fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #32 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 434-9): 21 years old, 20 ha (49 acres), diameter at breast height (± SD) = 18 ± 4 cm (5-9 inches), height = 19 ± 1 m (57-67 feet), percent live crown = 22 ± 11, basal area = 36 ± 7 m^3 / ha (124–186 ft^2 / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within this area of the stand. (continued on next page)

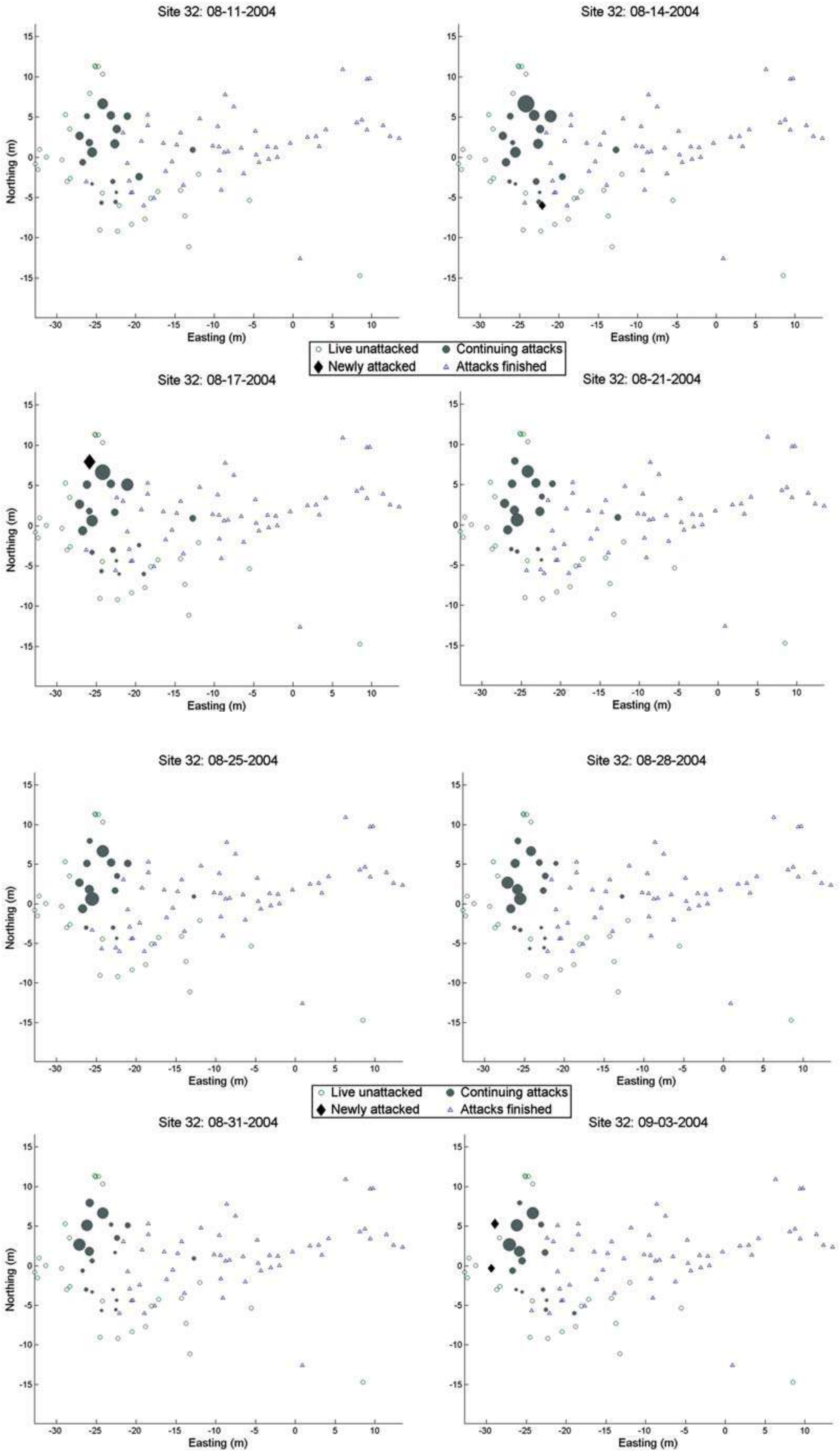

Figure 5.2 (continued)— The progression of tree attacks within a moderately fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #32 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 434-9): 21 years old, 20 ha (49 acres), diameter at breast height (± SD) = 18 ± 4 cm (5-9 inches), height = 19 ± 1 m (57-67 feet), percent live crown = 22 ± 11, basal area = 36 ± 7 m^3 / ha (124–186 ft^2 / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within this area of the stand.

Lorio 1980a, 1980b; Lorio and others 1982; Mason and others 1985; Nebeker and others 1985). Several possible explanations have been proposed. The time-honored explanation is that trees growing in relatively high density (overstocked) have smaller crowns that produce less photosynthates for oleoresin synthesis, and are therefore less well defended against beetles (Brown and others 1987, Lombardero and others 2000b, Matson and others 1987). This hypothesis is weakened by the observation that spot growth is lower even in mixed stands of pine and nonhost hardwoods where total basal area is still high (presumably limiting crown size and defensive capabilities just as it would if it was a pure pine stand; Schowalter and Turchin 1993, Zhang and Zeide 1999). An alternative hypothesis is that beetle aggregation efficiency declines as the distance between host trees increases (Turchin and others 1999a). A weakness of this model is that the distance among tree stems declines as stands mature (similar basal area but fewer larger stems per hectare), and yet mature stands can also support high spot growth if the basal area of host trees is high. A third hypothesis is that spots grow faster in overstocked stands because the relatively dense closed canopy, limits air movement below the canopy, which results in greater integrity of the pheromone plumes and makes it easier for beetles to locate and join attacks in progress. The effect of canopy structure on plume integrity has been experimentally validated (Thistle and others 2004), and is probably of considerable importance, but this model, like the tree defense model, still fails to explain why mixed pine-hardwood stands with closed canopies are less suitable than pure pine stands for spot growth. Further research is required to understand why high densities of host trees promote spot growth. This is especially important because forestry management tactics that limit stand susceptibility to spot growth are arguably the best long-term solution for mitigating undesirable impacts of SPB (Belanger and others 1993, Nowak and others 2008).

Stand Age

At least for loblolly pine, spot growth appears to be related to stand age. During a large epidemic in the Bankhead National Forest of northern Alabama, the extent of infestations within infested stands was highest in loblolly pine stands that were 20-40 years of age and declined in older stands (Ylioja and others 2005). This could be because interstem distances increase in older stands, because canopy closure (and therefore the integrity of pheromone plumes) is less in mature stands, because larger trees require more SPB to overwhelm defenses, or perhaps just because older stands are a selected subset that have survived previous epidemics partly because they were initially more resistant for any reason. Notably, the pattern of reduced susceptibility in older pine stands runs counter to the common generalization in forest entomology that trees and stands become increasingly susceptible to pests with increasing age (Edmonds and others 2000).

Tree Defenses

There is high intraspecific variation among trees in their constitutive resin flow, and the amount of resin has demonstrable effects on the reproductive success of SPB (Blanche and others 1983, Nebeker and others 1992, Tisdale and others 2003a). In trees with relatively high resin flow, attacking adult beetles spend more time moiling in the resin and less time excavating galleries and laying eggs, leading to markedly lower per capita reproductive success (Reeve and others 1995). Thus stands where the trees have low average resin flow must permit greater spot growth, with other things being equal. However, this probably does not explain very much of the variation in spot growth across a forest because average constitutive resin flow does not vary greatly among stands across a ranger district—rather most of the variation is among trees within stands, even at the relatively fine scale of a beetle spot (Martinson and others 2007). It is probable that there is more variation among stands in the inducible capacity for resin flow because this is more strongly related to crown size and tree physiological status (Knebel and others 2008, Lombardero and others 2000b, Tisdale and others 2003b), but consequences for the growth of SPB spots is not well known. It is probable that pronounced seasonal and interannual variation in resin flow influences tendencies for growth in the population of spots across a forested landscape (Lorio 1986, Lorio and others 1990, Wilkens and others 1997).

The Predator *Thanasimus dubius*

The predator *Thanasimus dubius* is of well demonstrated general importance in the population dynamics of SPB (Frazier and others 1981, Reeve 1997, Reeve and others 1980, Thatcher and Pickard 1966, Turchin and others 1991). The abundance of *T. dubius* tends to be quite uniform across the scale of a

National Forest Ranger District (Cronin and others 2000, Friedenberg and others 2007b), so it is not obvious that variation in predation by *T. dubius* would produce important variation in the growth of spots within a forest in any given year. There is conspicuous variation in the abundance of *T. dubius* among years and among forests separated by at least a few hundred kilometers (Billings and Upton 2002, Martinson 2007), so this coarser variation is likely to make some forests in some years more or less likely to support high spot growth. Indeed, the ratio of *T. dubius* to SPB that are captured during spring dispersal is recognized as a predictor of regional risk for high growth of SPB populations (Billings and Upton 2002). Some of the interannual variation in abundance of *T. dubius* is explained by abundance of SPB the previous year (Reeve and Turchin 2002, Turchin and others 1999b). Within a summer, the abundance of *T. dubius* relative to SPB tends to decline quite markedly; e.g., Martinson (2007) reported that the predator: prey ratio from captures on sticky traps within spots declined from about 0.19 to 0.02 from early July to late July. Presumably, the effect of predators is greatest in the early summer. Friedenberg and others (2007a) estimated that relatively modest changes in predation rate during the early life of a spot could affect the probability of the spot dying by midsummer from a break in the continuity of attacks. Any features of trees or stands that influence predation by *T. dubius* could have important effects on the growth of SPB spots.

Interactions with Mites and Fungi

Community interactions involving mites and fungi are of surprisingly high importance in the population dynamics of SPB (Hofstetter and others 2006a, Lombardero and others 2003). SPB larvae depend upon the presence of one of two species of mutalistic (mycangial) fungi for their nutrition: *Entomocorticium* sp A and *Ceratocystiopsis ranaculosus* (Ayres and others 2000, Klepzig and others 2001a). Their relative abundance within SPB populations varies over space and time (Hofstetter and others 2006b). *Entomocorticium* seems to be a generally superior associate from the perspective of SPB (Coppedge and others 1995), and spots with a higher proportion of beetles carrying *Entomocorticium* appear to have higher reproductive success (Bridges 1983). Another common fungus, *Ophiostoma minus*, easily outcompetes the mycangial fungi (Klepzig and Wilkens 1997), and its abundance is highly variable from year to year and forest to forest, largely due to variation in the abundance of *Tarsonemus* mites that transport, propagate, and feed upon *O. minus* (Hofstetter and others 2006a, Lombardero and others 2000c). Spots in which the abundance of *Tarsonemus* mites is high tend to have low growth because of the resultant proliferation of *O. minus* within host trees. When the percentage of phloem occupied by blue stain (signaling the presence of *O. minus*) exceeds about 34 percent, spots tend to go extinct during the summer and fail to contribute SPB to dispersal flights the following spring (Hofstetter and others 2006b). Monitoring, and perhaps even manipulation, of *Tarsonemus* mites and *O. minus* has potential for predicting and managing SPB spot growth.

Climate

Climate—temperature in particular—has strong affects on most aspects of SPB biology. Development rates, oviposition rates, re-emergence rates, and probably the location of host trees by flying adults generally increase from approximately zero at 5°-10 °C, to a maximum at 27°-32 °C, and decline at higher temperatures (Wagner and others 1981a, 1984a). As a result, the rate at which growing spots enlarge (as in Figure 5.1) follows about the same pattern with temperature. Longevity tends to decrease across temperatures (Wagner and others 1984b), so the rate at which collapsing spots become inactive goes faster with increasing temperatures. The temperature-dependence of spot growth has been modeled by Coulson and others (1989), Feldman and others (1981a), and Lih and Stephen (1989). The temperature-dependence of generation time and cohort structure (eggs: larvae: pupae: adults) has been modeled by Friedenberg and others (2007a), who hypothesized that regional and interannual variation in temperature, through its effects on cohort structure, can influence the probability of spots dying because of an interruption in the continuity of pheromone plumes that structure attack behavior. Extreme temperatures can produce mortality of SPB that increases the probability of spot death prior to producing dispersing adults the following spring and reduces the number of dispersing adults that are produced by surviving spots. When the minimum winter temperature drops below about -14 °C (the approximate lower lethal temperature for SPB), populations tend to decline (Tran and others 2007). Effects of extreme summer temperatures are less studied, but there is evidence that temperatures can

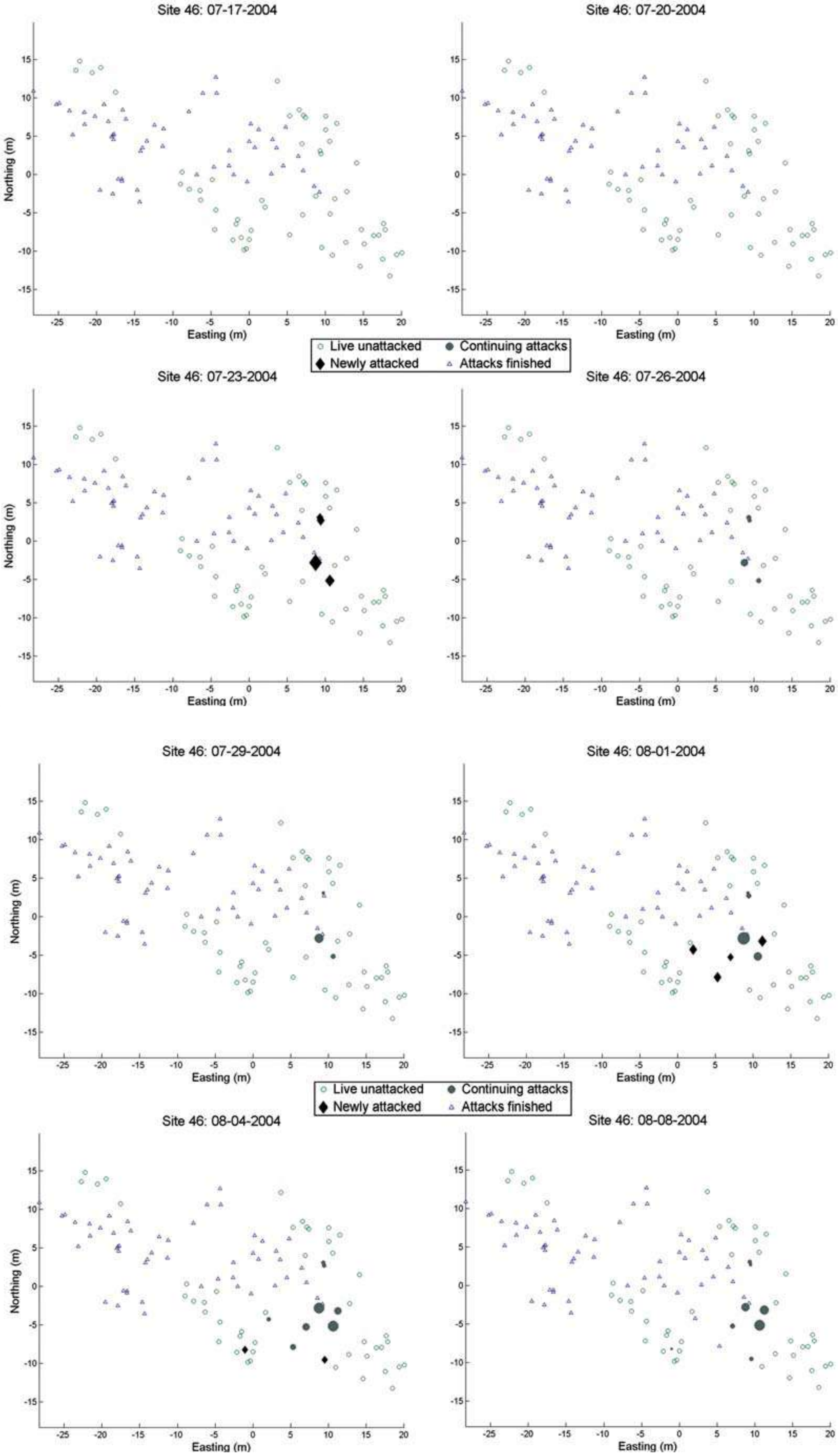

Figure 5.3 —The progression of tree attacks within a slow-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #46 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 389-18): 24 years old, diameter at breast height (± SD) = 17 ± 5 cm (5-9 inches), height = 19 ± 3 m (53-72 feet), percent live crown = 29 ± 11, basal area = 32 ± 14 m^3 / ha (81–191 ft^2 / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand. (continued on next page)

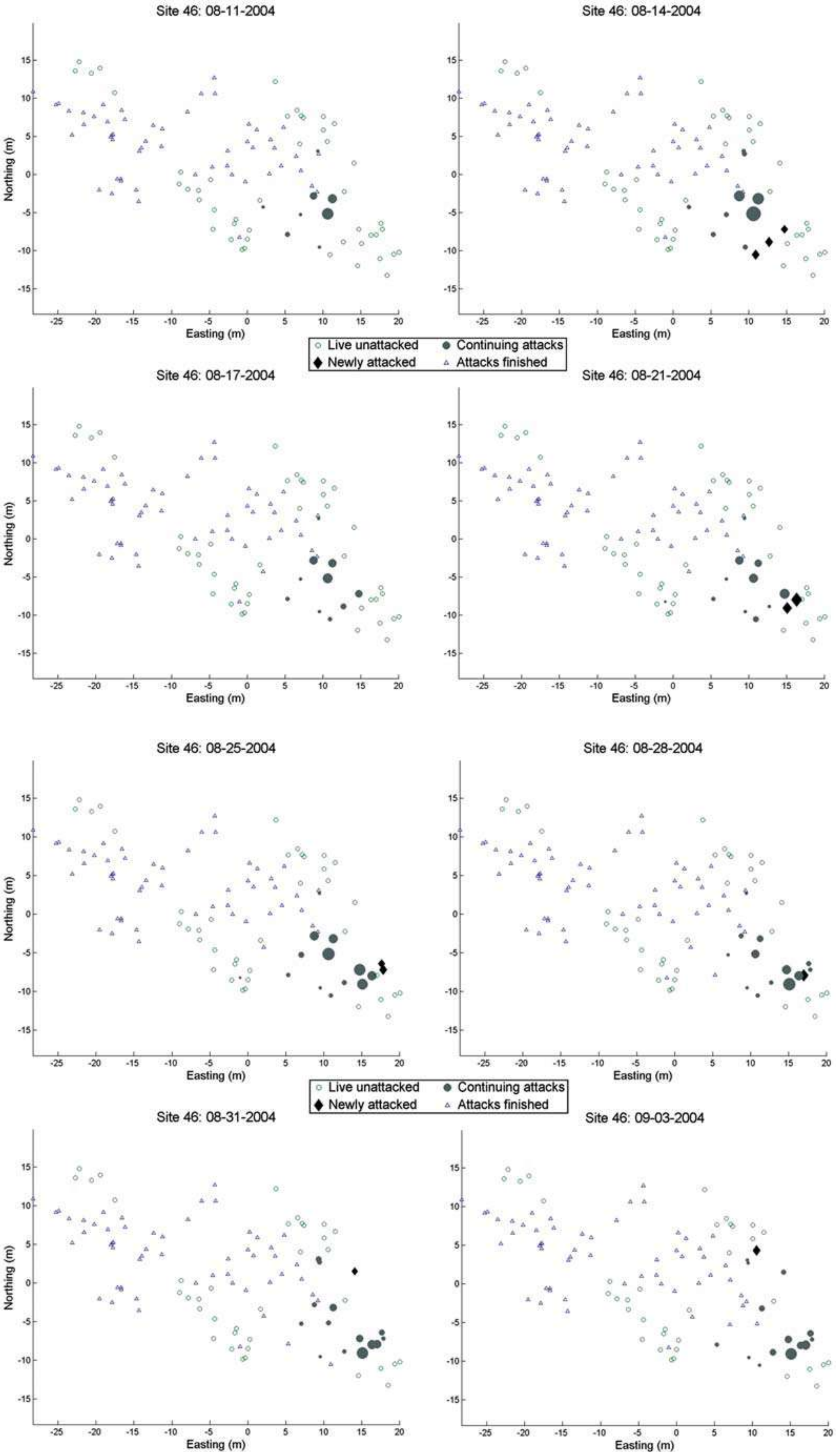

Figure 5.3 (continued)— The progression of tree attacks within a slow-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #46 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 389-18): 24 years old, diameter at breast height (± SD) = 17 ± 5 cm (5-9 inches), height = 19 ± 3 m (53-72 feet), percent live crown = 29 ± 11, basal area = 32 ± 14 m^3 / ha (81–191 ft^2 / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand.

sometimes get warm enough to kill beetles (Beal 1933, Wagner and others 1984b), and that spots have a greater tendency to collapse when temperatures exceed about 32 °C (Friedenberg and others 2008). There may also be important but less conspicuous effects of temperature on SPB populations via effects on species interactions within the community (Hofstetter and others 2006b, 2007; Lombardero and others 2003).

Other Community Interactions

Some other community interactions may also be of importance in influencing the growth of SPB spots. Competition with other species of bark beetles may be important in the early stages of spot formation (Bryant and others 2006; Flamm and others 1987b, 1989, 1993), and competition (and incidental predation) from cerambycid beetles, especially *Monochamus* spp., could influence SPB populations under at least some circumstances (Clarke and Billings 2000). Some parasitic hymenoptera prey on SPB (Moore 1972), but seem to be restricted to relatively low abundance under most circumstances (VanLaerhoven and Stephen 2008).

Immigration and Emigration

Although the population dynamics of spots from midsummer onward appear to be chiefly determined by patterns of SPB birth rates and death rates within the spot, immigration into spots might be important under some circumstances. SPB are capable of flying a kilometer or more (Turchin and Thoeny 1993). Some SPB that were marked with florescent powder within one spot have been later detected in nearby spots (Cronin and others 1999). It appears that many spots that go inactive during the summer (e.g., due to a break in the continuity of attacks and lack of a local pheromone plume) continue to produce SPB that disperse into the forest (Gara 1967). The demographic impact of these beetles on other spots is frequently assumed to be small (indeed the suppression tactic of cut-and-leave assumes this to be true; USDA 1987), but this remains a debatable point (Cronin and others 1999, Fitzgerald and others 1994). For untreated spots that remain active, there has been little consideration of how emigration might influence the growth of spots from which SPB are departing. New evidence suggests that emigration might be more important than generally recognized as a factor in spot growth. Martinson (2007) estimated high population growth for two spots based upon conventional measures of per capita reproductive success within trees, but independent measurements indicated that population sizes were actually stable or declining over the same time period. One explanation is that half or more of adult beetles emerging from the trees where they developed failed to locate the pheromone plume at the spot head and wandered out of the spot. If emigration can be this high, it would only require modest variation in emigration rates among spots to have a large impact on spot growth. Further studies would be useful.

5.5. SPB SPOTS FROM WINTER TO THE END

While SPB spots have been studied quite intensively during the summer months, less is known about their winter biology. There is no diapause or endogenously enforced seasonal cessation of activity in SPB (Payne 1980). In the Southeastern United States all life stages can be found at all times of year (Beal 1933; Thatcher and Pickard 1964, 1967), indicating that the same processes are occurring as during the summer (emergence, flight, attacks, oviposition, larval development, and pupation). But the processes go slower. Biophysical measurements indicate that SPB generation time is about 50 days at 25 °C, 100 days at 17 °C, and 200 days at 12.5 °C (Friedenberg and others 2007a, Wagner and others 1984a). At the same time, resin flow from attacked trees is slower (Lorio and Sommers 1986), growth rates of fungal and mite associates are slower (Hofstetter and others 2007, Lombardero and others 2000c), and development rate of the predator *Thanasimus dubius* is slower (Nebeker and Purser 1980). Presumably because of natural selection for sustaining activity during the winter months, SPB are physiologically capable of flight at unusually low temperatures for a bark beetle (≈ 7 °C; Moser and Thompson 1986). Besides going generally slower, the process rates for different life stages of SPB are affected differently. As a result, the relative frequency of the various life stages change during the winter. In western North Carolina and East Texas, studies indicate a preponderance of larvae by late winter (Beal 1933, Thatcher 1967). In New Jersey, at the extreme northern edge of SPB distribution in the United States, Tran and others (2007) observed 99 percent of the population to be prepupae in February. When the stage structure of the population becomes concentrated as larvae, it becomes increasingly likely that there will be a cessation of adult activity and a break in the continuity of pheromone plumes that would be required to organize the attacks of the dominant cohort when they complete development and emerge as adults in early spring (Friedenberg and others 2007a). This provides a parsimonious explanation for the characteristic dispersal of adults away from their natal spots in spring, which generally terminates the life of spots that were born the previous spring and survived into the winter. Hedden and Billings (1977) found relatively high lipid content in SPB adults emerging in spring, which they interpreted as an adaptation for supporting the energetic requirements of spring dispersal flights (but see Coppedge and others 1994). Forest Health personnel in New Jersey report that some individual SPB spots have remained active for multiple years, so there may be regional variation in the tendencies of SPB to disperse in the spring.

6

Population Dynamics of Southern Pine Beetle in Forest Landscapes

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Abstract

Southern pine beetle (SPB) is an important pest of Southeastern United States pine forests. Periodic regional outbreaks are characterized by localized areas of tree mortality (infestations) surrounded by areas with little or no damage. Ultimately, this spatiotemporal pattern of tree mortality is driven by the dynamics of SPB populations—more specifically, by rates of survival, reproduction, development, and dispersal. In turn these rates are driven by the interaction between SPB and its hosts, predators, and climate. In this chapter, the relationship between these factors and SPB population ecology are discussed. Particular emphasis is placed on mechanisms that could explain the temporal changes of the population from outbreak to nonoutbreak phases, the dispersal of SPB across a complex forest landscape, and the importance of interpreting the environment using current knowledge of SPB ecology.

Keywords

landscape
population dynamics
southern pine beetle

6.1. INTRODUCTION

Like all organisms, the population dynamics of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) are intrinsically tied to its spatial and temporal environment. The pattern of damage exhibited by SPB is patchy (heterogeneous) through both space and time. SPB population dynamics exhibit two phases: an endemic phase, when populations are so low that damage is almost undetectable within the forest, and an epidemic phase, when populations reach high densities and tree mortality is considerable. During epidemic phases or outbreaks, damage is aggregated into discrete areas (infestations or spots) that occur within a much larger area of unaffected forest landscape. This pattern is a crucial component of the pestilence of the SPB. This heterogeneity ensures that some areas of the forest (hence individuals who manage it) will incur damage while others do not.

One possible explanation for the patchiness of SPB damage is that it is driven by the heterogeneity of the forest landscape itself. Figure 6.1 shows the juxtaposition of different land uses within a typical East Texas landscape where SPB outbreaks are prevalent. This heterogeneity may be driven by a number of factors including the dynamics of tree growth and forest management; natural disturbances such as logging, fire, weather damage, and pests (including the SPB); and socioeconomically driven land management (for example, forestry and agriculture). The survival, development, reproduction, and movement of the SPB are intrinsically tied to such forest landscapes. It is these processes that ultimately lead to high density populations, tree mortality, and pestilence. However, the biggest problem with interpreting Figure 6.1 is the temptation to visualize this landscape from a human point of view. The central thesis of this chapter is that to understand SPB population dynamics, this environment needs to be interpreted with reference to the life history, behavior, and ecology of SPB.

The goal of this chapter is to review the population and life history processes that drive SPB population dynamics across forest landscapes. These processes include development, survival, and reproduction; movement of SPB within and between infestations; interaction between the SPB and its hosts; and the interaction between the SPB and its predators. Practically, the extensive nature of forest ecosystems and the cryptic nature and small size of the SPB make it

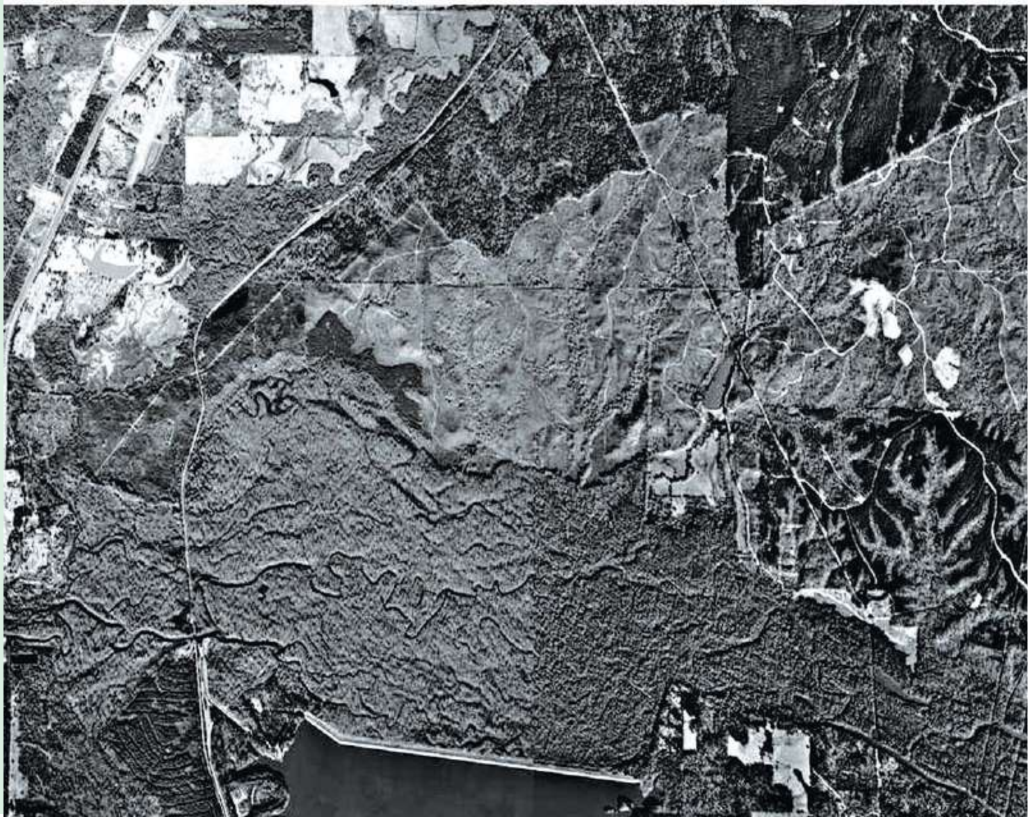

Figure 6.1—Photograph of a typical East Texas forest landscape. The image shows a mosaic of different land types including forest, pasture, urban areas, and water. Forest patches of various sizes and shapes can be seen with boundaries delineated by roads, creeks, or different land uses. Within this matrix, forest patches may be further classified by tree species, planting densities, age, and the type of management. The landscape is also dynamic, experiencing seasonal changes in temperature, soil water, and tree growth, and longer term changes caused by growth and management. One of the goals of SPB ecology is to understand the factors that drive population dynamics and damage, and thus be able to interpret landscapes such as the one depicted at right from the point of view of the beetle. (image courtesy of the USGS)

difficult to measure SPB population dynamics directly. However, many of these life-history processes can be measured independently. With some interpretation and speculation, this knowledge can be integrated into an overview of population dynamics useful for understanding and managing SPB damage. This "bottom-up" approach to understanding the SPB equips forest managers to understand why certain areas of forest incur damage while others do not. By focusing on the agent of damage itself (SPB) rather than just on the properties of the forest, this approach also arms forest managers with the knowledge needed to determine the extent and pattern of future SPB outbreaks.

6.1.1. The Range of SPB and the Physical Landscapes it Inhabits

The core range of the SPB extends from East Texas, across the Gulf States to Florida, and northwards to Virginia (Figure 6.2). Within this range, large variations occur in climate, topography, and the composition (abundance) and configuration (pattern) of host species. This large geographic range suggests that the life-history processes of the SPB (movement, development, reproduction, and longevity) define an organism capable of exploiting a wide variety of landscapes and climates.

Figure 6.3 shows patterns of SPB damage throughout its range between 1960 and 2000. A feature of this spatial and temporal pattern is that outbreaks do not occur at the same frequency throughout the SPB's range. An outbreak is formally defined as at least one SPB infestation per 405 Ha (Gumpertz and others 2000). The simplest explanation for differences in outbreak frequency is that they are driven by the amount of SPB hosts in a region. However, SPB outbreaks are only weakly (if at all) related to the abundance of potential hosts (Gumpertz and others 2000). A number of researchers have explored other simple hypotheses that might explain the spatial pattern of outbreaks. For

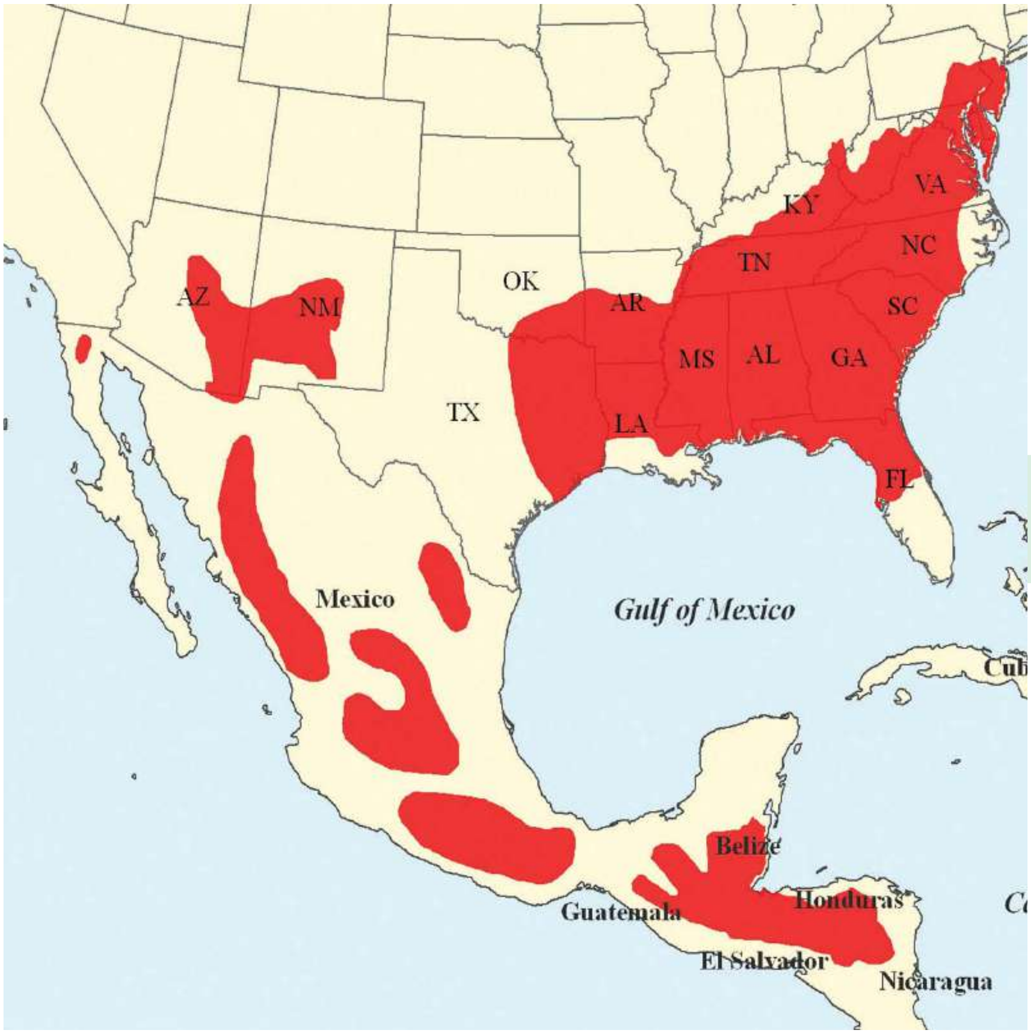

Figure 6.2—Geographic range of SPB. (redrawn from Payne 1981 by E. Takow)

example, Gumpertz and others (2000) used saw timber volume, along with other variables such as climate, elevation, and longitude, to develop a logistic regression model for the incidence of outbreaks in North Carolina, South Carolina, and Georgia. Similarly, Gan (2004) developed a statistical model that incorporated 16 selected climatic variables in an attempt to predict outbreak frequency. One conclusion from these studies is that SPB incidence and damage is not strongly related to any single, simple property of the landscape. Rather, it would appear that SPB damage is driven by complex population dynamics that we currently do not fully understand.

6.1.2. Why are Landscape Population Dynamics Important for SPB Management?

Patterns of SPB damage have both spatial and temporal components. Outbreaks occur infrequently through time (at periods of between 5 and 15 years depending on geographic location), with each outbreak comprising a number of discrete infestations, or spots, and localized damage. A number of statistical models have been developed to explain or predict the likelihood of infestations occurring in a particular area based on the local characteristics of the forest (e.g., soils, landform, and the age, BA, and DBH distribution of trees). Some of these models are reviewed in chapter 22. However, despite the utility of these models for SPB management, one trend that emerges is that although they can tell us which stands are most likely to incur damage (i.e., risk), they are unable to predict exactly where and when infestations will occur.

This lack of predictive power can be attributed to the fact that current models are missing vital information needed to fully describe the system. This missing information may fall into one of the following categories:

1. It is not possible to measure environmental variables accurately enough or at resolutions fine enough to permit accurate predictions.
2. Environmental variables used in these models are not those that are most relevant to SPB damage.
3. The models fail to account for the dynamic nature of the agent of damage itself—namely, SPB population dynamics.

Points 2 and 3 are especially relevant to this chapter. First, properties of the forest most relevant to SPB dynamics should be identified by understanding the basic population ecology of the SPB. This ecology includes mechanisms of host location; the speed, longevity, and habitat preferences during dispersal; and the relationship between life-history processes (development, survival, and reproduction) and temperature. Understanding the ecology of the SPB will undoubtedly lead to a different interpretation of the forest landscape as first registered by the human eye (Figure 6.1) and is arguably the first step in formulating hypotheses

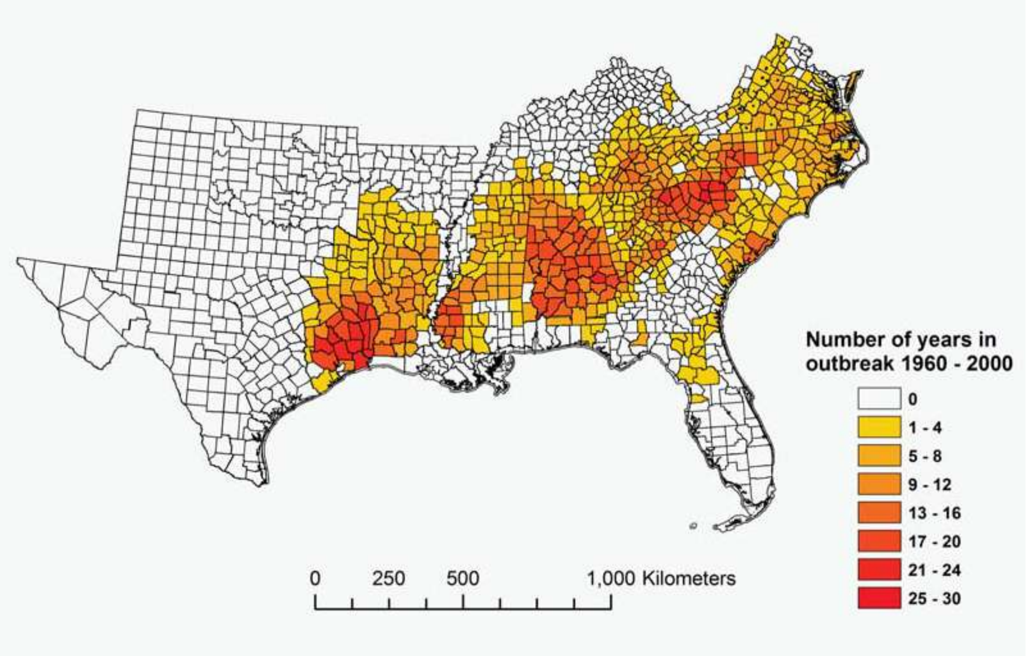

Figure 6.3—Map showing the number of outbreaks experienced by counties across the Southeastern United States between 1960 and 2000.

and models that explain the dynamics of SPB populations. Second, tree mortality is ultimately driven by changes in the abundance of SPB populations at a single point in space and time. Understanding the environmental factors that drive these changes should allow more effective SPB management.

Is it Necessary to Understand Population Dynamics to Predict Damage?

A fundamental question that surrounds SPB management is whether it is necessary to understand the dynamics of their populations in order to predict where damage will occur. More specifically, two competing hypotheses might be proposed:

H1. SPB populations are either homogeneously distributed through space and time, or are able to rapidly and efficiently disperse and/or locate potential hosts such that static, measurable properties of the forest (measurements of host suitability) become the most important factors for predicting future damage.

H2. SPB populations are unevenly distributed through space and time, have limited host-finding and dispersal ability such that patterns of damage can only be predicted by understanding the spatial and temporal patterns of the population.

These hypotheses mark endpoints of a continuum. Hypothesis 1 suggests that predictions for when and where damage will occur can be made by only measuring properties of the forest landscape, assuming the most relevant variables are measured. In contrast, Hypothesis 2 suggests that predicting the location and timing of damage depends upon both the properties of the landscape and the temporal and spatial distribution of beetles within the landscape. Given knowledge of SPB outbreaks, it is clear that H1 cannot be entirely correct. For a given region, SPB populations fluctuate between endemic and outbreak phases. In addition, outbreaks tend to occur locally such that the spatial extent of an outbreak can be defined.

Hypothesis 2 has important consequences for understanding the validity of current SPB management tools. Most risk models (reviewed in chapter 22) use only static properties of the forest to predict damage. In a sense, they estimate the potential for damage. Their formulation assumes that during outbreaks, populations are homogeneously distributed across a landscape. They also assume equal population densities during each outbreak, and since they do not account for variations in population dynamics through time, outputs from these models represent the long-term average probability that a stand or forest will become damaged (see following section).

If current risk models are correctly interpreted, they remain useful tools for SPB management. However, it is clear that many of their assumptions can be contested, given current knowledge of SPB population dynamics. In addition, there are many questions important for SPB management that cannot be addressed using existing risk models. These include:

1. How does the structure of the forest landscape affect SPB dispersal and the initiation of new infestations?
2. To what extent is the outbreak frequency of the SPB predictable?
3. To what extent are active infestations contagious?
4. Do regional SPB populations become locally extinct during nonoutbreak periods?

As mentioned previously, it is the patchiness and current unpredictability of damage that largely characterizes SPB pestilence. The challenge for population ecologists is to develop models (herein “model” refers to either a conceptual or a mathematical explanation of a process) that explain fluctuations in the abundance of SPB populations through space and time, and how these dynamics contribute to patterns of tree mortality.

6.1.3. Population Regulation

One central debate in SPB population ecology surrounds the mechanisms by which populations are regulated. Without some form of regulation (changes in the vital rates of the organism), populations either grow or decline infinitely. Southern pine beetle populations do neither. Instead they fluctuate from periods of high density populations (outbreaks), to extended periods of low density populations (endemic). Two classes of regulatory mechanisms have been suggested to explain these fluctuations. Proponents of exogenous regulation suggest that population dynamics are largely regulated by density-independent factors such as weather. Endogenous regulation suggests that the dynamics of the SPB are influenced by density-dependant effects such as the reciprocal relationship between predators, hosts, or intra-specific competition.

Many SPB management issues can only be answered with full confidence if all of the mechanisms that cause populations to oscillate between low and high densities are understood. However, to make inroads into the SPB problem it is necessary to break down the complexity of population dynamics into discrete units. For example, it is possible to model SPB populations within infestations in order to understand the growth of infestations and to produce practically useful estimates of damage. Such models may be useful even if they do not attempt to explain why an infestation occurred, or do not account for immigration and emigration. Similarly it is useful to model populations at low densities in order to understand the dynamics of extinction within a region, or to develop simple temporal models that ignore the effects of space in order to investigate density-dependant effects (Turchin and others 1991). In all cases, the art of modeling (whether models are conceptual or mathematical) is to simplify population dynamics by choosing a level of complexity that contributes to an improved understanding of the system.

6.2. DRIVERS OF POPULATION DYNAMICS

The majority of data for the SPB have been collected from active infestations where SPBs are relatively easy to study. However, epidemic populations comprise only a fraction (but the most visible one) of SPB's population dynamics. It could be argued that the most important phase for understanding SPB dynamics is the endemic phase. An understanding of SPB populations between outbreaks and the factors that contribute to the shift from endemic to outbreak conditions is currently not well developed.

In the absence of data from endemic populations, conceptual or mathematical models must be built using life-history processes that can be more easily studied. The following sections deal with data and conceptual models that contribute to an understanding of how and why populations of the SPB oscillate from low density (endemic) to high density (epidemic) proportions. More specifically, they deal with mechanisms that could explain:

1. How and why SPB populations are regulated at low densities (between outbreaks).
2. How changes to this system (either endogenous or exogenous) lead to an increase in population growth rate and relatively short periods of high density populations.
3. How and why the system reverts back to an extended period of low density population dynamics.

6.2.1. Temperature and Climate

Figure 6.4 shows the time taken for SPB to develop at constant temperatures. Development is optimal at approximately 30 ^{o}C, and there is a reduction in development at temperatures above and below this mark. Similar relationships have been measured for reproduction and survival. Because of these relationships, temperature has long been proposed as an important regulator of SPB population dynamics, and there is little doubt that seasonal changes in temperature drive much of its dynamics. For example, at the onset of outbreaks, SPB infestations tend to be detected within the landscape in spring or autumn, when temperatures fluctuate around the optimum for development. Conversely, population activity and the initiation of new infestations tend to decline in midsummer and winter when temperatures become unfavorable for population growth.

These seasonal declines are a consistent and important component of SPB population dynamics. During winter, low temperatures curtail development and reproduction, and therefore population growth. Reductions in developmental processes affect the emergence of new individuals. Whereas under optimum conditions, a generation may be completed in 30 days, during winter it may take more than 90 days (Wagner and others 1984a). This extended development time may have a number of consequences. First, all other things being equal, extended development times and lower reproduction lead to a reduction in population growth rate (Birt and others 2009). Second, because there is intrapopulation variability in the development rates of individuals, longer development times increase the period over which emergence occurs. At optimal temperatures, individuals of the same age develop quickly and will emerge over a short period of time; whereas at low temperatures, individuals develop slowly and will

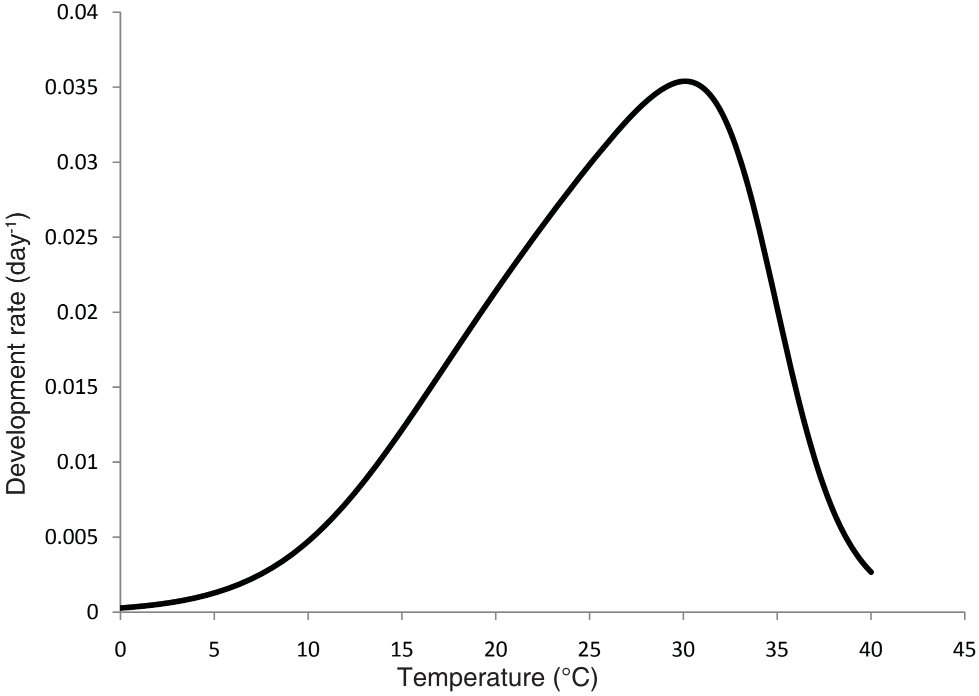

Figure 6.4—Graph showing the relationship between development rate (development time-1) and rearing temperature. Development is optimal at approximately 30 °C, leading to a development time of approximately 1/0.035 = 29 days. Note that development rate rapidly drops off at temperatures above 35 °C, but at sub-optimal temperatures the effect is more gradual. The graph serves as a basis to understand how seasonal climate (high summer temperatures and low winter temperatures) may curtail population growth by effectively halting development.

emerge over a much longer period of time. Low temperatures may also reduce the range of flight (Moser and Dell 1979a, Moser and Thompson 1986). Together, these interruptions to patterns of emergence are likely to reduce host-finding success and may be significant for populations at both endemic and outbreak conditions. Within infestations (epidemic populations), a reduction in attacking individuals may reduce the ability of the local population to overcome defenses of trees in the immediate vicinity. During endemic population phases, a decrease in attacking individuals may affect the ability of the population to locate and colonize highly susceptible hosts within a broader landscape (for example, lightning-struck trees).

Temperature may also have a direct effect on the mortality of individuals within a population. In the laboratory, 1 or 2 days of exposure to extreme low temperatures (-5 to -12 °C) causes >50 percent mortality (Lombardero and others 2000a). Through most of its range, such temperatures will occur infrequently, especially considering that bark may buffer temperatures by 1 to 4 °C (Tran and others 2007). But at high altitudes or in northern portions of its range, or during colder winters, extreme low temperatures may have significant effects on SPB overwintering. For example, Ragenovich (1980) recorded 95 percent brood mortality in areas of the Southern Appalachians that experienced temperatures <-20 °C. Ungerer and others (1999) suggest that the northernmost range of SPB is marked by a region where approximately 9 out of 10 winters experience minimum temperatures of -16 °C or less.

Extremely high temperatures may also directly increase mortality. For example, two of the methods used to manage active infestations, cut-and-leave and cut-and-top treatments, affect the microclimate of host trees and the mortality of brood stages within them (Fettig and others 2007). Such treatments are thought to reduce the emergence of attacking beetles within an infestation and the dispersal of individuals away from an infestation, thereby curtailing growth of infestations and outbreaks. In southern portions of its range, temperatures above the optimum for development (35 °C) and above its thermal tolerance (40 °C) may often occur.

Year to year differences in the overwintering (or high temperature) success of the SPB may affect the spatial distribution of SPB populations within a landscape and the ability of the population to outsource the following spring. Severe winters (or summers) may cause significant mortality of the SPB within a defined region, and population recovery may only occur following immigration from refuge populations that escaped the mortality. Under milder conditions, mortality may still occur, but at lower rates. In both cases, the effect could be to uniformly reduce the size of the population within every infested tree in the landscape or, possibly in conjunction with landscape heterogeneity, temperature may impart differential effects on each metapopulation (each actively infested tree in the landscape). In the latter case, in addition to reducing the overall size of a regional population, low temperatures may serve to disaggregate infested trees and thus reduce the distance between actively infested trees in the landscape. Such effects may be especially important where topographical features (for example, mountains) may buffer excessive temperatures. Considering the importance of aggregation for SPB populations (see following sections), changes to the spatial pattern of metapopulations may have an important role to play in the broadscale and long-term dynamics of the species.

Although temperature has clear, demonstrable effects on both directly measured population dynamics and the life history of individuals, its role in the mechanisms that lead to endemic-epidemic-endemic oscillations is contentious. The principal difficulty with this hypothesis is that it would require long-term and broadscale growth of the population to be close to zero. It suggests that in the long run (for example, over a 100-year period), the population should not significantly grow or decline, but within this period local populations would occasionally be driven (by year-to-year variations in climate) to epidemic levels and then return to endemic levels. More specifically, a temporary increase in growth rate would have to be followed by a corresponding decrease in order to complete the cycle to an original population size. This is plausible for predictable, seasonal dynamics where spring, summer, or autumn growth might be offset by winter (or high summer) declines. It is less likely that interannual variation in environmental conditions (alternate sequences of favorable and unfavorable conditions) are capable of driving the characteristic temporal patterns of outbreak and nonoutbreak conditions.

Another criticism of this model is that strong, consistent relationships between climate and SPB outbreaks have rarely been demonstrated. Gan (2004) did find relationships between selected climatic variables (including temperature and precipitation) and outbreaks, but the statistical model used does not necessarily point to these variables as direct drivers of population growth. Despite the difficulties of a pure hypothesis of climatic regulation, there can be little doubt that climate (temperature in particular) is an important driver of SPB population dynamics. However, it is suggested that the most likely role of climate is that it works synergistically with another regulatory mechanism. Two plausible mechanisms are discussed in the following sections—namely predator-prey and host availability. In both cases, it is possible that interannual variations in climate may act as a catalyst for these other processes.

6.2.2. Predator-Prey Dynamics

The most complete explanation of SPB population regulation involves the interaction between SPB populations and its predators. Turchin and others (1991) developed statistical and mechanistic models suggesting that patterns of SPB populations in East Texas are more attributable to delayed density-dependant effects (with a time lag of 2 years) than inter-annual differences in climate. In other words, the rate of population change in a given year is negatively related to the size of the population 1 and 2 years previously. Predator-prey interaction (a lag between the rate of change in predator populations in response to the abundance of their prey) is one mechanism that can drive delayed density dependence.

There is considerable evidence that predators can exert significant pressure on SPB populations. Populations of the SPB tend to be associated with a wide variety of potential SPB predators and competitors (Moser and others 1971). *Thanasimus dubius*, commonly associated with SPB populations, has been observed to exert considerable mortality on adult bark beetles on external bark surfaces (Reeve 1997). It is also considerably more mobile than the SPB, which suggests that it may be capable of efficiently locating its prey over large distances (Cronin and others 2000). The most compelling evidence for predator-prey regulation (in particular the delayed density independence known to cause cycles) comes from a 5-year field study (Turchin and others 1999b) where significant differences were found between survival rates of the SPB in trees where predators were excluded by cages vs. populations exposed to predators. More specifically, in agreement with a model of delayed density dependence, low density SPB populations were less affected by predation, whereas at high SPB densities (i.e., at the peak of SPB activity and during the first year of SPB decline) predator-induced mortality increased considerably.

The evidence that SPB populations are regulated by predator-prey mediated delayed density dependence is thorough but by no means conclusive. In particular, there is no evidence for delayed density population cycles outside of East Texas. Ideally, SPB population dynamics should be explained by a universal model, with mechanisms and parameters that are consistent throughout the range of the SPB. The model proposed by Turchin and others (1991) exhibits quasi-periodic cycles of approximately 6 years. However, the frequency of SPB outbreaks varies considerably across the United States (see Figure 6.3). To account for changes in these interoutbreak periods, the model will require a different set of parameters for different locations. To maintain plausibility, regional differences in these parameters must be explicable in terms of differences in climate, landscape structure, or some other measurable variable. Similarly, although the predator-prey hypothesis has driven much experimental work, these results have not yet been incorporated into detailed, explicit mathematical models that test the robustness of Turchin and others' (1991) original model. For example, a number of researchers have measured the growth rates of populations within individual trees with and without predators (Reeve and others 1998). In the original model, the rate of increase of the population corresponded to the number of infestations in the landscape rather than for the growth rates of populations within individual trees. It is argued that the plausibility of the hypothesis will be increased if these delayed density mechanisms can be demonstrated using finer scale population processes such as temperature-dependant development, reproduction, survival, and dispersal. In particular, these detailed mechanisms should be able to explain the characteristic spatio-temporal patterns of tree mortality of aggregated infestations during outbreaks and scarcity of damage during nonoutbreak conditions.

6.2.3. Host Availability

Southern pine beetle populations might also be driven by the availability of hosts. This might occur during both outbreak and low-density periods. The rapid growth rates of populations within infestations and the observation that free-flying, adult SPBs are relatively short-lived (Gagne 1980, Ragenovich and Coster 1974) suggest that a constant availability of new hosts is necessary in order to sustain the growth of an infestation and, in turn, outbreaks. For endemic populations, dynamics might be driven by a balance between the growth rate of a population occupying an infested tree and the mortality costs associated with emerging individuals that need to locate new hosts.

Central to a host-limitation hypothesis is the idea that there are differences in the susceptibility of SPB hosts within a forested landscape. These differences may occur through space and time and could be driven by climatic conditions such as drought, flooding, lightning strikes, or other tree stressors; genetic differences in hosts including different species; or the age, size, or density of trees or stands. In such cases, the functional heterogeneity of the landscape might be best envisaged as a complex mosaic of susceptible and nonsusceptible host patches. As such, the potential for SPB population growth and the spatial and temporal pattern of damage will depend on the arrangement and abundance of these susceptible hosts through space and time and the ability of the SPB to locate and utilize them.

It is widely acknowledged that host-finding (location and successful attack) depends on both the numbers of attacking individuals and the intrinsic susceptibility of a host. Figure 6.5 shows a conceptual model of this behavior inspired by dose-response relationships in toxicological studies. This model suggests that high population densities (large numbers of attacking individuals) will increase the probability of a new host becoming infested. But it also indicates that low density populations may also be capable of overcoming the defenses of highly susceptible trees; for example, those damaged by lightning (Coulson and others 1999b). Shifts along the x-axis represent differences in the susceptibility of hosts in the landscape (left shifts leading to increased susceptibility and vice versa). This conceptual model of susceptibility may help to explain the pattern of endemic and outbreak dynamics. Most directly, the decline of an infestation could be driven by the depletion of susceptible hosts, but also by the number of attacking beetles available in the local population. In turn, the number of attacking beetles in the environment may be driven by seasonal changes in climate or increased predation (see sections above). Such mechanisms could begin to explain how small changes in climate might lead to the much larger changes in population growth rate necessary to drive an entire population cycle. For example, endemic-to-outbreak transitions might occur when conditions conspire to create local population densities large enough to

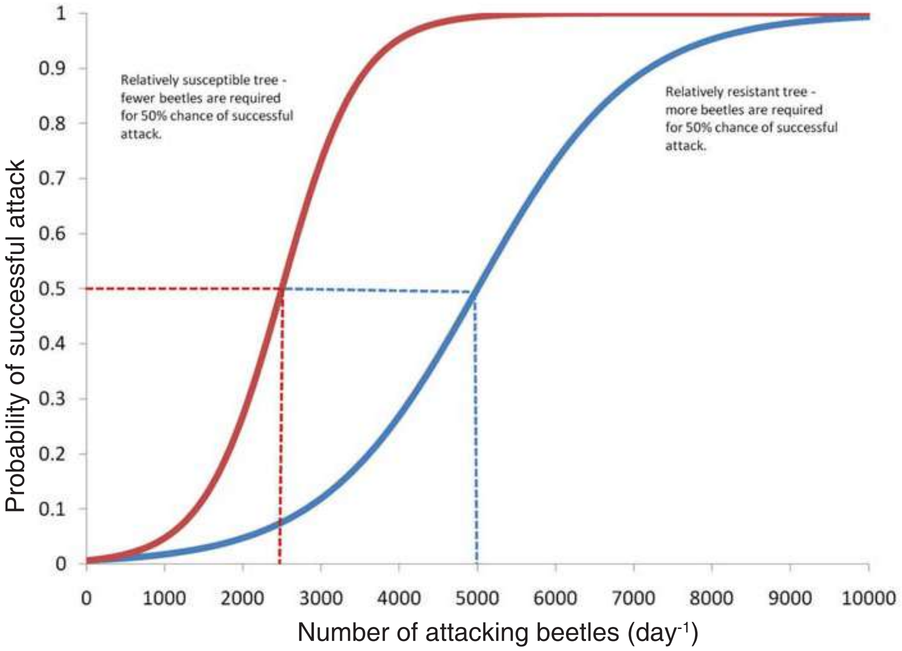

Figure 6.5—Graphs illustrating a conceptual view of tree susceptibility to SPB attacks. The graph describes mathematically how the probability of a successful attack may depend on the number of beetles available for attack, and some measure of the inherent susceptibility of the tree. The red and black lines show relatively susceptible and resistant trees, respectively. Susceptibility can be described by curves at any point on the x-axis—shifts to the left indicate increased susceptibility (e.g., lightning-struck trees) and to the right, increased resistance to attack. The models are based on dose-response functions common in toxicology studies.

overcome otherwise resistant trees, with the subsequent return to endemic conditions occurring through a combination of seasonal interruption of population dynamics and a reduction in the most susceptible trees in the landscape.

One problem with the host susceptibility hypothesis is that it relies upon a model that is highly conceptual. Unlike the predator-prey hypothesis, no mathematical representations exist with which to test its likelihood. Such representation is important in order to test the validity of conceptual, qualitative logic and turn it into testable and quantitative ideas. Nevertheless, there are large amounts of empirical data that suggest that at least some parts of SPB population dynamics are driven by interactions with its hosts. Most notably, SPB risk models are based on site conditions within a stand. Factors such as basal area (crowding of trees leading to increased stress and susceptibility) and soil conditions (the ability of the soil to drain or hold water and moderate water stress) have been shown to be important determinants of where infestations are likely to occur (see Lorio 1980b for a review).

The role of lightning-struck trees as highly susceptible hosts and sources of SPB populations has also been extensively studied. Using explosive detonator cord, Miller (1983) simulated lightning strikes in loblolly pine trees at various times between March and December, and within 10 days observed colonization of the tree first by black turpentine beetle (*Dendroctonus terebrans*), followed by *Ips calligraphus*, and finally SPB. In a similar study Coulson and others (1986) simulated lightning damage in 40 trees in East Texas and observed that bark beetles (including the SPB) colonized each tree. This colonization occurred after 6 months for trees injured in February and 5 days for trees injured in June, August, and September. In addition, approximately half of the disturbed and subsequently colonized trees spawned multiple tree infestations in neighboring untreated trees (two infestations grew to 45 and 35 infested trees). Lovelady and others (1991) extended these studies by exploring the availability of lightning-struck hosts in an East Texas landscape. They conclude that during endemic periods, lightning-struck trees are sufficiently available, both temporally and spatially, to provide an important refuge for the SPB and a mechanism for population persistence. However, during epidemic phases a large number of infestations occurred in areas that were not subject to lightning strikes, suggesting that the SPB is able to exploit less susceptible hosts at high population densities. Rykiel and others (1988) propose a conceptual model for the propagation and amplification of lightning strike damage by the SPB into large-scale forest disturbances. They conclude that lightning alone is unlikely to cause epidemic beetle outbreaks, but attribute outbreaks to synergies between lightning and other factors such as climate and the average susceptibility of a landscape. In turn, they suggest that average landscape susceptibility (an aggregate measure of the composition and susceptibility of hosts within a landscape) is driven by a feedback loop involving the damage caused by SPB outbreaks, leading to depletion of suitable hosts, followed by regeneration of the forest and a return to conditions ripe for another outbreak.

Host Susceptibility, Population Dynamics, and Risk Models

Lightning-struck trees, water stress, wind and storm damage, silviculture, and tree genetics may all contribute toward a forest landscape comprising trees or stands with different susceptibility to the SPB. The SPB has also been observed to attack felled green timber (Moser and others 1987), preferentially select trees with active red cockaded woodpecker cavities (Conner and others 2001b), and utilize trees infested by other bark beetle species.

SPB risk models quantify the likelihood that damage will occur within one particular location over another. They characterize the heterogeneity of the forest landscape, usually based on properties of a stand. These models are usually based on historical data sets that document properties of stands (for example, soil, vegetation characteristics, slope, and aspect) that did or did not incur damage during an outbreak. Simple statistical models are then used to weigh these variables by importance and to estimate risk to damage in other unsampled stands. Stand level risk models have been successful tools for SPB managers over the last 30 years but cannot provide definitive, 100 percent accurate measures of infestations or damage. Many of the reasons for this are related to the population dynamics of the SPB.

First, these risk models only measure static properties of the forest and do not account for the agent of damage itself—SPB populations. Consequently, it is feasible that during an outbreak, a stand that a model predicts is at high risk (through an assessment of its physical and silvicultural characteristics) does not incur damage because it is under no pressure from dispersing beetles. Paine and others (1984) present a similar argument and a conceptual model that illustrates the concept of stand risk.

A more subtle problem arises because data used to develop risk models may be collected from a number of different outbreaks. In some years or locations, outbreaks may be severe, leading to high population densities and, if the relationships in Figure 6.5 are to be believed, a higher probability that a stand of a given susceptibility will be infested. It follows that data sets used to develop risk models may be biased by regional population size. Although it is difficult to experimentally control population size, increased knowledge of the spatial and temporal dynamics of populations during outbreaks may help to account for errors in the risk model and allow them to be applied more objectively and successfully.

Second, although it is known that the SPB preferentially attack certain hosts, it is not fully understood why this occurs. In other words, it is not possible to consistently predict the location of susceptible hosts in the landscape because the direct mechanisms involved in tree susceptibility are currently unknown. For example, susceptibility might be broken down into a number of factors including:

1. The influence of trees or silviculture on host-finding (for example, stand location, production of green leaf volatiles, relationship between stand structure, and pheromone diffusion)

2. Defenses against attack and reproduction (for example, measurements of resin flow and chemical defenses)

3. Nutritional value (for example, nutrient content, phloem thickness, and water balance) and its influence on brood survival

Many of these factors may also vary seasonally or over shorter time frames. The challenge for SPB ecologists is to develop repeatable methods to measure these factors and to relate them to relevant SPB life-history processes and population success. In the absence of knowledge of these susceptibility mechanisms, risk models usually use surrogate measurements of susceptibility such as basal area (presumably an indicator of competition among hosts and potentially stress), soil type or depth (which may indicate the likelihood of flooding or drought), or age (a possible indicator of nutritional status). These surrogate measures are used because they are relatively easy to measure. But as aggregate measurements of a stand, they may not always be indicative of susceptible trees. For example, high basal area stands might not be particularly susceptible (stressed) if other environmental conditions remain near optimal. Conversely, within a large stand, there may be localized anomalies (e.g., flooding or drought) that lead to small patches of susceptible trees that could serve as epicenters of SPB activity.

Such conditions may be driven by fine-scale, practically immeasurable differences in site conditions; for example, soils or topography.

By developing a more detailed understanding of SPB population dynamics, it should be possible to increase the accuracy of the next generation of risk models. Understanding the spatial and temporal distribution of populations during outbreaks should drive the measurement of forest conditions at the most appropriate scales and resolutions. And an enhanced, more fundamental understanding of why certain trees become infested may drive the development of novel ways to measure forest heterogeneity. Most of all, a most basic knowledge of SPB population dynamics clarifies what the results of current risk models actually mean and how they should be used. Given the discussion above, it is perhaps not surprising that risk models are unable to indicate exactly where damage will occur. However, far from diminishing the utility of these models, it is argued that this fact adds value by clarifying how their success should be measured (e.g., what level of predictive accuracy is acceptable) and how their results should be interpreted so that they can be used for practical management.

SPB as an Optimum Organism

In simple population models, faster development rates among individuals in the population (all other processes being equal) contribute to greater population growth rates (Birt and others 2009, Nylin and Gotthard 1998). Because they must kill the trees they infest, progeny of successfully reproducing adults must continually find hosts to ensure population persistence. This presents a paradox for low density vs. high density populations. At high densities (for example, within infestations), optimum development rates should lead to increased population growth because hosts are plentiful (the Allee effect is in play). However, at low population densities this may not be the case. If the growth of endemic populations is regulated by a limited supply of highly susceptible hosts (for example, lightning-struck trees), then rapid turnover of the population (shorter development times) may not be optimal. During nonoutbreak periods, or periods when there are fewer attacking individuals, it is conceivable that population persistence involves changes in life-history processes that mitigate the problem of locating hosts. For example, Coppedge and others (1995) and Wagner and others (1984a) found differences between the body mass of individuals collected at different times of the year. This may be an adaptive response to increase host-finding efficiency, and this extra mass may be explained by longer development times (Atkinson and Sibly 1997). Such plasticity has been observed and extensively studied in a number of other arthropods (Peckarsky and others 2001). Other important adaptive mechanisms might involve second generation individuals reproducing in their natal tree, or synchronized emergence after periods of unfavorable population growth. Although speculative, such arguments are a reminder that, by the nature of the system, most of the observations and data collected for the SPB are from epidemic populations.

6.3. SPB DISPERSAL AND HOST FINDING

The SPB must kill a host in order to successfully reproduce. Over much of its range, warm, moist conditions lead to rapid decomposition of dead trees, curtailing the length of time that a host remains nutritionally favorable. During endemic periods, individuals must continually locate hosts that may be sparsely distributed across the forest landscape. During outbreaks, and in particular within active infestations, competition for nutritional resources (Reeve and others 1998) may drive the location of fresh hosts both within an infested stand and within the broader forest landscape. The SPB's ability to efficiently disperse, locate hosts, and generally utilize a heterogeneous spatial environment is therefore a critical component of its population ecology.

6.3.1. Dispersal

Because of its small size, it is difficult to observe the movement of SPB individuals directly, especially during endemic periods. As a result, movement must be inferred using properties of the system that are measurable (e.g., mark-recapture data) and models of movement. Figure 6.6 shows a simple model that encapsulates one of the fundamental aspects of SPB movement and its impact for population dynamics. The graph describes differences in the density of SPB populations if individuals were to move different straight line distances from a source population (for example, their natal tree) and follows a simple mathematical relationship between the area of a circle with radius r and the local density of a population. Although it does not explicitly represent the movement of the SPB, it illustrates a fundamental tradeoff for populations exploiting a heterogeneous forest landscape. If individuals move large distances from a natal tree, population densities become diluted, but moving smaller distances may severely limit the ability to locate fresh hosts. These reductions in population densities are important. At the very least, the success of a sexually reproducing population requires the presence of males and females, an event that is likely to become increasingly difficult as population densities decrease. But for the SPB in particular, the efficiency of host location and successful colonization is increased when large numbers of individuals are able to attack *en masse.*

The model illustrated by Figure 6.6 demonstrates some simple, physical consequences of diffusion. Mean SPB dispersal, measured using mark-recapture experiments, has been estimated at approximately 0.25 km, with some individuals moving greater than 1 km from their release site (Turchin and Thoeny 1993). Gara (1967) and Moore and others (1979) found marked beetles at approximately 0.3 km and 1.6 km away from a release site. Mark-recapture studies actually measure the endpoints of beetle movement (or spatial distribution) after a given period of time. In turn, these endpoints are driven by a number of more fundamental processes including:

1. Speed of movement expressed as distance per unit time
2. The amount of time a beetle spends dispersing, driven by motivational states and the loss of beetles from the dispersing population
3. The directionality or tortuosity of movement; for example, does it move in long straight lines or in shorter, non-directed hops

Flight Speed and Time Spent Dispersing

Tethered SPB flight experiments have recorded average flight durations of at least 1 hour during which time individuals covered an average of approximately 1 km (Kinn 1986). Although these experiments do not allow the SPB to exhibit natural behavior (for example, it is unclear whether flight is terminated because beetles are exhausted or whether these durations are indicators of true dispersal behavior), they do yield useful estimates of flight speed (13 m/minute). To place this figure into perspective, the flight speed of honeybees has been estimated between 200 and 300 m/minute (Nachtigall and others 1995).

Flight activity has been shown to be dependent on weather conditions. Moser and Dell (1979a) developed a predictive model of flight based on trap counts and estimated the minimum temperature threshold for flight as 14 ^{o}C. Moser and Thompson (1986) suggest that the threshold may be even lower (approximately 5 ^{o}C) and suggest that discrepancies between these values may be caused by solar insulation. They also estimate maximum temperature thresholds of approximately 38 ^{o}C and suggest that rainfall may also reduce flight activity. Given the relatively slow flight speed of the SPB, it is also suggested that wind may have a large impact upon flight activity, or at least the ability of the SPB to undertake directed flights. In these flight activity studies, the SPB were captured in a network of baited traps, and the number of captures related to weather conditions. Trapping success is therefore dependant on the average size of the dispersing population, in part driven by patterns of emergence and reemergence within the entire population. However, the size of this dispersing population and the length of time an individual spends dispersing may be affected (reduced) by two additional factors: mortality and successful host location. Southern pine beetle adults are short-lived and are unlikely to survive more than 7 days as dispersing adults, but this background mortality may be driven by additional factors such as the weather conditions, the heterogeneity of the landscape (amount of nonhost landscape), and predation. The size of the dispersing population may also be affected by the time it takes for dispersing individuals to locate and colonize a host. In turn, this may vary according to whether dispersal is within an active infestation (with high densities of attacking individuals) such that individuals are able to readily find suitable hosts. Changes in population size and losses from the dispersing population may therefore bias results from trapping experiments and movement patterns inferred from them.

The size of the dispersing population relative to the total population (population within trees) may be a strong indicator of the efficiency of an SPB population. Dispersing individuals, though clearly important for population persistence, are unable to produce offspring and therefore do not make immediate contributions to population growth. In addition, the process of dispersal is costly both in terms of energy expenditure and mortality costs. This suggests that the motivation for dispersal is primarily to find fresh hosts and possibly to escape the effects of competition and predation. This motivational state, along with constraints imposed by beetle morphology and physiology (limitations of flight), and the forest landscape provides the backbone necessary for understanding fine-scale dispersal behavior.

Flight Directionality

The directionality of SPB movement is another fundamental driver of SPB spatial distribution. Host selection by insects has been broken down into a series of four steps: host-habitat finding, host recognition, host acceptance, and host suitability (Kogan 1994, Strom and others 1999). The speed and tortuosity of movement, in both two and three dimensions, of a dispersing population is important because it is related to the ability of individuals to sample or encounter potential hosts and conspecifics. Little is known about this fine-scale movement behavior. For example, it is not known whether individuals undertake large numbers of short flights, moving from tree to tree to continuously evaluate potential hosts, or whether they undertake flights of relatively longer durations before landing on a host.

Kinn (1986) observed that in an absence of an attractant or at distances greater than 20-25 feet (6.1-7.6 m) from an attractant, SPB will tend to disperse (meaning long range dispersal) (Gara 1967, Gara and Coster 1968). Under such conditions beetles tended to fly upwards at a steep angle of ascent. In contrast, individuals within the range of an attractant were observed to fly 1-5 m above the forest floor. Given the model outlined in Figure 6.6, it is plausible that the SPB employs different behaviors while dispersing within infestations (high density populations) compared with long-range dispersal. A number of authors have noted that infestations occur in the direction of prevailing winds, suggesting that long-range dispersal may occur above the canopy. It has also been suggested that the heterogeneity of the landscape itself may affect the speed and directionality of dispersal; for example, Turchin and Thoeny (1993) found aggregation of beetles within stands with high basal areas, and it is possible that understory development, the height of forest canopies, and the juxtaposition of different stands may also lead to marked three-dimensional corridors that affect SPB dispersal.

6.3.2. Host Location and Selection Mechanisms

The need to find new hosts each generation, the dilution of local population densities, and

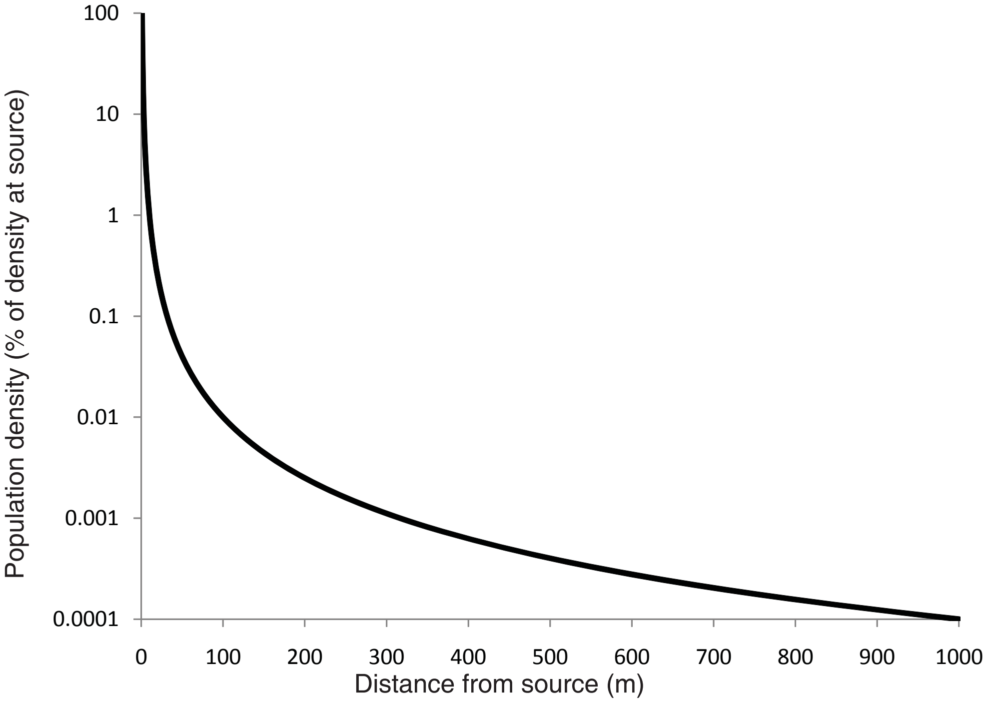

Figure 6.6—A simple model for the reduction in population density (individuals per unit square) with distance *r* from a population source. Note the use of log10 scale on the y-axis. The relationship is based on a fixed number of individuals evenly distributed over the area of a circle with radius *r* so does not account for a gradient of population density from a point source.

the speed and fine-scale movement behavior of dispersal drive much of the spatial distribution of SPB populations. But for the SPB, the ability to detect and respond to chemical (either host volatiles or pheromones) or visual cues in order to locate hosts is another important component of dispersal, hence population dynamics. Figure 6.6 is relevant as a base for exploring the relationship between movement and local SPB densities, and highlights the importance of chemical or visual cues for increasing the efficiency of host-finding and beetle aggregation. These host-finding mechanisms therefore provide much of the detail necessary to fully understand SPB dispersal. An indepth discussion of the role of chemical and visual cues for host-finding has been discussed elsewhere in this volume, and this review will focus on the consequences of these mechanisms.

Host volatiles alone (α-pinene) are unlikely to attract SPB (Payne 1980), especially over large distances. As a result, beetles are most likely to locate fresh unattacked hosts through a process of random searching. However, once a suitable host has been located, pheromones produced by attacking beetles (most notably frontalin) attract conspecifics and drive the aggregation of beetles. Although no detailed experiments have been conducted (Byers 1989b), it is reasonable to assume that the concentration of pheromones increases as the host accumulates individuals. It follows that the attractiveness of new, actively infested trees may follow a positive feedback loop driven by the spatial and temporal distribution of beetles around the host. In two dimensions, this might be conceptualized as a radius of pheromone influence—individuals that move within this radius will become affected by the chemical. Figure 6.6 suggests the importance of this process to the SPB. As individuals disperse further away from a population source, the likelihood of finding a conspecific by chance are greatly reduced. For low density, endemic populations, assuming susceptible hosts are rare and the mortality costs associated with attacking a fresh host are high, any mechanism that facilitates aggregation is likely to be important for population growth. Byers (1996) developed a model of host-finding based on these concepts and concludes that host-finding efficiency is greatly increased when this feedback mechanism occurs, and that even endemic populations may be able to locate rare, highly susceptible hosts relatively efficiently. The model could also be expanded to three-dimensional space. Here, this area of influence could be envisaged as a volume of influence that may extend above the forest canopy but is bounded by the forest floor or understory. The extent, shape, and longevity of such plumes are likely to be driven by wind, humidity, canopy closure, rainfall, and temperature. While quantification of the diffusion of pheromones and the attractiveness of beetles is difficult to measure, this three-dimensional view of the forest may be useful for understanding the potential advantages of dispersal above or below canopies.

In addition to driving the aggregation of beetle populations, it is possible that chemical cues affect SPB populations in other ways. For example, assuming that aggregation pheromones are driven by the presence of SPB, they also present a consistent cue that can be used by predators. Clerid beetles and *Monochamus* spp. have been shown to respond to chemicals associated with beetles (Allison and others 2001, 2003; Mizell and others 1984), while parasitoids also use chemical cues to distinguish between preferred life stages within such trees (Sullivan and others 2003).

Populations of the SPB are also often associated with other pine beetle species (for example, *Ips* spp., *Dendroctonus terebrans*). Each species minimizes competition by occupying different niches within infested trees (Wagner and others 1985), but as species colonize suitable hosts they may also facilitate host location and successful attack by the SPB. The extent to which olfactory cues are used interspecifically is subject to debate. Payne and others (1991) found a behavioral response by SPB to compounds produced by *D. terebrans* but not to those produced by *Ips spp*. In contrast, *Ips* spp. did respond to SPB compounds. Whether the SPB is a pioneer species in such guilds or makes use of trees already weakened by other species, the fine-scale interactions between species within the guild of southern pine bark beetles may be important for understanding broadscale SPB populations.

Although aggregation of beetles is important for host attack, intraspecific competition occurs in high density populations (Reeve and others 1998). Here, antiaggregation pheromones may serve to repel beetles from an infested host that is either too old or contains excessively high populations densities, such as may occur within large infestations. Antiaggregation effects are interesting not only for driving the ecology of SPB populations but also for direct management. Within infestations they drive the mechanisms that cause attacks to switch from infested hosts to fresh hosts; hence, the magnitude of damage within an infestation. Possibly of greater importance, it is conceivable that they drive the mechanisms that determine the timing and amount of dispersal away from active infestations and thus affect the contagion of infestations. A paradox for SPB populations is that assuming the benefit of aggregation, it is unclear how it can be advantageous for individuals or genotypes to move away from high density population sources (infestations). Assuming a high cost of dispersal and the rapid reduction in population density away from an infestation, it is difficult to see how it would be advantageous for individuals to intentionally move away from infestations. The following hypotheses might be proposed:

1. Emigration is unintentional. It may be caused by strong winds affecting the SPB's ability to undertake directional flight or by a breakdown in pheromone communication during periods of unfavorable weather, or by an infestation growing too large too quickly and leaving infested trees (therefore individuals emerging from them) too far away from pheromone sources at the head of the infestation.
2. Emigration is a response to predation.
3. Emigration is a response to seasonality, a factor that consistently leads to a reduction in local population densities. If densities become too low to overcome the defenses of local trees, the dispersal may be a more optimal strategy.
4. Emigration is a response to intraspecific competition and occurs when the mortality costs associated with dispersal are lower than those associated with competition.

These hypotheses are speculative but are also testable. Depending on the hypothesis, emigration will be proportional to population growth, related to measurable weather indices or to predator numbers. In the case of a response to intraspecific competition, one might expect that during early stages of infestations, individual beetles will tend to remain within an infestation because they have a high value for infestation growth, and emigration as a proportion of the population size will increase as the population density within each tree increases. In turn, densities of within-tree individuals might increase as a result of changes in the susceptibility of trees (for example, if the infestation reaches a stand boundary) or as a result of other environmental changes such as seasonal temperature changes that interrupt the emergence of beetles, reduce the Allee effect, and thus limit the availability of new hosts.

However speculative these hypotheses may be, understanding why beetles disperse is important to understanding when and where damage will occur. Armed with knowledge of why the SPB disperses, it is possible to develop robust models, whether conceptual or mathematical, driven by the motivational state of the organism. In turn, these motivational states are likely to be driven by local environmental conditions including population size, temperature, and predation that may drive different dispersal strategies across the SPB's range. One of the tools that ecologists can use to complete this process is to measure, map, and visualize the landscape from the SPB's rather than human perspectives. Population models often assume that organisms move or behave in predefined ways, usually based on real-world measurements. But armed with an SPB-centric view of the environment, a method based around the concept of SPB populations seeking to optimize environmental resources may offer a fruitful perspective to the problem. Such concepts clearly depend on strong concepts of what an optimal behavior actually is (maximized population growth, population persistence, or the success of individuals or genotypes) and on the tradeoffs and limitations of certain life-history processes. Clearly 100-percent survival and infinite reproduction would be optimal but unrealistic. For the SPB, one of these tradeoffs (dispersal distance) is readily apparent and may be the cornerstone necessary to understand complete SPB population dynamics.

6.4. CONCLUSIONS

Southern pine beetle population dynamics are complex. After 40-plus years of study there are no definitive explanations for why populations oscillate between high density (outbreaks or epidemics) and low density (endemic) populations. They are also difficult to study directly, which makes it imperative that processes that can be or have been measured are integrated into more complete descriptions of population dynamics. One conclusion from this review is that although much is known about the ecology of the SPB, there are still too many unknowns for a complete, definitive model of population dynamics to be developed. Given the difficulty of studying SPB populations directly, it is suggested that much can be gained by piecing together these ecological processes into more comprehensive models of dynamics.

How these observations are pieced together is important. In the long run, it is desirable to develop models capable of explaining the entire dynamics of the SPB—models that include spatial and temporal dynamics and that explain the characteristic patterns of outbreak and nonoutbreak dynamics. But realistically, these real-life processes are complex. In the short term, smaller modules of SPB population processes can be developed; for example, models of infestation growth, dispersal and host-finding, population regulation, contagion of infestations, and so on. These smaller portions of population dynamics are relatively easy to develop, understand, and validate compared to models representing complete SPB dynamics. Some may also have an immediate practical value for SPB management. Most important, once models are assembled and documented they provide tangible, testable descriptions of population dynamics. Since there are a large number of ways in which SPB ecology can be interpreted, the development of multiple working models, each with respective merits and weaknesses, should greatly contribute to overall understanding of SPB population ecology.

Throughout this review, the word “model” refers to a conceptual or mathematical explanation of how some components of the SPB system work. Three conceptual models have been proposed that offer an explanation for changes in SPB populations. A number of other models have been proposed that describe dispersal and host location. These conceptual models are an important first step to understanding SPB dynamics. However, population ecology is a quantitative disciple. It links quantitative rules for reproduction, death, and movement to changes in the number or distribution of individuals through space and time. The advantage of mathematical over conceptual models is that they demand a logical integrity that helps to translate conceptual models into testable ideas. At present, the predator-prey hypothesis is the only complete model of population regulation that has been represented in this way (Turchin and others 1991). At the very least, the model demonstrates that a predator-prey model is capable of explaining the oscillations shown by SPB populations. By incorporating an error term in the model, the authors allow for the fact that the model parameters (population growth) may be affected by other unexplained factors (e.g., climatic variations, changes in host susceptibility), some of which are also discussed in this chapter. These are ecological details currently only implied by the predator-prey model, and that need further explanation and research.

One of the conclusions of this chapter is that SPB dynamics are complex. But this complexity arises because many processes are responsible for driving patterns of birth, death, and movement. More specifically, the importance of each proposed mechanism changes according to the spatial or temporal scale at which a population is studied. Over a single year, changes in temperature clearly play an important role in population dynamics. During endemic phases, the availability of highly susceptible trees and the ability of the SPB to find them may be the important factors. Within infestations, temperature, the size of the attacking population, and its effect on host susceptibility (the Allee effect) may drive overall patterns of damage. And within an infestation, populations in a single tree may be primarily driven by competition and predation. This complexity, driven by the spatial and temporal scale of any particular study, is likely one reason why SPB dynamics are currently not well understood. An advantage of a quantitative approach is that it disambiguates the spatial and temporal scale of any conceptual model and clarifies the importance of different processes and mechanisms.

Finally, data is required in order to test and evaluate models. Southern pine beetle populations are difficult to study directly, but spatial distributions of beetles can be estimated using trapping experiments or by documenting visible signs of tree mortality. In addition to population or damage data, measurements are required that document the state of the forest, predator populations, climate topography, or any other factors that could be important drivers of population dynamics. To extract maximum value, the spatiotemporal scale and resolution of all data sets should be comparable, and the data sets should be well documented and readily available to researchers. Given the complexity of the SPB system, it is doubtful whether any individual, using observation and experience alone, could ever effectively organize the vast amounts of information associated with the SPB. Extensively managed forests, a large geographic range, infrequent and unpredictable outbreaks, and the importance of both spatial and temporal dimensions present large challenges for data collection and organization. In a given year, outbreaks might occur simultaneously at opposite ends of SPB's geographic range. These outbreaks might occur in landscapes with very different environmental conditions, and each may exhibit subtle differences in the spatial and temporal patterns of damage detectable only through meticulous observation or data collection. Some outbreaks may be so severe that it is impossible to document each infestation in detail without using complex sampling methods. The organization of this information is imperative for understanding the SPB problem at all scales. Advances in GPS technology and Web-based data entry, storage, and retrieval tools are beginning to address these problems (see chapter 21). When populated with data, these tools should provide an unprecedented overview of SPB damage and population dynamics viewable at any number of spatial and temporal scales, and provide a comprehensive overview of historical SPB activity necessary to further the development of improved population models.

7

Regional Population Dynamics

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Keywords

population dynamics
region
southern pine beetle

Abstract

The population dynamics of the southern pine beetle (SPB) exhibit characteristic fluctuations between relatively long endemic and shorter outbreak periods. Populations exhibit complex and hierarchical spatial structure with beetles and larvae aggregating within individual trees, infestations with multiple infested trees, and regional outbreaks that comprise a large number of spatially distinct infestations. Every year at least some part of the Southern United States experiences outbreaks, and the large and unpredictable timber losses associated with these make the SPB the most important pest of southern forests. This chapter reviews the mechanisms that may drive SPB populations at a regional scale. More specifically, it focuses on the initiation and decline of outbreaks, the patterns of damage within them, and the utility of this knowledge for managing the SPB.

7.1. INTRODUCTION

Previous chapters have discussed the population dynamics of southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) at the spatial scale of a single tree, within a single stand or infestation, and across a broader landscape. A feature of this organization is that each viewpoint is intrinsically related —populations within trees drive stand level (infestation) dynamics, which in turn drive landscape-scale dynamics. In addition, each of these spatial units is associated with a distinct temporal scale. For example, population dynamics within a single tree may operate over approximately 30-120 days, a single infestation may last for 90 days to a year, while an outbreak within a landscape typically occurs between 1 and 3 years.

One outstanding challenge for SPB population biology is to integrate information at each of these basic spatial and temporal units into a complete and coherent picture of SPB dynamics. Another significant challenge is to understand how these biological processes ultimately impact humans and the management of the SPB. This chapter deals with SPB population dynamics at a regional scale. Although a definition of region is at least contentious, for the purposes of this paper it is defined as a spatial unit that allows the study and understanding of a complete, and as far as is possible, endogenous cycle of population dynamics from endemic to epidemic and back to endemic phases. The next section provides a historical overview of SPB outbreaks and discusses the appropriate spatial and temporal scales to study regional dynamics.

The question of what causes SPB outbreaks is central to a discussion of regional dynamics and has both economic and intrinsic ecological implications. The fluctuations characteristic of the SPB are an interesting case of population dynamics. This chapter also discusses hypotheses that may explain the causes of these outbreak dynamics and evaluates the evidence for each. Since this chapter takes a regional view, these hypotheses are evaluated based on factors capable of driving rapid population growth but also the subsequent decline of populations. In other words, they must account for the fact that populations are approximately stable in the long-term, but that stability is maintained by a finer scale temporal pattern of population increases and declines. However, in addition to intrinsic ecological interest, SPB research is also driven by its importance as a pest. The key components of this pestilence are large-scale tree mortality, depression of regional timber prices, and the disruption of local economies (see chapter 14 on economic impacts). Also important, the location and timing of SPB damage is largely unpredictable and pulsed. If the total damage caused by the SPB were metered out evenly through space and time, it is unlikely that the SPB would be such an important pest. A key to managing SPB pestilence is therefore to understand how regional population dynamics drive this spatio-temporal pattern of tree mortality. This chapter concludes by discussing how current knowledge of regional population dynamics could be used or are currently being used to manage the SPB.

7.2. HISTORICAL PERSPECTIVE

Figure 7.1 shows the historical record of SPB activity (counties in outbreak status) between 1960 and 2000 throughout the Southeastern United States. Outbreak status is defined as one or more SPB infestation per 1,000 acres of appropriate host type. In turn, an infestation, or spot, is defined as greater than 10 contiguously infested trees. Visually, the record shows a number of key features of the SPB problem:

1. Between 1960 and 2000, SPB outbreaks have occurred at least somewhere in the Southern United States.
2. There is considerable variation from year to year in the number of counties experiencing outbreak conditions, hence the severity of the regional or nationwide SPB problem.
3. The spatial pattern of outbreaks shifts from year to year, but outbreaks tend to be spatially and temporally correlated. In other words:
    a. Areas with SPB activity tend to be spatially and temporally aggregated (outbreaks tend to extend over a number of contiguous counties).
    b. A county is more likely to experience an outbreak in the current year if it experienced one the previous year.
    c. Counties bordering existing outbreaks are more likely to experience an outbreak the following year.

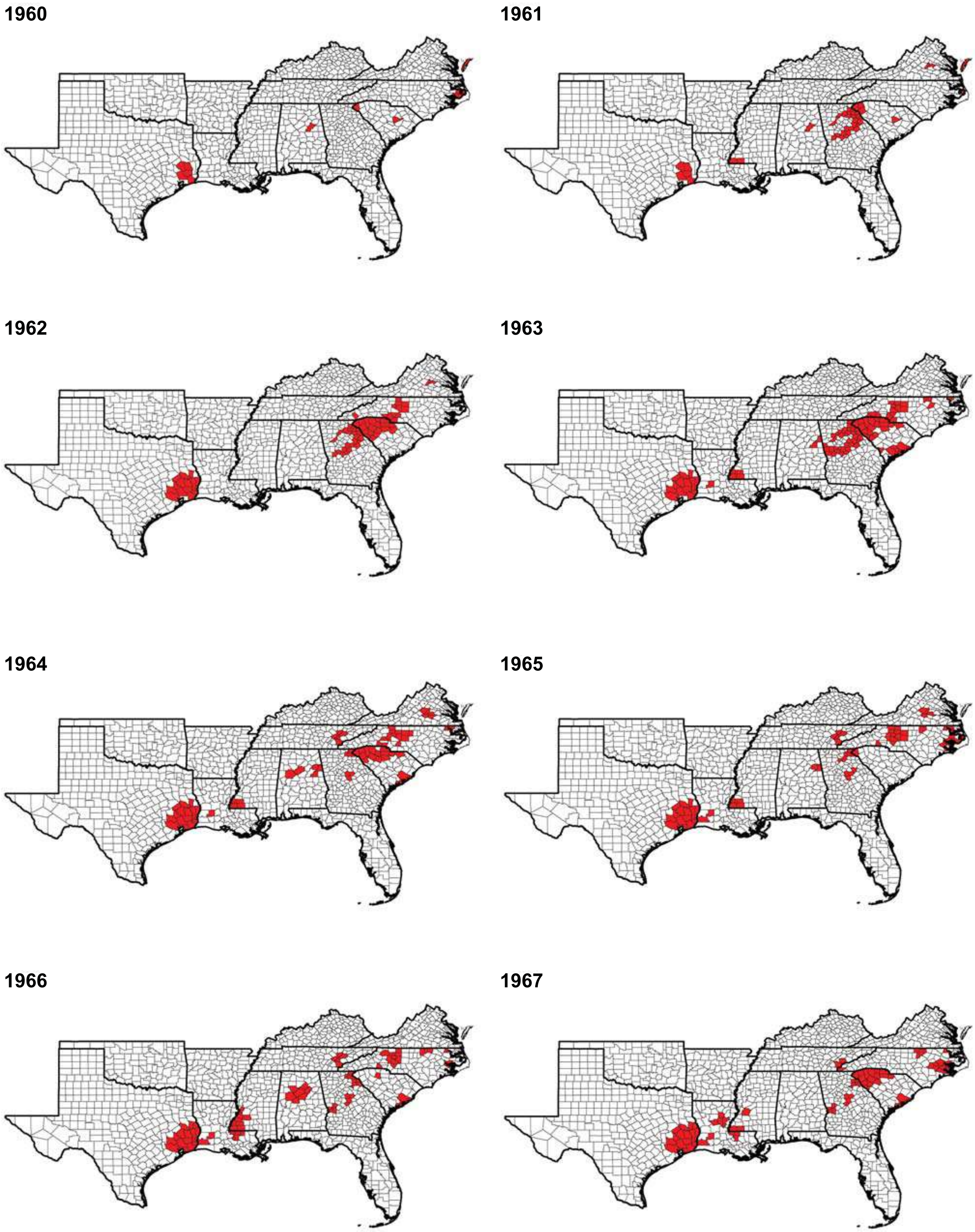
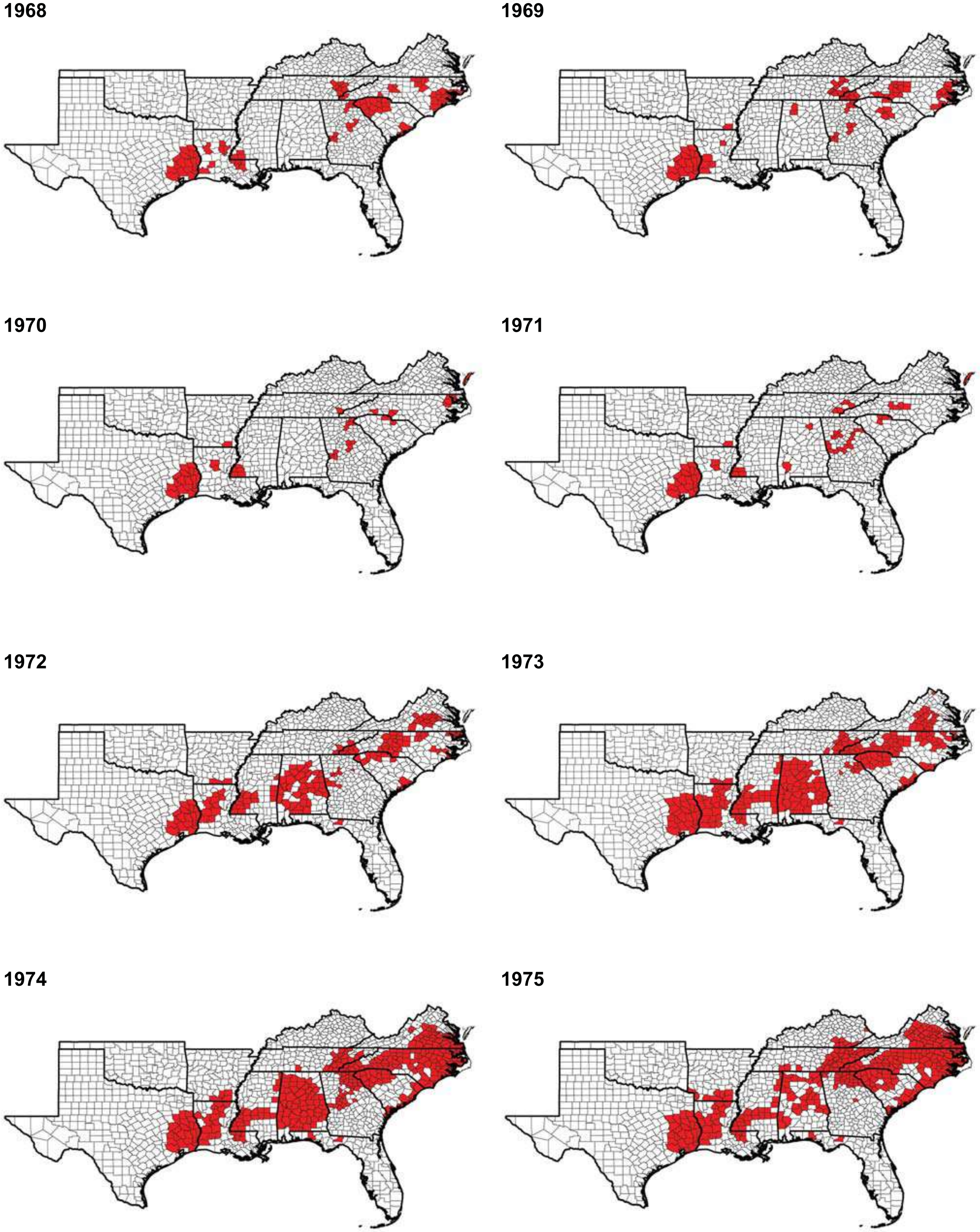


Figure 7.1—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)



1968

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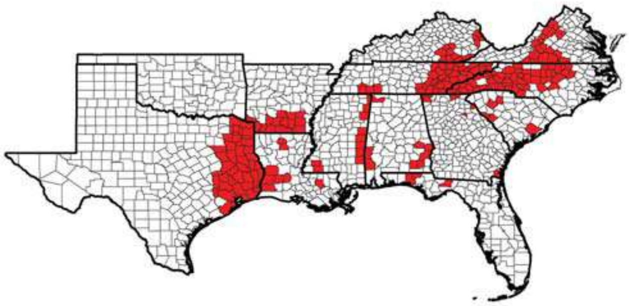
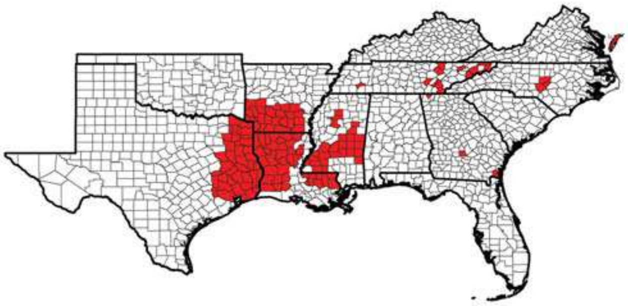
Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)

1976



1977



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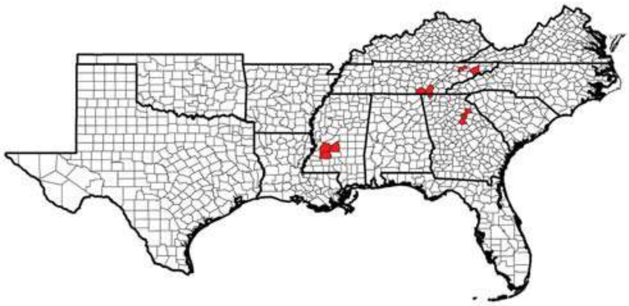

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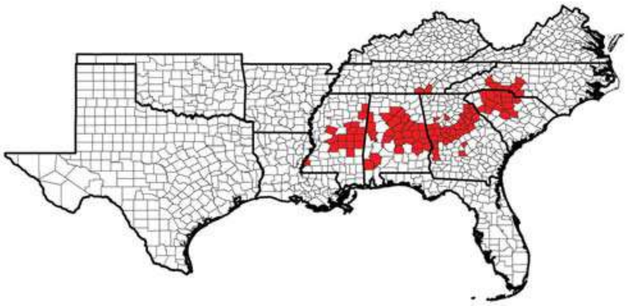

1980

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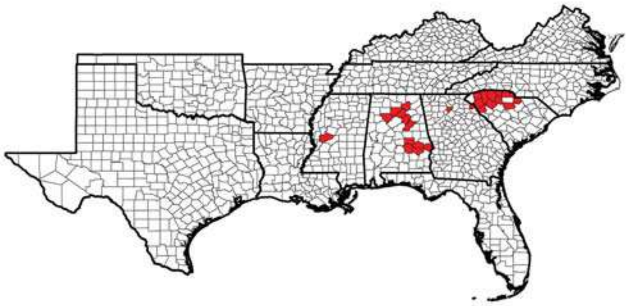
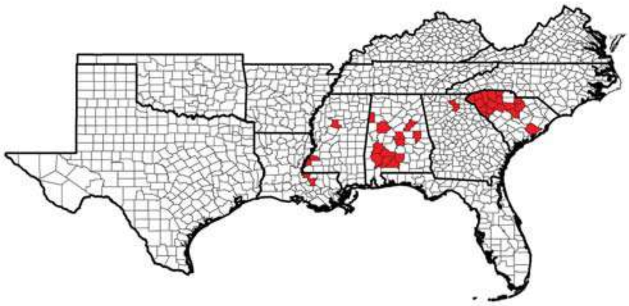


1982



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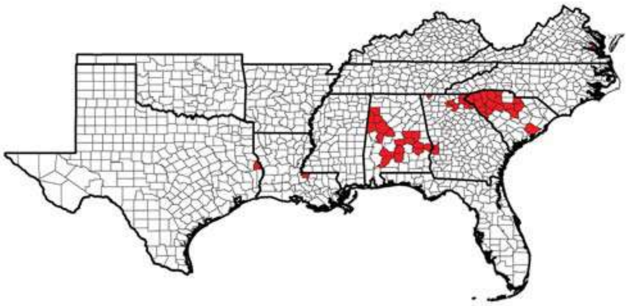

Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)

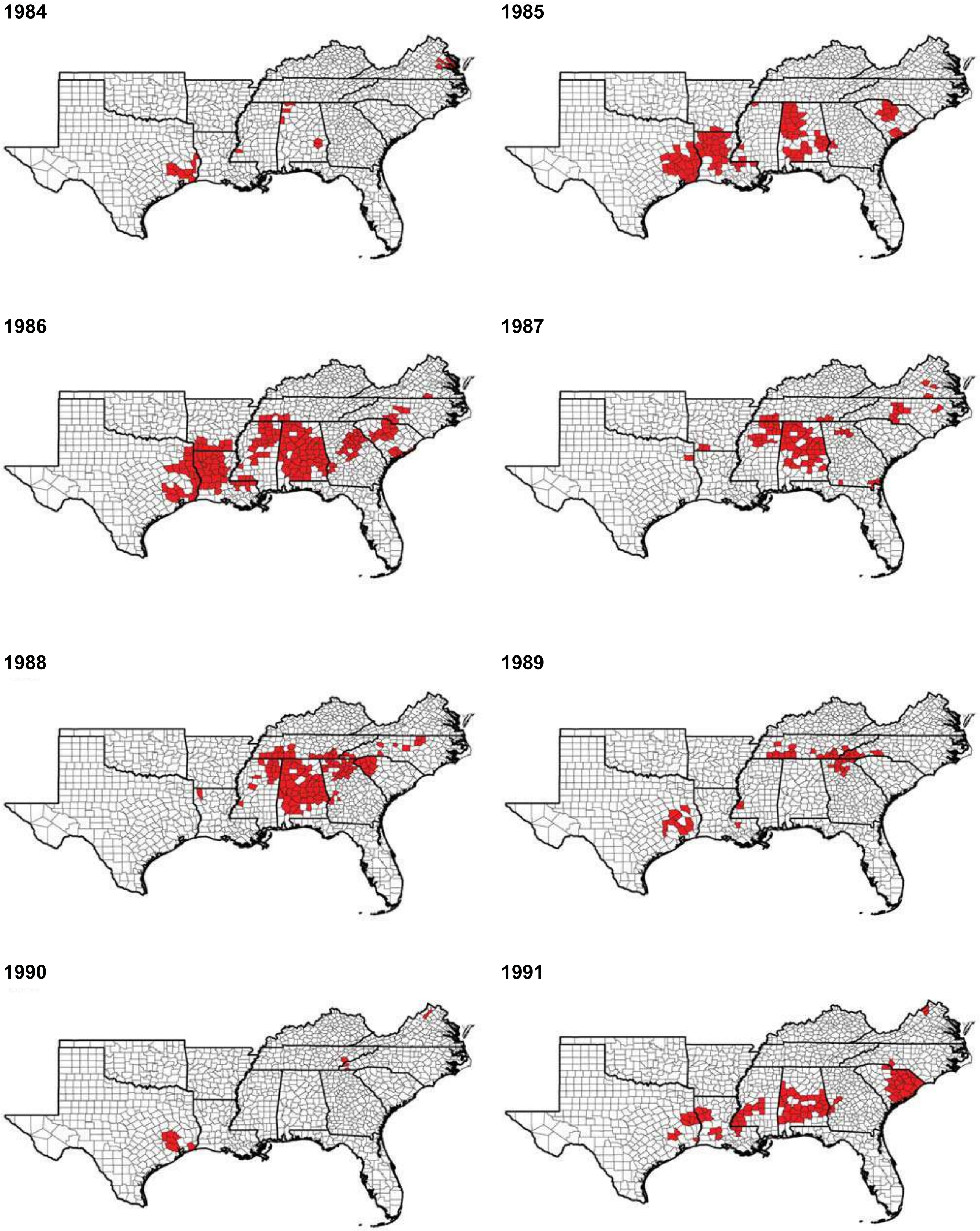

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Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)

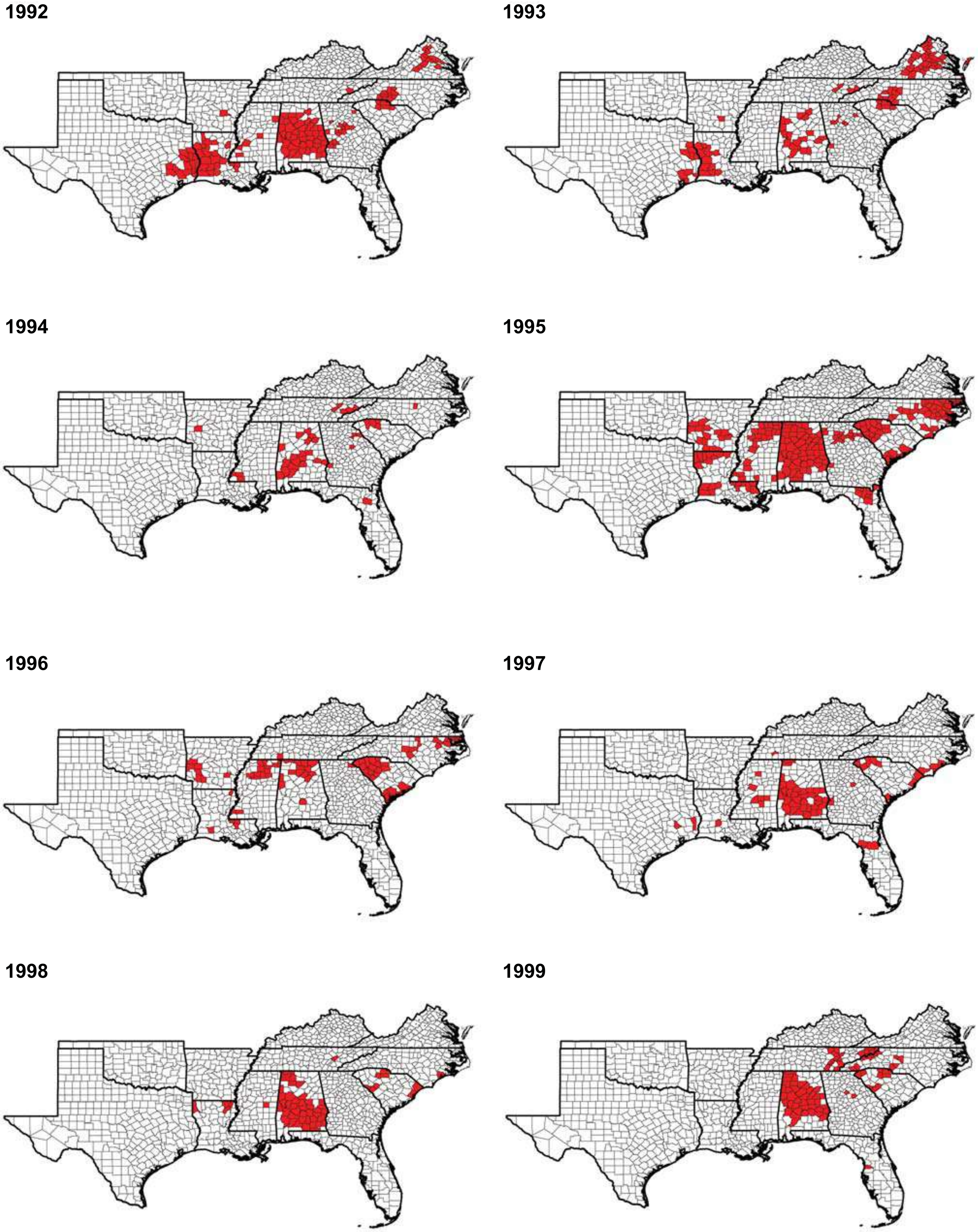

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Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red. (continued on next page)

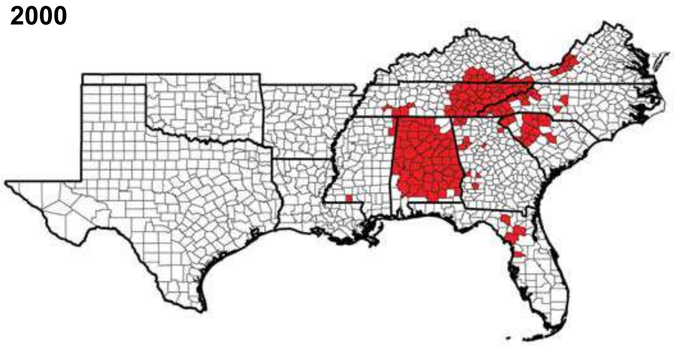


Figure 7.1 (continued)—Southern pine beetle outbreaks in the Southern United States between 1960 and 2000. Counties with outbreaks (defined as greater than 1 infestation per 1,000 hectares of host) are colored red.

4. Despite this spatial and temporal correlation, in some years outbreaks appear to occur spontaneously within a region; i.e., a county may become active even when spatially and temporally separated from previous outbreaks.

Figure 7.2 summarizes the detail presented in Figure 7.1 by reporting the frequency of outbreaks occurring in each county. Here the temporal pattern is lost, but areas that experience frequent outbreaks are clearly visible. These areas include East Texas, western Mississippi, central Alabama and northwest North Carolina.

7.2.1. Regional Patterns of SPB damage

Southern pine beetle population dynamics are complex and have strong spatial and temporal components. Figure 7.3 uses infestation counts and interpretations from known outbreaks to illustrate this concept approximately. Using the number of infestations per unit area as an index of population size, temporal fluctuations in the dynamics of the SPB within the Southeastern United States are relatively stable through time compared to fluctuations in populations within a single county (Hardin County, Texas), which in turn are more stable than for a single km^2 area. In other words, any observed pattern of population dynamics changes with the spatial scale of the observation. Figure 7.3 therefore highlights the importance of choosing the correct spatial and temporal scales for a study. A number of factors may affect this choice, including the availability of data, the known biology of the organism, and the socioeconomic implications (pestilence) of an organism's dynamics.

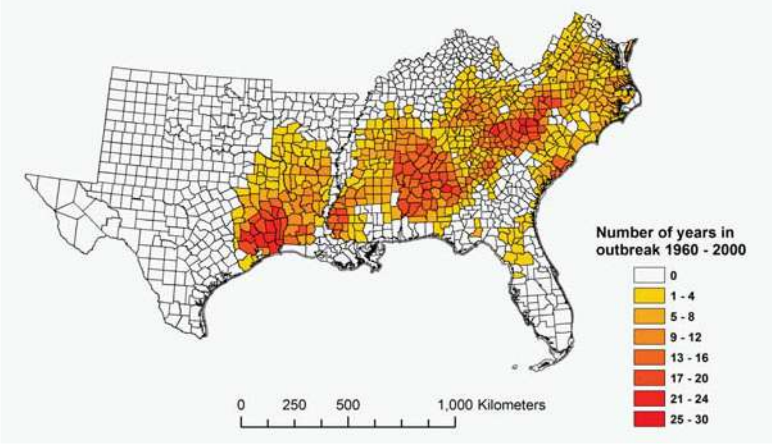


Figure 7.2—County map showing outbreak frequency in the Southeastern United States between 1960 and 2000.

Data Constraints

Although Figures 7.1 and 7.2 are useful summaries of SPB activity and abundance, the grain of the maps mask important information about the dynamics of the insect and the ecology that drives it. Central to this problem are precise practical and ecological definitions of both "infestation" and "outbreak." Practical definitions are relatively easy. An infestation is usually defined as a cluster of greater than 10 contiguous dead trees, while an outbreak occurs when greater than 1 in 1,000 acres of available host type incur an infestation (Gumpertz and others 2000). However, ecologically these definitions lack clarity. Whereas the spatial and temporal delineation of a population within a tree is very clear, for infestations and outbreaks this clarity is blurred. Infestations often grow into one another to create a large, single area of contiguous tree mortality or split into one or more divergent, active heads. Similarly, given the county level outbreak patterns illustrated in Figure 7.1, it would be reasonable to question the precise nature of the spatial pattern of infestations for a single year within a county. Figure 7.4 illustrates two possible, and contrasting, spatial patterns that might be extrapolated from county level maps, using 1990 as an example. Each would suggest very different spatial and temporal definitions for what constitutes a single, self-contained population. Similarly, Figure 7.5 illustrates three possibilities for the spatial and temporal pattern of infestations within an outbreak.

The complex spatial and temporal dynamics of the SPB therefore drive much of the difficulty of

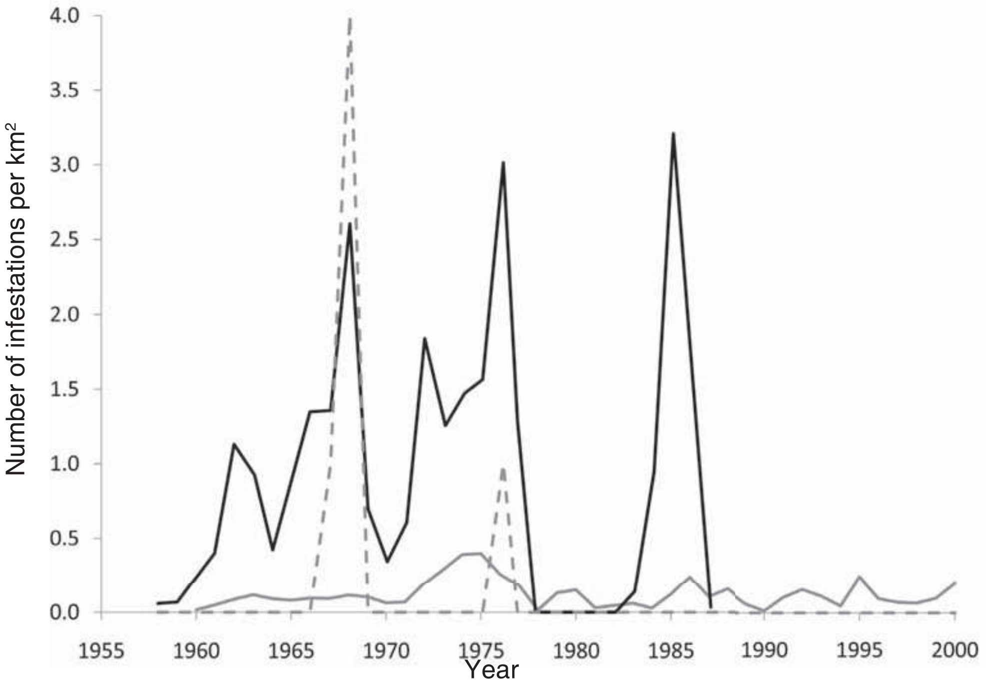


Figure 7.3—Graph illustrating how changes in spatial scale lead to changes in an observed temporal pattern of populations. Each line shows the number of infestations normalized to a single km^2 area. The solid grey line shows a relatively stable temporal pattern of infestations across the whole Southeastern United States. The solid black line shows the number of infestations in Hardin County, East Texas, and the dashed grey line shows the number of infestations in a single km^2 area of the Bankhead National Forest, Alabama. The graph and the pestilence of SPB illustrates the importance of spatial models of SPB populations.

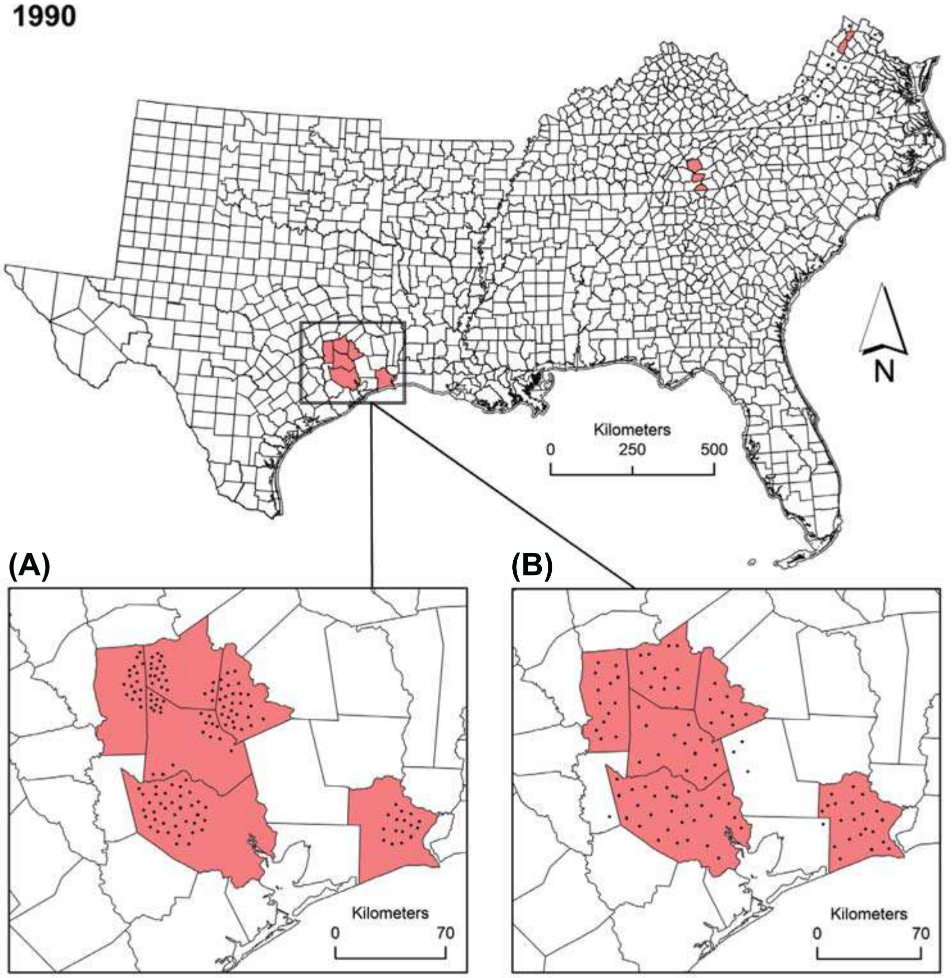
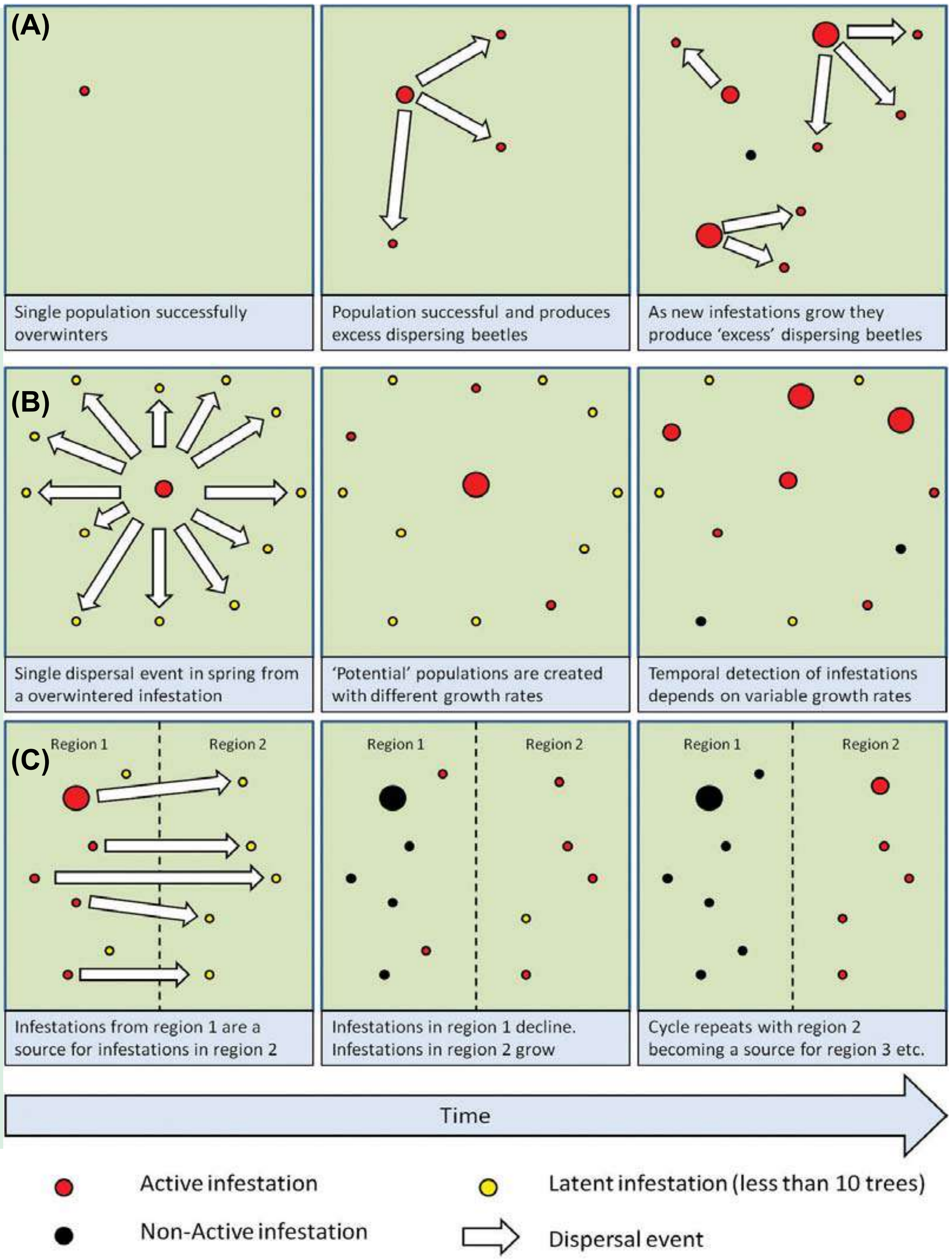


Figure 7.4—Two plausible patterns of the structure of infestations within an outbreak, extrapolated from county level observations as displayed in Figure 7.1; (A) illustrates a number of discrete, delineated populations. Each pattern is likely to be driven by different population processes particularly dispersal; (B) shows a homogenous pattern of infestations. Since the actual pattern of infestations within counties is unknown, the figure cautions against over interpreting the data displayed in Figure 7.1.

Figure 7.5—Diagram showing three plausible mechanisms of outbreak initiation and expansion. In the top panel (A) a single infestation (in early spring) grows and produces an excess number of beetles, which disperse across the landscape to initiate new infestations. In the second panel (B) a single infestation (possibly one that has successfully overwintered) leads to a single migration event and the initiation of new infestations. Through time, some of these infestations are successful and grow quickly; others grow more slowly and some die out. The final panel (C) illustrates a situation of mass movement from one region to another. To a large extent, the mechanisms in each panel represent the endpoints of a continuum, and owing to the difficulties of studying SPB, the exact spatiotemporal details of the pattern is unknown. One of the goals of population research is to understand how changes in basic ecological processes such as fecundity, survival, development, and dispersal relate to changes in the observed spatiotemporal structure of the population.



studying the insect and collecting and interpreting data. In truth, a complete picture of a typical outbreak is unknown because of these difficulties. First, the small size of the SPB and the sheer area of forested areas also make dispersal of individuals and the delineation of discrete populations difficult to determine accurately. Second, population dynamics tend to be observed indirectly through the symptoms of damage (the reddening of tree crowns) rather than the actual abundance of the insect. This reddening of tree crowns may also only appear some time after trees have actually been killed (Billings and Kibbe 1978), the delay depending on factors such as temperature, water availability, and the frequency that surveys are carried out. In short, however accurately field surveys are performed, measures of SPB population dynamics are indirect and subject to considerable errors. Finally, the geographic range of the SPB includes areas with different physical, vegetative, and climatic characteristics, and a landscape under constant change. In any analysis of population data, researchers must make allowances for all the variables deemed important. In effect, there are no true replicate or controlled data sets available for the study of large-scale SPB populations.

Spatial Scale and the Biology of SPB

Ideally, population dynamics should be described using simple, parsimonious ecological mechanisms for a system that is as enclosed or self-contained as possible. The hypothetical patterns shown in Figures 7.4 and 7.5 are driven by simple biological mechanisms such as quantities and timings of births, deaths, development, and dispersal. One goal of population ecology is to link basic life history of individuals to realized pattern of population dynamics, and in an applied context, to use this basic level of understanding to predict, prevent, and manage populations. Much of the difference in pattern illustrated by Figures 7.4 and 7.5 is likely driven by the timing and amount of dispersal away from growing infestations to initiate new ones. Figure 7.5A illustrates a situation where an outbreak is initiated by relatively few infestations, which grow throughout the season, producing excess beetles that initiate new infestations. In contrast, Figure 7.5B illustrates a situation where a number of infestations exist simultaneously at the beginning of an outbreak, some of which grow to large size and some of which decline before they become detected. Figure 7.5C illustrates a final hypothesis where the size of a regional population remains relatively constant through time and outbreaks occur as a population moves from one active region to an adjacent one. Each pattern must be driven by very different mechanistic population processes (e.g., development, survival, reproduction, and dispersal). Understanding these mechanisms is therefore crucial to predicting when and where SPB outbreaks are likely to occur in the future.

SPB Pestilence and Spatial Scale

Since the SPB is important as an applied problem, an appropriate spatial scale of study could be selected based on the outstanding needs of managing the population. For example, using the spatial hierarchy outlined in this text, within-tree populations of the SPB are relatively easy to study and relatively well understood but offer little direct value for practical management. Population dynamics within an infestation are also relatively easy to study and relatively well understood and offer some practical value in understanding the intrinsic hazard of particular stands should they become infested. Populations within a landscape and at a regional scale are, however, much more difficult to study, but arguably offer the most benefit for managing the SPB. In particular, regional scale dynamics are dominated by fluctuations between outbreaks and nonoutbreaks that cause massive, pulsed timber losses. This glut of timber may lead to depressed timber prices and costs of restoring forests that have long-term effects on local economies. Socioeconomic effects are therefore driven by the loss of value that occurs when trees are killed by the SPB at a regional scale.

Defining an Appropriate Regional Scale

The following sections describe three hypotheses that could explain regional fluctuations in SPB populations and the transition from endemic to outbreak and back to endemic populations. For clarity, regional is defined as a spatial scale of between 2500 km^2 (a typical southeastern county and the smallest outbreak given Figure 7.1) to 150 000 km^2 (corresponding to roughly size the size of the largest outbreak area). This scale is relevant to the economic impact of SPB dynamics, but also because it is probably large enough that the dynamics of the population can be described endogenously. However, since we have neither definitive patterns of SPB populations through space and time nor absolute knowledge of its life history and behavior, this definition may be subject to future debate. The remainder of this chapter will discuss how basic life history processes of births, deaths, development, and dispersal (for which other chapters in this text describe much valuable detail) may lead to the characteristic and economically important fluctuations of SPB populations at this regional scale.

7.3. REGIONAL POPULATION DYNAMICS

Several hypotheses have been proposed to explain the periodic outbreaks of SPB. The most significant of these are:

1. Outbreaks are driven by predator-prey interactions.
2. Outbreaks are driven by host interaction and intraspecific competition.
3. Outbreaks are driven by annual and geographic variations in weather.

It is noteworthy that after approximately 50 years of study, none of these hypotheses have been unanimously accepted by SPB researchers. To a large part, this can be explained by the inherent difficulties involved in studying the SPB and devising long-term, large-scale experiments to test hypotheses. As a result, much of our knowledge of the SPB has been derived through experiments at spatial and temporal scales where the insect is easy to study (for example, within-tree or within-infestation dynamics). This section presents a detailed review of mechanisms important to each hypothesis and an interpretation of how these pieces of SPB ecology might be pieced together to form a cohesive view of regional dynamics.

7.3.1. Predator-Prey and Interspecific Competition as Drivers of Regional Outbreaks

The most complete explanation for the pattern of population cycles displayed by the SPB involves delayed density-dependence driven by insect predators. In delayed density-dependence, the rate of population change in a given year is inversely related to the size of the population during one or more previous years. Using time series data collected from 1958 to 1990, Turchin and others (1991) developed statistical and mechanistic models to show that cycles in the abundance of the SPB in East Texas can be explained by delayed density-dependence with a lag of 1 and 2 years. In other words, the rate of population growth or decline in any given year is inversely related to the size of the population 1 and 2 years previously. They hypothesized that natural enemies are the principal drivers of this density-dependant effect. Subsequently, a 5-year experimental test of this hypothesis found that survival of SPB broods was significantly higher in trees protected from predators than in control trees (Turchin and others 1999b). In addition, they found that annual changes in the population density of the SPB (detected using a broader network of pheromone traps) were correlated with changes in predation (see chapter 29 for an alternative explanation).

Although these experiments did not explicitly identify a predator that drives this system, the clerid beetle *Thanasimus dubius* is generally considered one of the SPB's most important regulators based on its direct observations and association with SPB populations (Reeve 1997), predation of SPB adults, and dispersal capabilities (Cronin and others 1999). However, ecologically significant predation may not be limited to this species alone. The aggregation of the SPB into infestations, resulting in locally high population densities, offers a potentially large resource for predators and competitors to exploit. It is therefore not surprising that a complex of predators and interspecific competitors are known to associate with SPB infestations (Moser 1971).

Spatial detail is not explicitly included in the model of Turchin and others (1991), but regulation by predators or competitors must involve mechanisms that explain the efficiency with which they are able to locate infestations. As with any model, some imagination and interpretation are needed to conceptualize the mechanics of these real-world details and evaluate whether its assumptions are ecologically plausible. In particular, it is interesting to speculate whether infested trees will always be located by predators, given the dispersal capabilities of both species. Inefficient prey location might cause infestations that escape predation to exhibit increased population growth and possibly outbreaks. By introducing more ecological detail (e.g., dispersal of both predators and prey) it is possible that the model will exhibit quite different behavior. Such arguments serve as a reminder that, by definition, no model can represent a complete description of an ecological system. In particular, given the importance of space and unpredictability to SPB pestilence and management, a major criticism of Turchin and others (1991) delayed density-dependence model is that it is capable of explaining regional outbreaks, but does so without considering the spatial pattern of infestations within an outbreak. It would be interesting to find whether the delayed density-dependence hypothesis would be strengthened or weakened by a spatially explicit version of the original model.

Although delayed density-dependence is most often associated with predation, it may also be driven by other ecological factors. For example, Hofstetter and others (2005) highlight significant interactions between SPB, *Tarsonemus* mites (phoretic parasites of the SPB), and blue stain fungi (*Ophiostoma minus*). The latter species often infects the phloem of infested trees and inhibits the development and survival of SPB brood, and its spread appears to be facilitated by the presence of *Tarsonemus* mites on the SPB. Moreover, the authors conclude that the potential for population regulation by blue stain fungi is greater than that measured for clerid beetles. They suggest that an increase from 8 to 49 percent blue stain infestation corresponds to an 85 percent decline in progeny per beetle; whereas high densities (relevant to field observations) of predators reduce SPB survival by about 60 percent (although it should be pointed out that the overall effects on a population depend not only on the amount by which a life history process is reduced, but also on which life history process and which lifestage is affected). Although not as comprehensively studied as the predator-prey (clerid-SPB) system, it is possible that these interactions at the scale of individual trees may drive the kind of regional delayed density effect proposed by Turchin and others (1991) model.

One of the strengths of the predator-prey hypothesis is that there is supporting evidence from a variety of spatial scales. For example, Turchin and others' (1991) original model provides a simple, regional explanation of more detailed predator-prey processes that have been measured at the scale of an infestation or an individual tree. The belief fostered by this body of research has led to practical methods of monitoring and predicting SPB outbreaks. Since 1987 a Southwide network of pheromone traps has been employed to capture SPB individuals and its main clerid predator (Billings 1988). The results from this long-term ongoing survey have been used to predict likely trends and levels of SPB populations during the next season. One of the advantages of such prediction is that the results can be used to effectively plan aerial and ground surveys important for region-wide control. Weekly counts of adult SPB and clerids are recorded for 4 consecutive weeks in spring (marked locally by the flowering of dogwood *Cornus florida*). Data from each state are sent to a central location for analyses and predictions of SPB infestation trend and relative population level for the current year. These predictions are based on mean numbers of SPB per trap per day and percent SPB (defined as the number of SPB divided by the combined number of SPB plus clerids caught per trap and expressed as a percentage) (Billings 1988).This index is plotted onto the SPB prediction chart (Figure 7.6) to provide a prediction of SPB population trend or level.

Table 7.1 shows that this prediction system is fairly accurate. Actual SPB infestation trends and levels are obtained by comparing the number of spots reported in a given locality or State in the current year with the number reported for the same locality or State in the previous year. The model allows annual population trend to be predicted between 62 and 80 percent of cases, where a case represents a prediction for a State in a given year, while prediction of actual SPB population level is less successful (between 32 and 85 percent). When interpreting these success rates one should be wary that a base level of prediction will be roughly 33.3 percent; i.e., with three categories one would expect to be correct one in three times if a prediction were made entirely randomly (though one should also consider that long periods of endemic population phases suggest that it is also inherently more likely that there will be no changes to the population trends). One less tangible measure of the success of this survey is that most States in the South continue to remain involved with data collection and reporting, suggesting that the work involved with the monitoring system is worthwhile.

The success of this regional monitoring program is evidence for the importance of predator-prey interactions as a driver of SPB dynamics. However, it is also instructive to consider exactly how this practical, predictive index fits into an ecological explanation of the hypothesis. The predator-driven delayed density-dependence model (Reeve 1997; Turchin and others 1991, 1999) suggests that at a regional level there should be relationships between the relative size of the predator population and SPB rates of increase, a gradual buildup of SPB numbers through time, a predictive relationship between current populations and populations 2 years earlier, and a strong cyclical component (i.e., consistent periodicity) to SPB outbreaks. Currently, however, the predictive index uses only the first of these characteristics (i.e., a relative measure of predator density). Given the complex nature of the SPB system, it is argued that a large part of the belief in any predictive index stems as much from its relationship to the theoretical, ecological underpinnings of the system as to a statistical analysis of its success.

7.3.2. Host Dynamics and Intraspecific Competition as a Driver of Regional Outbreaks

The ecology of the SPB is intrinsically tied to the biology of its host. A population cycle within a single tree begins with adults congregating and attacking a suitable host, which produces a defensive resin to "pitch out" beetles. During initial colonization, SPB mortality may be high and attacks may be unsuccessful. However, if the tree's defenses are overcome, attacking beetles will produce tunnels and galleries within the phloem that eventually girdle the tree and kill it. Eggs are laid within these galleries, and after some period of time—most likely driven by the decline in nutritional quality of the host and the density of eggs— the original attacking adults reemerge to target another potential host. Finally, the eggs develop through larval, pupal, and teneral adult stages before emerging from their natal tree in search of a fresh host to complete the cycle.

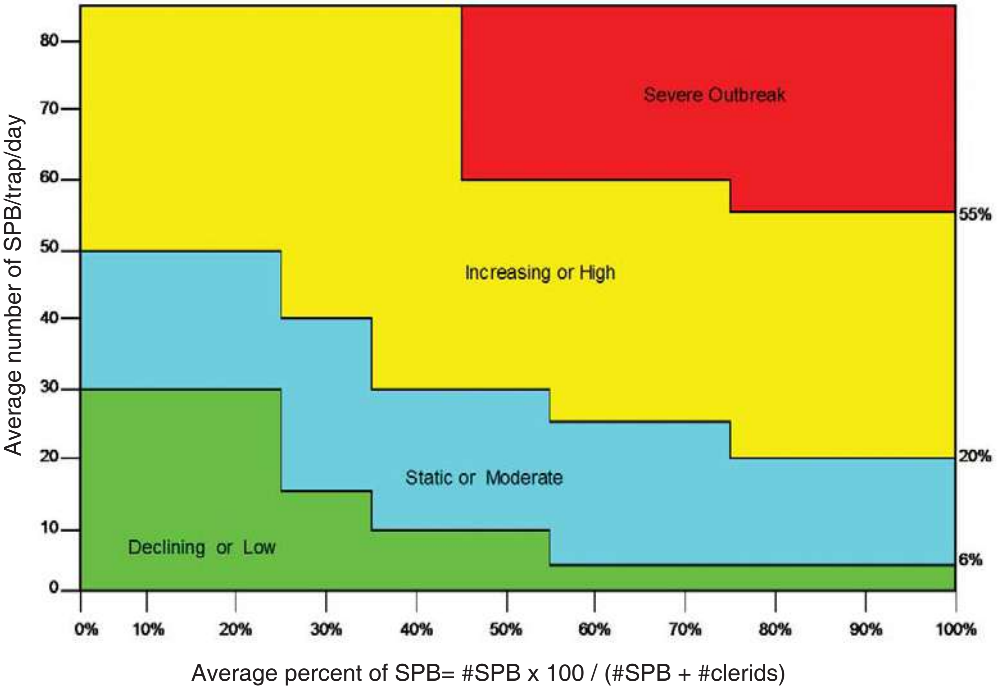


Figure 7.6—Graph used to determine regional risk (separated into outbreak risk, increasing, static, and declining population trends) using trapping data for predators and SPB.

Table 7.1—Prediction accuracy of predator-SPB regional risk prediction. The upper table shows the accuracy of predictions for the trend in SPB predictions (i.e., whether populations are declining, static, or increasing), and the lower table illustrates results of predicting the density of the SPB population (low, moderate, or high).

Predicted	Actual		
	Declining	Static	Increasing
Declining	80% (84/105)	9% (6/67)	23% (17/73)
Static	10% (10/105)	76% (51/67)	15% (11/73)
Increasing	10% (11/105)	15% (10/67)	62% (45/73)

Predicted	Actual		
	Low	Moderate	High
Low	85% (84/157)	38% (6/63)	12% (3/25)
Moderate	14% (10/157)	54% (51/63)	56% (14/25)
High	1% (11/157)	8% (10/63)	32% (8/25)

This simple, descriptive view of a population cycle masks many details important to a full understanding of regional population dynamics, including:

1. How many beetles does it take to kill a tree?
2. How do attacking beetles select a potential host?
3. Do trees have different susceptibilities or abilities to defend themselves, and what drives this characteristic?
4. Do different trees have different nutritional value to developing SPB?
5. How does the nutritional value of an infested tree decline through time, and what drives this decline?
6. How do beetles locate and target hosts across infestations (short distances) and across landscapes?

These questions form much of the ecological detail required to understand the dynamics between the SPB and its hosts and ultimately the initiation of outbreaks. The importance of host dynamics was discovered early in human-SPB interactions when foresters and early SPB researchers observed that SPB infestations occur more frequently in some stand types compared to others. Over time, researchers have used these observations to develop practical risk models that can be used to assess the risk of a stand becoming infested, based on characteristics of the host pines such as tree density (BA), age, tree size (DBH), and crown ratio (see chapter 22). These models are the underpinning for understanding the type of trees or stands in the forest that are most vulnerable to SPB damage. Given this information, it is reasonable to assume (though this assumption remains largely unevaluated) that the conditional state of the forest environment (host trees) drives the initiation and the severity of SPB outbreaks. An outstanding need of SPB research is to bridge the gap between these empirical observations and the population ecology that drives the presence of the SPB in certain stands and contributes to regional outbreaks.

One of the central tenets of the SPB-host hypothesis is that the vulnerability of a host tree is a function of both its innate susceptibility (driven, for example, by genetics, resin production, and *in situ* growing conditions) and the local density of attacking SPB individuals. Figure 7.7 illustrates this concept. It shows that a highly resistant tree may be successfully colonized if there are enough beetles available to overcome its defenses. Equally, trees with low resistance may require relatively few beetles for successful colonization.

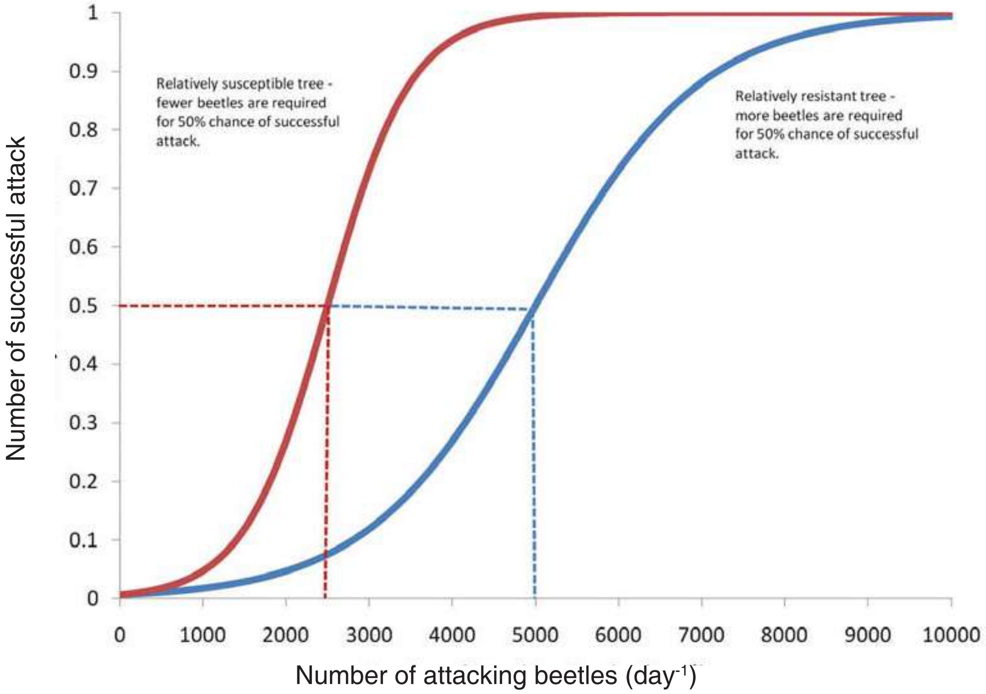


Figure 7.7—Graph illustrating a conceptual view of tree susceptibility to SPB attacks. The graph provides a mathematical description of attack success driven by population size. The red and black lines show relatively susceptible and resistant trees, respectively. Susceptibility can be described by curves at any point on the x-axis – shifts to the left indicate increased susceptibility (e.g., lightning-struck trees), and to the right, increased resistance to attack. These conceptual models are based on dose-response functions common in toxicology studies.

A number of authors have shown, empirically and experimentally, that damaged trees (for example, from lightning strikes) are readily colonized by SPB (Coulson and others 1986, 1999b; Rykiel and others 1988), and that relatively few attacking beetles are needed to overcome their defenses. One of the central tenets to the SPB-host hypothesis is that the forest environment is a distinctly heterogeneous environment, comprising a mix of hosts that vary greatly through both space and time in their vulnerability to SPB attack. Many researchers believe that damaged, highly susceptible trees are responsible for both the maintenance of low density populations within a region and the initiation of infestations. For example, Lovelady and others (1991) suggest that these trees are numerous enough to provide temporal steppingstones for endemic, low-density SPB populations. It is thought that under these conditions, relatively few progeny beetles are produced, making it unlikely that they are able to overcome the defenses of healthy, neighboring hosts such that populations are effectively regulated by the availability of such trees. However, if a number of vulnerable trees occur in close proximity through time and space, and/or a number of generations can be completed in close proximity, local populations may increase to densities capable of attacking more resilient hosts, serving as an epicenter of an infestation and outbreak. During epidemic phases, damaged trees may attract large numbers of dispersing beetles, as demonstrated by Coulson and others (1986). Under these circumstances, it may not be necessary for populations to complete several generations before surrounding trees become infested. During epidemic phases, then, vulnerable trees may act as attractors for beetles that have dispersed away from their natal infestations, thereby concentrating populations and serving as epicenters for new infestations.

Another detail important to the SPB-host dynamics is intraspecific competition. The importance of intraspecific competition is ecologically intuitive, given that host trees are a limited resource in the forest, both at high and at low population densities, and that the location and attack of hosts increase the risk of beetle mortality. Different types of competition have been characterized at different stages of tree colonization:

1. Contest competition: In established infestations, large numbers of adults may attack a tree in a relatively short period of time. Under these circumstances, parents tend to spend less time in the tree (reemerge after a shorter period of time), and hence construct less gallery and lay fewer eggs. This has been characterized as a form of contest competition because the organism is actively moderating its behavior to efficiently compete for resources (in this case by moving to another tree). In the SPB this behavior is thought to occur in response to pheromones that repel attacking beetles from colonized to uninfested trees (Payne 1980).
2. Scramble competition: At high larval densities (as a result of high adult attack densities) individuals (because of their sedentary nature) must compete for increasingly limited resources. As a result, larval mortality increases, and it is possible that the next generation of adults emerge with a lower fitness (Reeve and others 1998).

Intraspecific competition may be an important factor in driving the aggressive spread of a single infestation, the initiation of new infestations, and the decline of infestations. Southern pine beetle adults may respond to high adult densities by switching attacks to neighboring trees, thus accelerating the rate of spread of infestations, or possibly by dispersing more widely into the landscape to initiate new infestations (as suggested by Figure 7.5B).

Intuitively, optimal host-switching behavior must be underpinned by a set of tradeoffs involving the relative costs of using an established, currently infested host and the risk of progeny experiencing scramble competition during late developmental stages vs. switching to the attack of a fresh host and the risk of direct mortality associated with finding a suitable host and overcoming its defenses. Population densities within infestations may decline when mechanisms that regulate intraspecific competition break down; i.e., cease to be optimal. For example, the timing of changes in the focus of attacking beetles may sometimes be suboptimal, leading to overcrowding, competition for limited resources, and increased scramble competition. Reeve and others (1998) suggest that this may occur at attack densities of greater than 6 beetles/100 cm^2 of bark surface, densities that have regularly been observed in established infestations (Fargo and others 1978, Lih and Stephen 1996). In turn, suboptimal responses to competition during initial tree colonization may be explained by uncertainty in future environmental conditions that the population will experience. For example, seasonal changes in weather (which drives the emergence of the next generation of attacking adults) or the availability of suitable host trees may both affect the ability of the SPB to efficiently allocate resources between trees.

The role of temperature in the development, fecundity, and survival of SPB is well known (and discussed in the next section). Across its range, the SPB exists within a seasonal climate that may include high and low temperatures that exceed its thermal tolerance. Interannual variations in these seasonal cycles may be responsible for outbreaks (discussed in the next section). However, seasonal temperatures may also interact with the ability of the SPB to locate and attack fresh hosts. For example, extreme temperatures, either high summer or low winter, slow down population processes and curtail population growth. This seasonal dormancy may lead to lower densities of attacking adults, and in line with Figure 7.7, a reduction in the probability that the population will successfully attack a new host. The opposite may also be true. During periods of optimal temperatures, emergence may be concentrated within shorter time spans, leading to a higher local density of attacking adults and increased probability of successful colonization. In both cases it is easy to see how these processes may act synergistically with the presence of suitable hosts. In the case of suboptimal population growth, if a reduction in attacking beetles occurs in addition to the depletion of susceptible hosts, population decline may be exacerbated. Such an event might occur at a stand boundary, for example. Similarly, the simultaneous occurrence of a lightning-struck tree (or any highly vulnerable one) and a sustained period of weather conducive to population growth might create conditions suitable for multitree infestations, which in turn could be precursors to a regional outbreak.

7.3.3. Weather as a Driver of Outbreak Dynamics

Temperature has been shown to drive the reproduction, survival, and especially the development of the SPB (Gagne 1980, Wagner and others 1984a). The time taken for a single generation of the SPB to develop ranges from approximately 100 days at 15 °C to about 30 days at 30 °C (see Figure 7.8). Weather has been shown to directly affect SPB flight thresholds (Moser and Dell 1979a, Moser and Thompson 1986) and the survival of dispersing SPB. Drought, flooding, hurricanes, lightning, and ice storms may also indirectly drive SPB population dynamics by affecting the vulnerability of hosts. Seasonal variations in weather are therefore undoubtedly responsible for many consistent characteristics of SPB

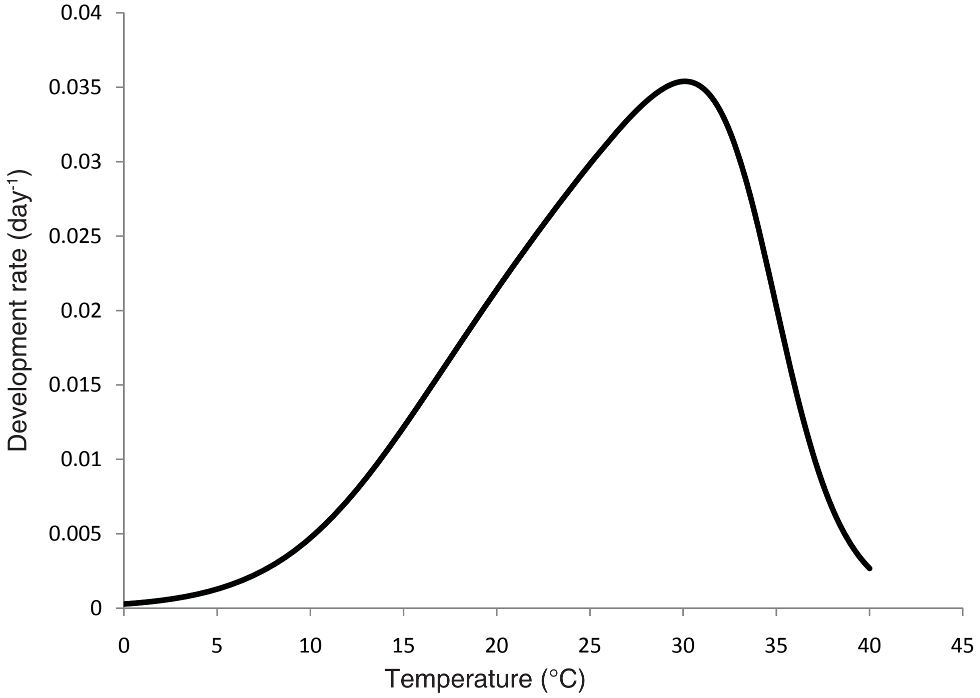


Figure 7.8—Graph showing the relationship between development rate (development time-1) and rearing temperature. Development is optimal at approximately 30 °C leading to a development time of approximately 1/0.035 = 29 days. Note that development rate rapidly drops off at temperatures above 35 °C, but at suboptimal temperatures the effect is more gradual.

dynamics such as the length of generations, the timing of infestation enlargement (mainly during the spring and autumn), the decline of infestations during winter, and the utilization of lightning-struck trees. In short, given empirical and experimental knowledge, there is no doubt that temperature and other seasonal weather factors are significant drivers of SPB population dynamics.

However, the most important questions for regional dynamics are:

1. The extent to which climate is responsible for differences in the frequency of outbreaks between regions
2. The extent to which interannual variations in weather drives outbreaks dynamics (endemic-epidemic transitions)

Figure 7.9A shows the average number of generations of the SPB (voltinism) expected to occur across its range, based on local temperatures. Cross-referenced with Figures 7.2 and 7.3 (showing regional outbreak frequency), the map suggests that areas of high SPB activity tend to coincide with areas that have host incidence and areas that support a large number of generations. However, this observation is not universally true. For example, southern Georgia has considerable areas of host and climatic conditions conducive to six or seven SPB generations per year, but has relatively low outbreak frequency. Similarly, the mountainous regions of North Carolina are predicted to support relatively few generations per year, yet exhibit considerable outbreak frequency. In short, regional differences in climate driving voltinism of the SPB does not, at least at first glance, appear to be a particularly strong predictor of the frequency of outbreaks.

Figure 7.9B shows the interannual variation in the voltinism of the SPB across its range, expressed as a standard deviation of the mean development time (as shown in Figure 7.9A). A practical interpretation of this map suggests that, even in areas with relatively large annual variation in voltinism (namely, southern Alabama, southern Georgia, and East Texas), an extra generation (above the mean) is expected approximately 1 year out of 40 or 2.5 percent of all years (note that approximately 95 percent of the time voltinism will be within two standard deviations of the mean, with the remaining 5 percent being split between an unusually high or low number of generations). Put simply, annual variation in SPB voltinism is relatively low. On this evidence alone, it would appear unlikely that such small changes in year-to-year voltinism are responsible for initiating outbreaks.

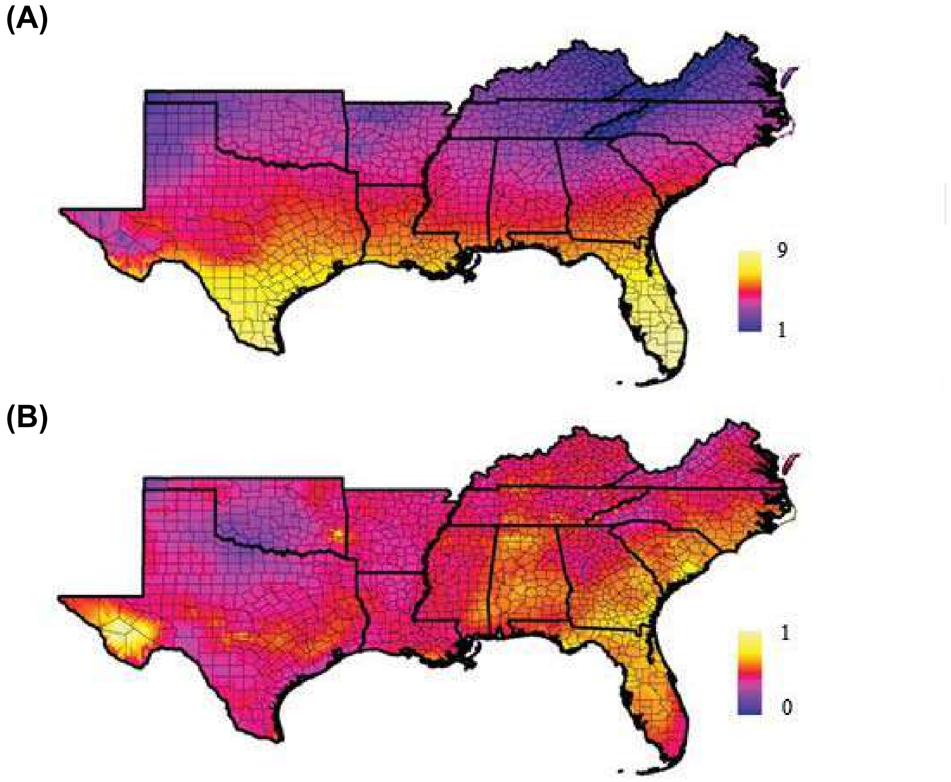


Figure 7.9—(A) Mean, and (B) Standard Deviation, of annual SPB voltinism across the Southeastern United States.

Why Weather May Still be Important Driver of Population Dynamics

Before the role of climate in driving outbreak dynamics is dismissed entirely, it is important to understand why its effects may be difficult to uncover. First, Figure 7.9 shows a single, surrogate measure of population performance – namely, voltinism. It is an assumption that areas that support the greatest number of generations are most suitable for SPB populations. Given that the SPB is an obligatory host killer, an essential (and costly in terms of mortality) part of its population dynamics is the need to continually locate fresh hosts in what is most likely to be a resource-limited environment. Under such conditions, it is possible that fewer generations might actually increase the stability of populations. Figure 7.9 may also be misleading in the sense that it reports only whether a county is in outbreak rather than the severity of the outbreak. It is possible that voltinism (or any other measure of population performance) is more relevant to the severity of an outbreak than the frequency with which outbreaks occur.

Second, statistical methods allow hypotheses to be formulated (for example, that annual voltinism is related to outbreak frequency) and then tested, given observations and data. However, climate (or weather) includes a large number of variables and dimensions and infinite ways by which they could be summarized as inputs into statistical models. For example, Figure 7.9 uses annual temperature, arbitrarily bounded by January 1 and December 31, as the input to the voltinism model. Yet it is possible that a different temporal timeframe might be a more appropriate driver of outbreaks. For example, a 2- or 3-year stretch of weather might be proposed as a better predictor of outbreaks perhaps representing a period more conducive to a buildup of SPB populations. Alternatively, the minimum length of time it takes for the SPB to complete one, two, or three generations, or weather patterns that influence other important life history processes such as overwintering (or high temperature) survival or host vitality (e.g., flooding, drought, storms) may be considered more important for driving outbreaks. In each case, although it is possible to test a proposed hypothesis against observed data, it is not possible to eliminate the importance of every possible interpretation or summary of climate.

Other authors have explored the relationship between outbreaks and weather with varying results. For example Gan (2004), using a model fit to county level data, found significant relationships between various temperature indices (lagged spring, summer, fall, and winter temperatures, and precipitation) and SPB infestation rates. He concludes that temperature has a greater effect on outbreak risk than precipitation and discusses these results in the context of global climate change. Working at the finer spatial scale of East Texas, Friedenberg and others (2008) developed a model that bridges the gap between exogenous and endogenous population regulation. The model uses delayed and direct density functions, and under certain assumptions about the nature of this density-dependence, found the number of infestations (used as a measure of population growth) was negatively affected by consecutive daily temperatures above 32 ^{o}C and by either higher than average or lower than average winter temperatures.

Given that seasonal weather patterns drive much of SPB population dynamics, it is difficult to believe that annual or regional variations in weather do not exert some effects on outbreak frequency or severity. Perhaps the most important deficiency in this hypothesis is the reliance on empirical studies alone. In contrast, evidence for delayed density-dependant predator-prey interactions comprises a theoretical model demonstrating how delayed density-dependence can result in outbreak dynamics—a fit of this model to empirical infestation data and detailed, *in situ*, experimental studies showing the population level effects of predation. Given the essential characteristics of the SPB problem (a large geographic range, regional data collection, a small insect in an extensive forest landscape, and infrequent outbreaks with both frequency and severity dimensions), it is argued that, even with 50 years of data, empirical studies alone are unlikely to uncover (and foster belief) climatic indices that can explain patterns of outbreaks. Like the predator-prey hypothesis, the climate-driven hypothesis warrants a bottom-up approach that pieces together the detailed life history processes of the SPB (which are undeniably driven by temperature) to form a coherent hypothesis for regional dynamics.

7.4. CONCLUSIONS

In previous sections, the population ecology of the SPB was organized around three theories that represent the conventional wisdom of how, when, and why regional outbreaks occur. Although no firm conclusions can be made about which of these (or to what extent each of them) is responsible for the characteristic patterns of SPB damage, a wealth of detailed ecological information exists about the population ecology of this species. One challenge for ecologists is to piece together existing knowledge into coherent, quantitative models of SPB population dynamics. Another is to use these models to identify deficiencies in our current knowledge of the SPB and devise experiments or observations capable of filling these knowledge gaps.

Although there is merit to understanding SPB population dynamics from a purely academic point of view, research into SPB damage is largely driven by its importance as a pest of southern forests. This pestilence is driven by the value of forest products and the magnitude and spatiotemporal unpredictability of SPB damage. However, given the importance of the SPB as a pest, it is also important to address how this knowledge can be used to manage future outbreaks. Regional population dynamics are particularly important for SPB management, and the hypotheses presented here have very different implications. In all cases, the ecological objective is to understand what drives regional outbreaks and the pattern of damage that comprises them. Management should include elements of prediction (forecasting when and where damage will occur), prevention (taking steps to reduce future damage), and remediation (accepting damage will happen but limiting its effects) based on this ecological knowledge.

Often, prediction of SPB damage is seen as the ultimate goal of SPB ecological research. However, it is likely that each of the hypotheses discussed in the previous section would need to be applied in different ways to enable it to be used in effective regional management plans. For example, even if population dynamics were found to be entirely driven by temperature, it is possible that the inherent unpredictability of long-range weather might prevent this knowledge being used to make practically useful predictions. If this were the case, the most valuable use of this knowledge would be to direct SPB management resources away from prediction towards methods of reducing its impacts. In contrast, knowledge from predator-prey research is currently being used to predict future SPB activity but probably offers little hope for prevention. Uniquely, knowledge from SPB-host research is currently used to predict and prevent damage (via risk models).

This chapter has taken a mechanistic, modeling approach to the description of regional SPB dynamics. In most cases, these models are qualitative and conceptual rather than quantitative. The reasons for this stem largely from the difficulty of observing the SPB and collecting data at all relevant spatial scales. Although quantitative models can be difficult to interpret without real-world data to validate results, the mechanisms by which SPB populations shift between small, benign endemic populations and problematic outbreaks are central to the SPB problem, and one of its defining characteristics. Any successful regional model should therefore recreate the aggregated pattern of trees within infestations and the disaggregated pattern of infestations within a landscape. Preferably, this pattern should be driven by a self-contained, endogenous population: Population dynamics should be determined by interactions between a defined environment and the SPB, rather than through open-ended processes such as immigration or emigration. Although it is relatively easy to model steady-state or infinitely growing or declining populations, repeated patterns of growth and decline are much more difficult to mimic. A theme of this chapter is that each of the hypotheses discussed is underpinned by considerable ecological detail (much of which is described in other chapters of this text), but that this detail may be interpreted or integrated in different ways. The advantage of a quantitative approach over the largely conceptual models described here is that the rigor of a mathematical formulation leads to unequivocal outputs. Although a quantitative model that reproduces population cycles is not necessarily correct, it would at least demonstrate that the ecological mechanisms it incorporates are capable of producing the endemic-outbreak dynamics so typical of SPB populations. Of the three hypotheses presented here, the only one that has been described quantitatively, and for which SPB-like population cycles can be demonstrated even theoretically, is the predator-prey explanation. Arguably, this shortfall in competing quantitative models represents the biggest barrier to understanding regional SPB dynamics and the translation of this knowledge to more effective management strategies.

8

Parasitoids of the Southern Pine Beetle

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Keywords

biological control
natural enemies
parasites
parasitoids
predators
SPB mortality

Abstract

Hymenopterous parasitoids make up a significant portion of the natural enemy complex associated with the southern pine beetle (SPB). Collectively, parasitoids can affect the growth of individual SPB infestations and area populations by reducing the survival rates of developing SPB larval/pupal broods. A substantial body of information on parasitoids has been accumulated, mostly during and after research supported by the Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP) during the 1970s. The parasitoids most closely associated with the SPB have been identified, and a key to larvae of the most abundant species is available. The sequence of arrival of parasitoids at infested pines relative to SPB attack and brood development has been documented. Some chemical cues by which parasitoids locate trees infested with SPB broods that are in susceptible developmental stages have been determined. However, the precise mechanism by which parasitoids locate specific hosts beneath the bark has not been described, although it is thought to involve specific olfactory cues. Factors that affect parasitoid efficacy such as host density and bark thickness have been quantified, and the overall contribution of parasitoids to natural enemy impact has been estimated and incorporated into population growth models.

8.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is attacked by a number of parasitoids that directly affect developing SPB broods and reduce numbers of emerging adults. Because the SPB is difficult and expensive to control once infestations develop, there have been a number of studies on SPB parasitoids and other natural control agents that detail life histories, impact, and so forth, and provide information to help assess the potential for integrating this natural control into forest management programs. The development of integrated suppression tactics will require an understanding of the life processes of the beetle and its important associates such as predators, parasitoids, and competitors. Although the existence of SPB parasitoids has been known since the beetle was first studied in the late 1800s, indepth inquiries mostly began during investigations supported by the Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP) during the 1970s (Thatcher and others 1980).

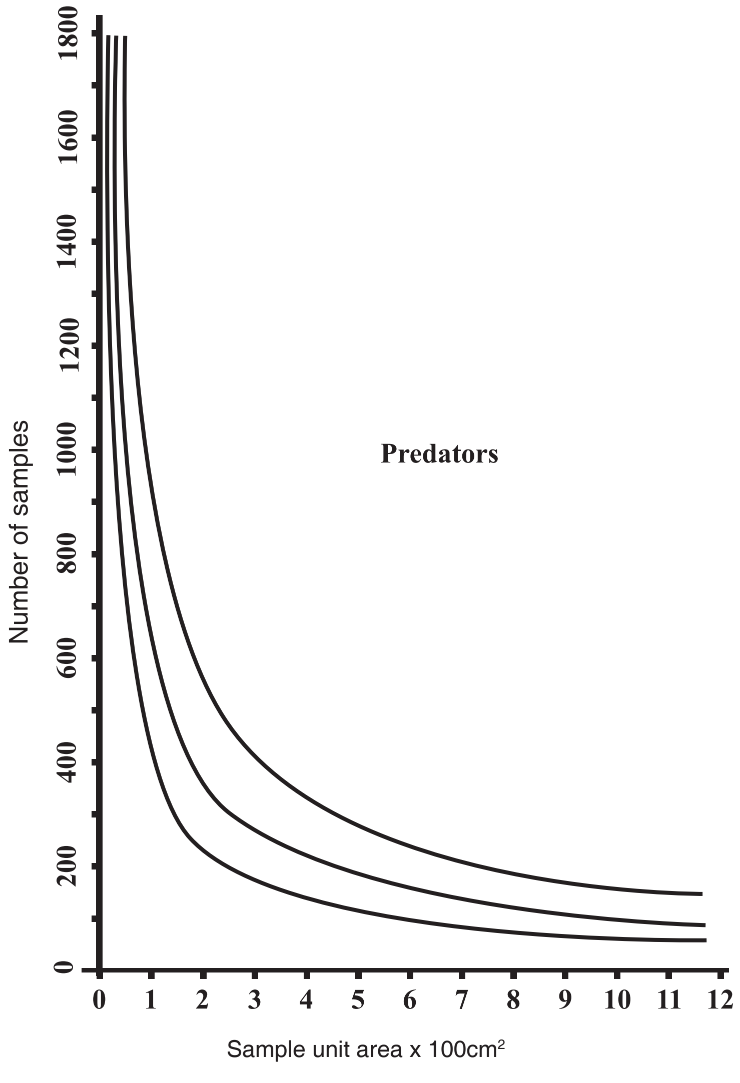


Figure 8.1—Number of samples and size of the sample unit needed to estimate the density of SPB predators. (illustration from Stephen and Taha 1976)

Studies of SPB natural enemies prior to ESPBRAP dealt primarily with compiled lists of SPB associates, usually based on collections of arthropods reared from bolts or bark excised from SPB-infested trees. Most of the attention was focused on insects, mites, and nematodes. The known or suspected roles for associated arthropods and other organisms were usually included (Coulson and others 1972, Dixon and Osgood 1961, Franklin 1969, Moore 1972, Moser and Roton 1971, Overgaard 1968, Thatcher 1960). However, the individual or combined impacts and interactions of these associates were generally unknown. Some studies supported by ESPBRAP were oriented toward determination of the specific roles and impacts of associates, particularly parasitoids and predators. This type of information was considered to be essential for the development of realistic SPB population models that can detect and/or forecast population trends, and to implement appropriate control strategies.

Other insects are among the principal natural enemies of the SPB. Some studies have identified these mortality agents and described their general biologies, plus seasonal, geographic, and within-tree distributions. Other reports concentrate on one or a few species. Dixon and Payne (1979b, 1980), Gargiullo and Berisford (1981) and Hain and McClelland (1979) provided information on SPB associates attracted to infested trees and included data on numbers and their temporal and spatial distributions. An illustrated guide to insect associates of the SPB was developed by Goyer and others (1980). The guide includes color photographs and distinguishing characteristics of each insect. With this manual, individuals with minimal training in entomology can identify common SPB associates, including parasitoids. Stephen and Taha (1976) devised a sampling system for estimating numbers of natural enemies. The system describes a sampling protocol and includes curves for estimating numbers of samples and sample sizes for various statistical confidence levels (Figure 8.1).

8.2. PARASITOIDS VS. PREDATORS AND PARASITES

Parasitoids differ from predators in that parasitoids are more intimately associated with their host. Whereas predators are usually larger than their prey and feed as adults and/or immature stages on several different hosts during their lifetime (a one-meal association), parasitoids are usually only slightly smaller than their hosts and normally develop from egg to adult on a single host, ultimately killing the host (a lifetime association). Parasites, on the other hand, are usually much smaller than their hosts and do not necessarily kill the host in order to survive.

8.3. THE PARASITOID COMPLEX ASSOCIATED WITH SPB

Parasitoids known to attack the SPB are shown in Table 8.1. Some parasitoids are somewhat host-specific in that they attack only one species or a group of closely related species with similar habits. However, only a few host-specific parasitoids are known for the SPB, and most will accept other bark beetle hosts.

The most common SPB parasitoids frequently attack, or will at least accept, other bark beetle or ambrosia beetle species (Bushing 1965, Dixon and Osgood 1961, Thatcher 1960). Many parasitoids of SPB also attack one or more species of *Ips* bark beetles that are often associated with the SPB (Berisford 1974b; Berisford and Dahlsten 1989; Berisford and others 1970, 1971; Kudon and Berisford 1980). Parasitism of more than one bark beetle species is not surprising since one or more *Ips* spp. are often found in trees infested by the SPB.

8.4. IDENTIFICATION OF PARASITOIDS

The more common parasitoids are illustrated in an SPB associates identification guide (Goyer and others 1980). In addition, Finger and Goyer (1978) provided descriptions of the mature larvae of the most common hymenopterous parasitoids of the SPB and included a key for identifying larvae and adults (Table 8.2).

Table 8.1—Confirmed and suspected parasitoids of the southern pine beetle

Hymenoptera	
Braconidae	
	Atanycolus comosifrons Shenefelt
	Atanycolus ulmicola (Vier.)
	Cenocoelius nigrisoma (Rohwer)
	Cenocoelius sp.
	Coeloides pissodis (Ashm.)
	Compyloneurus movoritus (Cress.)
	Dendrosoter sulcatus Mues.
	Doryctes sp.
	Heterospilus sp.
	Meteorus hypophloei Cushman
	Spathius canadensis Ashm.
	Spathius pallidus Ashm.
	Vipio rugator (Say)
Ichneumondiae	
	Cremastus sp.
	sp. (undetermined)
Eupelmidae	
	Arachnophaga sp.
	Eupelmus cyaniceps cyaniceps (Ashm.)
	Lutnes sp.
Torymidae	
	Liodontomerus sp.
	Lochites sp.
	Roptrocerus eccoptogastri (Ratz.)
	Roptrocerus xylophagorum Ratz.
	Roptrocerus sp.
Pteromalidae	
	Dinotiscus (=Cecidostiba) dendroctoni (Ashm.)
	Heydenia unica Cook & Davis
	Rhopalicus pulchripennis (Crawford)
Eurytomidae	
	Eurytoma cleri (Ashm.)
	Eurytoma tomici Ashm.
	Eurytoma sp.
Scelionidae	
	Gyron sp.
	Idris sp.
	Leptoteleia sp.
	Probaryconus heidemanni Ashm.
	Telenonus podisi Ashm.
Bethylidae	
	Parasierola sp.

Table 8.2—Key to the final instar larvae of the major parasitoids of the southern pine beetle (from Finger and Goyer 1978)

1’	Body with some setae but without microspines; head with few if any sclerites; spiracles on segments 2-10.	4
2	Labial sclerite very thick and rounded, often with slight projection on ventral surface and flat on dorsal surface between arms; silk orifice on wide oval sclerite.	*Dendrosoter sulcatus* (figs. 1B, 2B, 3B)
2’	Labial sclerite not as above.	3
3	Thickness of ventral part of labial sclerite about two times as wide as where dorsal arms start; area inside labial sclerite more circular than ovoid; silk orifice forming a straight line (figs. 1A, 2A, 3A) .	*Coeloides pissodis*
3’	Thickness of ventral part of labial sclerite at least three times as thick as where arms start; area inside labial sclerite more ovoid; silk orifice often with slight “V” in middle (figs. 1C, 2C, 3C).	*Spathius pallidus*
4	Head with very long setae; stalk of spiracle with over 20 chambers (figs. 1D, 2E, 3D).	*Heydenia unica*
4’	Head with short setae; stalk of spiracle with less than 20 chambers.	5
5	Stalk of spiracle with less than nine chambers, each decreasing in size from the atrium, forming a continuous funnel-shaped spiracle (figs. 2F, 3E).	*Dinotiscus dendroctoni*
5’	Stalk of spiracle with more than nine chambers, only first three chambers and atrium forming enlarged club-shaped structure (fig. 2G).	*Roptrocerus eccoptogastri*

8.5. PARASITOID ATTACK BEHAVIOR AND HOST LOCATION

Adult parasitoids are attracted to a combination of insect- and tree host-produced odors to locate trees infested with advanced SPB larval brood stages (Camors and Payne 1973).

8.5.1. Parasitoid Responses to SPB-Associated Chemicals

The responses of parasitoids to beetle and/or host chemicals released from SPB-infested trees have received some attention. Camors and Payne (1972) showed that *Heydenia unica* responds to host tree terpenes and a component of the SPB aggregation pheromone. Dixon and Payne (1980) caught four species of SPB parasitoids in traps baited with various combinations of SPB- and tree-produced chemicals, plus pine bolts artificially infested with SPB females. Although no host larvae are present at the time of SPB mass attack, they (Dixon and Payne 1980) suggested that the compounds may serve to concentrate parasitoids in areas where suitable host life stages would soon become available. Kudon and Berisford (1981a) developed an olfactometer to evaluate the response of SPB parasitoids to insect- and tree-produced odors. Olfactometer trials can aid in preliminary screening of chemicals that may attract parasitoids. Final determinations of attractancy must be made in the field, however.

Sullivan and others (1997) identified chemicals from loblolly pines infested with SPB larvae, including many of the chemicals involved in parasitoid attraction. They subsequently showed that different species of parasitoids are attracted to different SPB developmental stages or different combinations of chemicals (Figure 8.2) (Sullivan and others 2003). The precise mechanism by which female parasitoids locate and attack hosts beneath the bark is still unknown. Some experimental evidence from studies of other bark beetles suggests that they may orient to physical cues such as sound (Ryan and Rudinsky 1962) or heat (Richerson and Borden 1972). However, a considerable body of evidence shows that SPB parasitoids and many species that attack other bark beetles use olfactory cues that are closely associated with developing broods of larvae (Birgersson and others 1992; Pettersson 2001a, 2001b; Pettersson and others 2000, 2001; Sullivan and others 1997, 2000). Female parasitoids generally oviposit through the bark onto 3rd or 4th instar SPB larvae and occasionally, onto pupae (Berisford and Dahlsten 1989). Most parasitoids apparently sting their hosts to immobilize and preserve them before depositing eggs. One of the most common SPB parasitoids, *Roptrocerus xylophagorum* Ratzeburg (Hymenoptera: Torymidae), enters egg galleries through beetle entrance or ventilation holes and oviposits onto nearby beetle larvae through the sides of the egg galleries. Another parasitoid, *Heydenia unica* Cook and Davis (Hymenoptera: Pteromalidae), arrives at SPB or *Ips*-infested trees during the beetle's attack stage, possibly to mate, since no late instar larvae would be available for oviposition at that time (Camors and Payne 1972, Dixon and Payne 1979). Most of the parasitoids associated with the SPB arrive at infested trees when large numbers of acceptable hosts are available (Berisford and Franklin 1969, Camors and Payne 1973, Dixon and Payne 1979b). Figure 8.2 shows arrival patterns of some common parasitoids relative to SPB brood development.

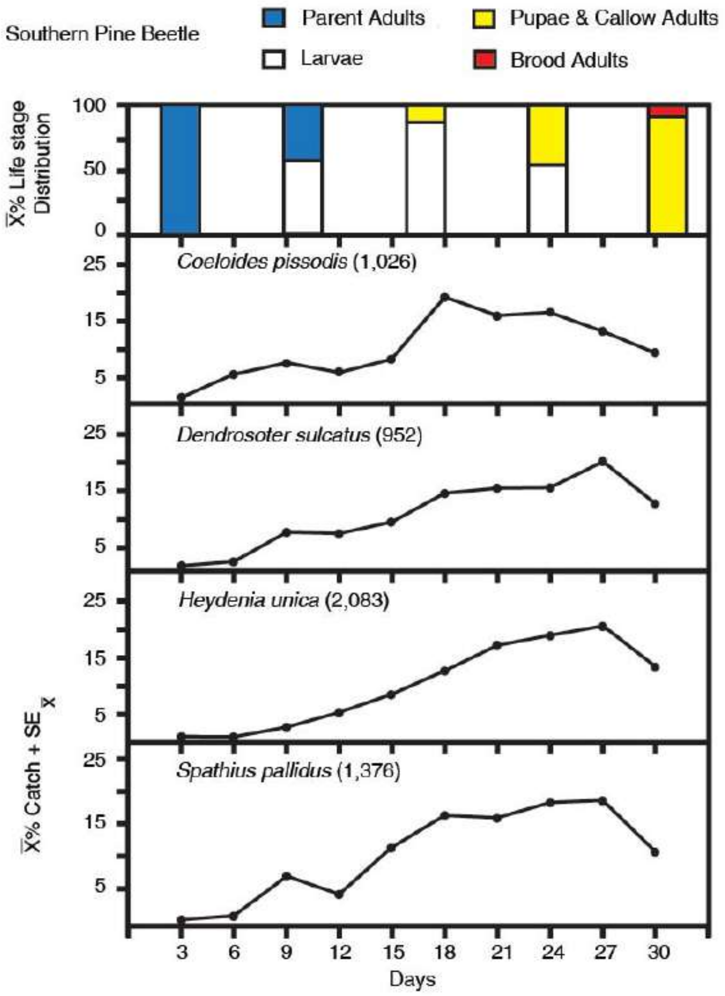


Figure 8.2—Sequence of arrivals of the SPB parasitoids: *Coeloides pissodis*, *Dendrosoter sulcatus, Heydenia unica*, and *Spathius pallidus*, in relation to SPB brood development. Numbers trapped are shown in parentheses. (illustration from Dixon and Payne 1979b)

8.6. FACTORS INFLUENCING PARASITOID IMPACT

Parasitoids in SPB-infested trees may be strongly influenced by bark beetle host brood density and bark thickness (Goyer and Finger 1980, Gargiullo and Berisford 1981). Regressions of numbers of parasitoids against SPB brood density for different bark thickness categories show the relative effect of each factor on different parasitoid species. Figure 8.3 shows regressions calculated for two common SPB braconid parasitoids, *Spathius pallidus* Ashmead and *Coeloides pissodis* Ashmead, both of which oviposit through the bark.

Parasitism by the most common hymenopterous parasitoids—*Heydenia unica* Cook and Davis (Pteromalidae), *Cecidostiba dendroctoni* Ashmead (Pteromalidae), *Dendrosoter sulcatus* Musebeck (Braconidae), *Coeloides pissodis* (Ashmead) (Braconidae), *Eurytoma* spp. (Eurytomidae), *Rhopalicus* spp. (Pteromalidae), and *Spathius pallidus* Ashmead (Braconidae)—increases as tree host bark becomes thinner (Gargiullo and Berisford 1981). *Roptrocerus xylophagorum* (Ratzeburg) (Torymidae) is strongly affected by bark thickness even though it enters SPB egg galleries to locate hosts. Most of the parasitoid species reach maximum parasitism rates at intermediate host densities (Figure 8.3), with the exception of *Eurytoma* spp. However, *Spathius pallidus* is apparently unaffected by host density, and *R. xylophagorum* becomes increasingly abundant as host density increases and bark thickness decreases. *R. xylophagorum* is the only parasitoid that shows a significant interaction with both bark thickness and SPB brood density (Gargiullo and Berisford 1981).

8.7. PARASITOID POPULATION FLUCTUATION

Hain and McClelland (1979) reported quantitative and qualitative differences in

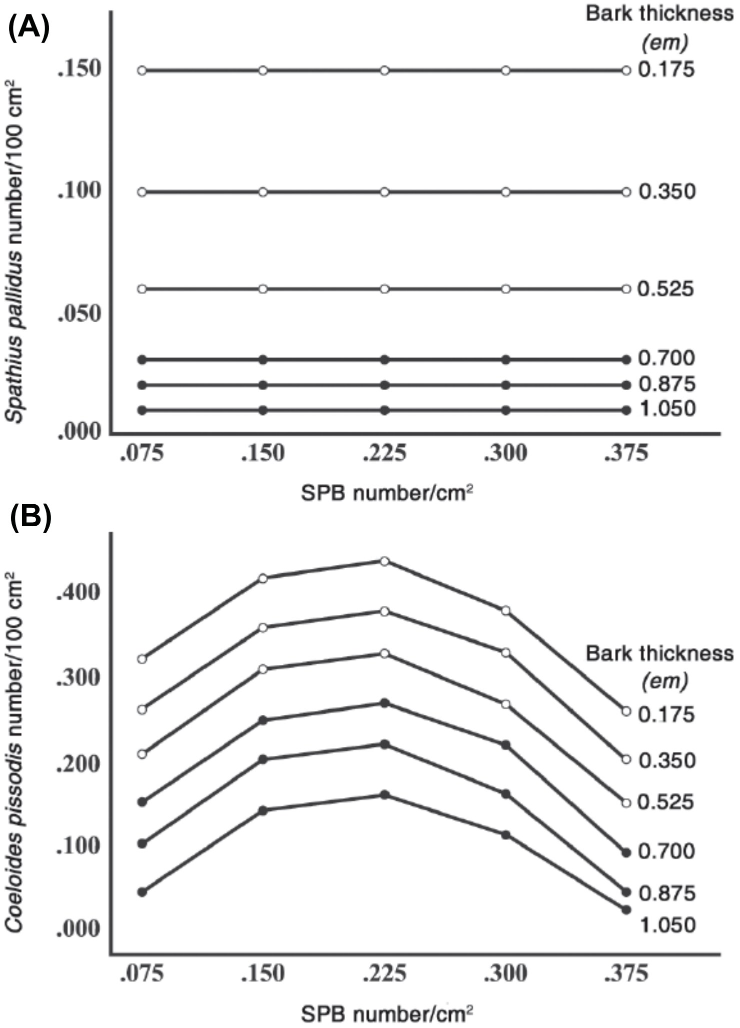


Figure 8.3—Numbers of the parasitoids (A) *Spathius pallidus* Ashmead and (B) *Coeloides pissodis* Ashmead relative to SPB host density and bark thickness. (illustration from Gargiullo and Berisford 1981)

natural enemy populations at three locations in North Carolina (Figure 8.4). A similar study in Louisiana found that natural enemy population differences were generally correlated with SPB brood adult densities (Goyer and Finger 1980). In Louisiana, highest numbers of parasitoids occurred during April to June, with a second peak in August. Lowest parasitoid populations were found in the fall and winter, when SPB populations were also low (Figure 8.5). Similar seasonal patterns were observed in Texas (Stein and Coster 1977).

Many of the parasitoids that attack SPB also attack other bark beetles, as noted previously. In fact, the parasitoid complexes associated with *Ips avulsus* Eichoff, *I. grandicollis* Eichoff, *I. calligraphus* (Germar), *I. pini* Say, and the eastern juniper bark beetle *Phloeosinus dentatus* (Say) share with the SPB three of the most common species—*Roptrocerus xylophagorum (= eccoptogastri), Heydenia unica,* and *Coeloides pissodis* (Berisford 1974b, 1974a; Berisford and Franklin 1971; Berisford and others 1970, 1971).

It has been assumed in the past that SPB parasitoids that are not host-specific would prefer the SPB even if other hosts were available, and that other bark beetles (e.g., *Ips* spp.) would serve as reservoir hosts when SPB populations were low or absent. However, Berisford (1974b) found that when both SPB and *Ips* spp. were available, parasitism did not readily shift from one species to the other, regardless of the relative abundance. This suggests that some degree of host preference may occur, at least temporarily, among parasitoids that are not considered to be host-specific. Kudon and Berisford (1980) found that when adult parasitoids were reared from SPB-infested logs and provided with simultaneous choices of logs containing late-instar larvae of SPB or *Ips* and SPB or Eastern juniper beetle (*P. dentatus*), a high percentage of the parasitoids selected logs with SPB (Figures 8.6A and B). Conversely, when parasitoids were reared from *Ips* or *P. dentatus*, they showed a preference for those species over the SPB (i. e., the hosts on which they developed as larvae) (Figures 8.6C and D). The preferences were accentuated when parasitoids could simultaneously select both beetle hosts (e.g., SPB vs. *P. dentatus*) and tree hosts (pine vs. cedar) instead of beetle hosts only (e.g., SPB vs. *Ips*) with both species infesting loblolly pine. Thus, it appears that the parasitoids, although not host-specific, may be at least temporarily entrained to initially select the host on which they were reared. This phenomenon appears to be a manifestation of Hopkins (1916) Host-Selection Principle. However, Hopkins' principle applies to phytophagous insects, and no references were made to predators or parasitoids.

8.8. IDENTIFICATION OF PREVIOUS HOSTS OF PARASITOIDS

Since several SPB parasitoids are known to attack other bark beetles, knowledge of the identity of previous hosts of parasitoids or predators that respond to SPB-infested trees would help to determine if other bark beetles are acting as alternate, competing, and/or reservoir hosts. Miller and others (1979) and Miller (1979) utilized immunodiffusion and immunoelectrophoresis techniques to produce antisera that were specific for the SPB and some of its bark beetle associates (e.g., *Ips* spp. and black turpentine beetle). These techniques were used to help determine the prey of SPB predators such as the clerid beetle *Thanasimus dubius* and may provide a means to estimate the number of prey consumed. Kudon and Berisford (1981b) found that the fatty acid composition of parasitoids reared from SPB and some if its common associates closely matched the fatty acid composition of their beetle host(s). Therefore, the host origin of a single parasitoid could be determined, provided that the host's lipid profile has already been established. Figures 8.7A and B shows the similarity between the lipid profile of the SPB and a parasitoid, *Heydenia unica*, reared on SPB. Figures 8.7C and D shows lipid profiles for *I. calligraphus* and *H. unica* that had been reared on *I. calligraphus*. The technique of comparing lipid profiles could also help to determine predator hosts, particularly if they feed on a single prey species. When *Thanasimus dubius* was fed either on SPB or the cowpea weevil (*Callosobruchus maculatus* [Fabricius]), the lipid profile of *T. dubius* reared on SPB matched the host profile well, but although the profile of clerids that fed on the weevil (an unnatural host) differs from that of clerids that fed on the SPB, it did not match the weevil profile. This technique, however, appears to need some refinement. The host-induced preferences of parasitoids may be a factor affecting the overall impact of the parasitoid complex on SPB populations. Although relatively high populations of *Ips* spp. usually present in logging slash, damaged trees, lightning strikes, and so forth, can support substantial parasitoid populations, *Ips* may not be a particularly good reservoir for SPB parasitoids in regard to biological control of the SPB, partially due to induced host preferences. On the other hand, the parasitoids are apparently able to attack other hosts if the preferred host is not readily available, and high *Ips* populations may maintain parasitoids for eventual attacks on SPB.

At this point, we do not understand the mechanism that determines how parasitoids switch from one host to another. If we assume that temporary host-induced preferences will create a lag in acceptance of nonpreferred hosts,

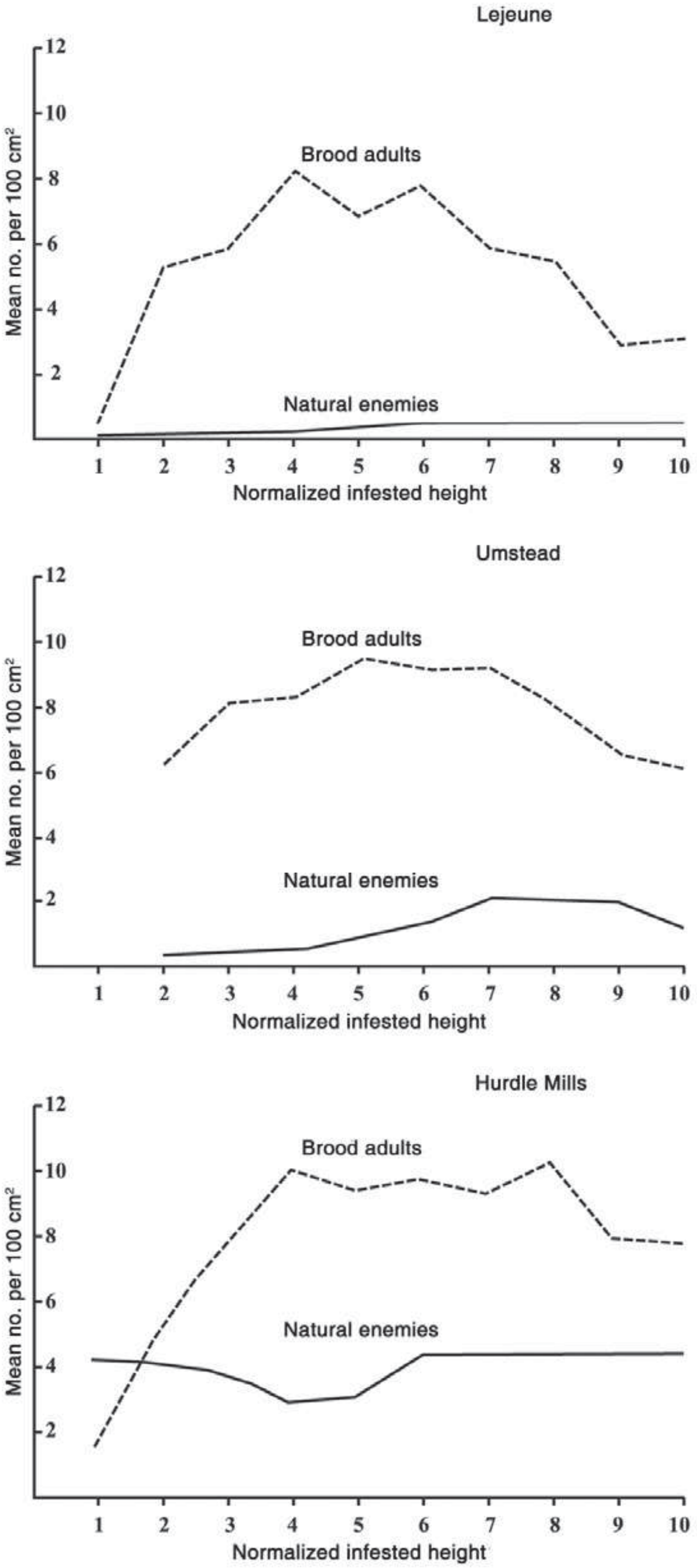


Figure 8.4—Numbers of natural enemies, including parasitoids, relative to numbers of SPB brood adults at three locations in North Carolina. (illustration from Hain and McClelland 1979)

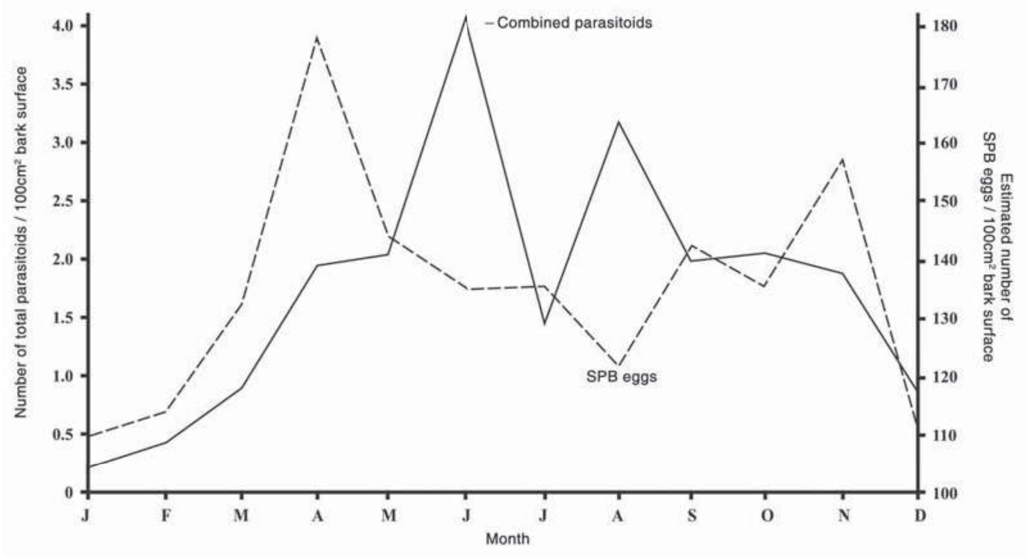


Figure 8.5—Seasonal abundance of parasitoids relative to numbers of SPB eggs in SPB-infested trees in Louisiana. (illustration from Goyer and Finger 1980)

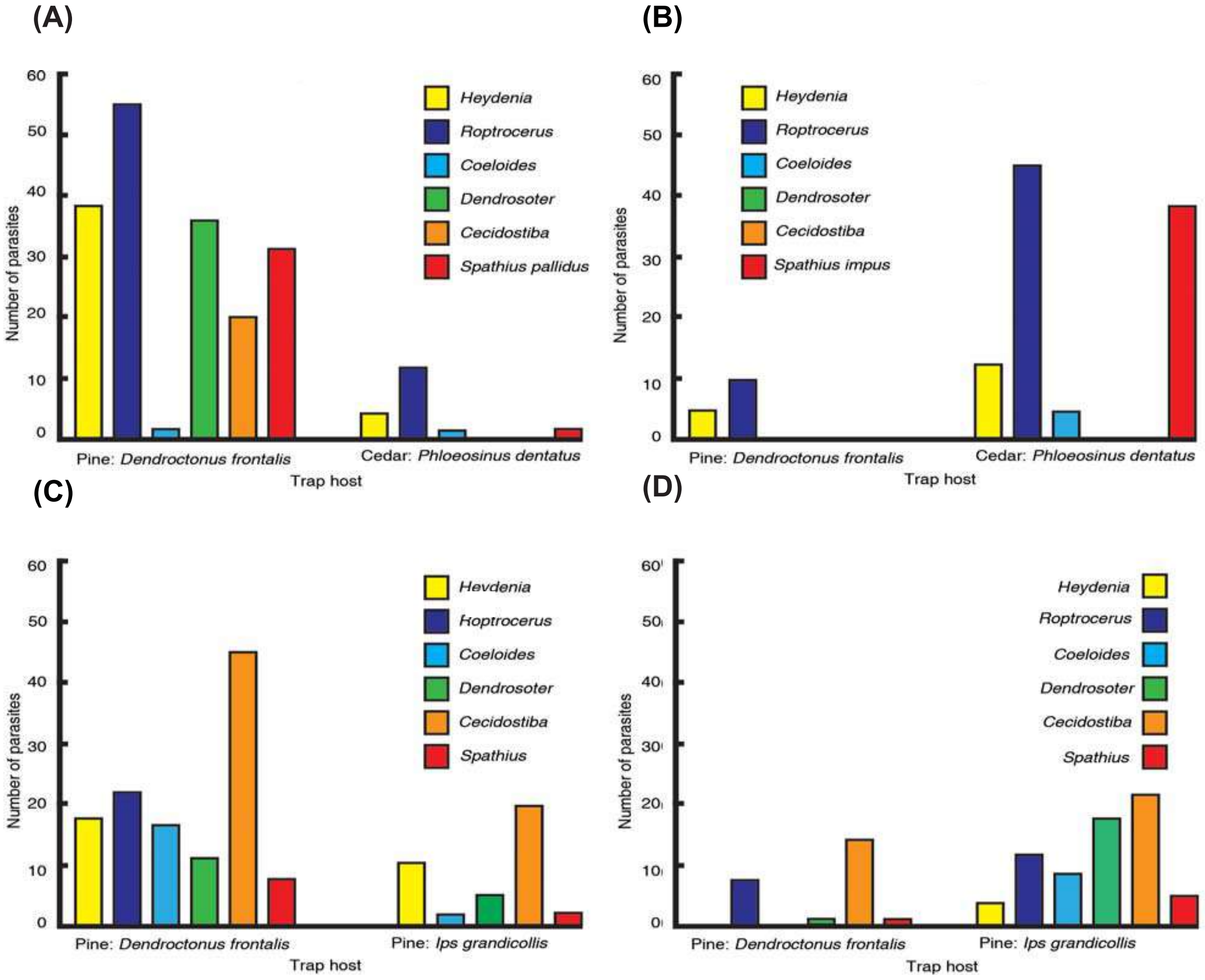


Figure 8.6—Parasitoids reared from (A) SPB and (B) *Phloeosinus dentatus* presented with simultaneous choices of logs infested with SPB or *Phloeosinus dentatus*. Parasitoids reared from (C) SPB and (D) *Ips grandicollis* presented with simultaneous choices of logs infested with SPB or *Ips grandicollis*. (illustration from Kudon and Berisford 1981b)

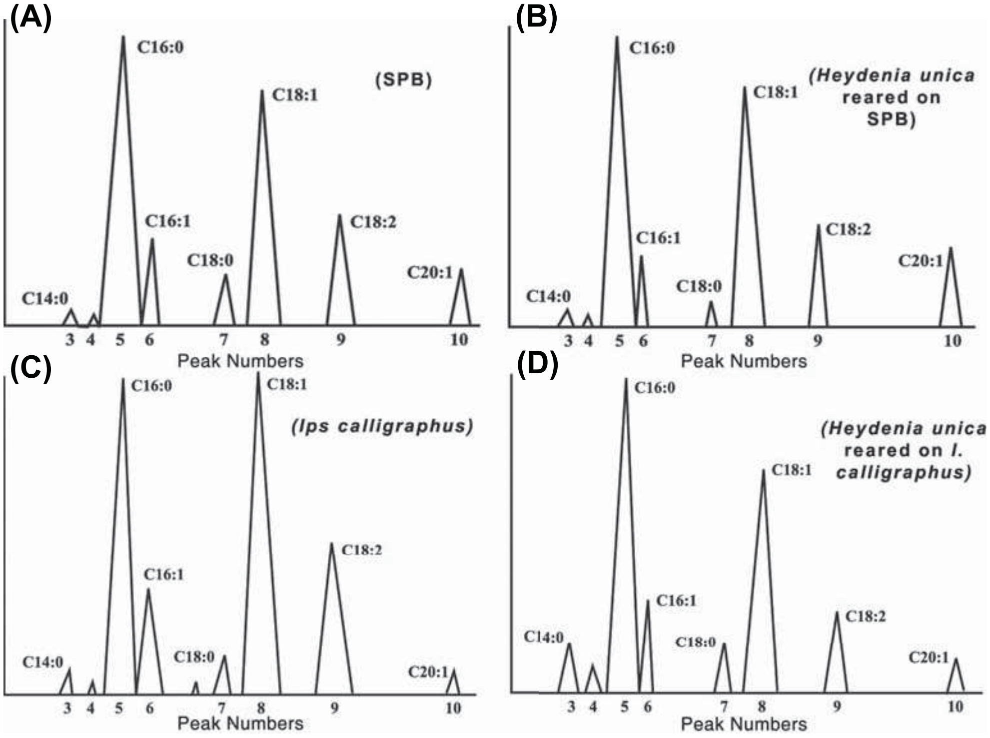


Figure 8.7—Lipid profile of (A) SPB and (B) a parasitoid, *Heydenia unica*, that had been reared on SPB. Lipid profile of (C) *Ips calligraphus* and (D) the same *Heydenia unica* that had been reared on *I. calligraphus*. (illustration from Kudon and Berisford 1980)

then potential SPB parasitism by parasitoids from *Ips* spp. might be reduced for at least one generation. A conceptual model of potential parasitoid-host interactions among SPB, *Ips*, and their common parasitoid complex has been proposed (Berisford 1980). The model assumes a relatively stable *Ips* population vs. fluctuating SPB populations and describes theoretical shifts of parasitoids among the beetle hosts as each host becomes more or less abundant relative to the other over time. During SPB epidemics, *Ips* populations will also increase since *Ips* spp. frequently attack SPB-infested trees. The relative populations, however, still fit the hypothesis of the model; i.e., that the relatively scarce host loses parasitoids to the relatively abundant one regardless of absolute populations (Figure 8.8).

The SPB and most of its associated bark beetle competitors produce aggregation pheromones (Birch 1978), or they cause the release of attractive host compounds during initial attacks. Some bark beetles may use pheromones as species isolation mechanisms (Lanier and Wood 1975, Wood 1970). Birch and Wood (1975) and Byers and Wood (1981) demonstrated that two closely associated bark beetles may utilize reciprocal inhibition to avoid competing for the same food. These species may colonize the same tree but occupy different parts due to inhibition of attacks by beetles that arrive after the species that makes the initial successful attacks. Predators of the SPB, particularly clerid beetles, respond to aggregation pheromones where adults feed on arriving SPB adults and females subsequently oviposit on the trees. Other natural enemies, including parasitoids, may use SPB aggregation or sex pheromones as kairomones to locate potential hosts. Birch and others (1980) determined the response of different beetles to logs infested with various combinations of SPB, *I. avulsus*, *I. grandicollis*, and *I. calligraphus*. The first beetles to arrive were generally SPB if SPB females were present in experimental logs. Southern pine beetles did not respond, however, to logs infested with any *Ips* species. Response by *I. avulsus* and *I. grandicollis* was enhanced when SPB plus males of either of the *Ips* spp. were present. The response of *I. avulsus* to its own attractant was also enhanced by the presence of *I. grandicollis*. This phenomenon was also reported by Hedden and others (1976). *Ips calligraphus* was inhibited by *I. avulsus*. Conversely, *I. avulsus* response was enhanced by the presence of *I. calligraphus*. Reciprocal inhibition occurred between the SPB and *I. grandicollis*. The olfactory interactions during attack on new host material resulted in rapid colonization of trees with minimal competition among different bark beetle species.

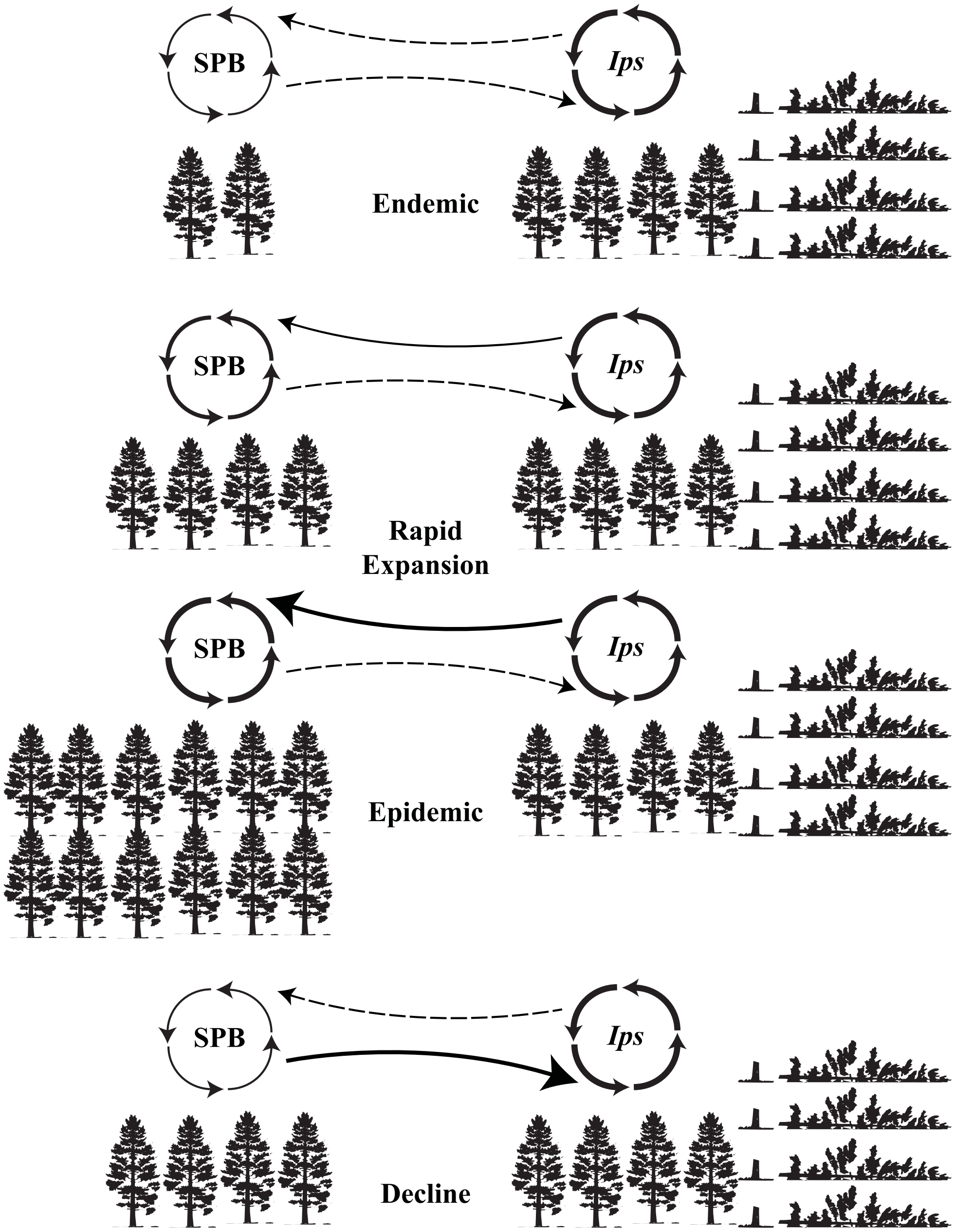


Figure 8.8—Theoretical model of parasitoid shifts from relatively scarce hosts to more abundant hosts (*Ips* spp. and SPB) during the buildup of SPB from endemic to epidemic levels and the subsequent decline to endemic populations. (illustration from Berisford 1980)

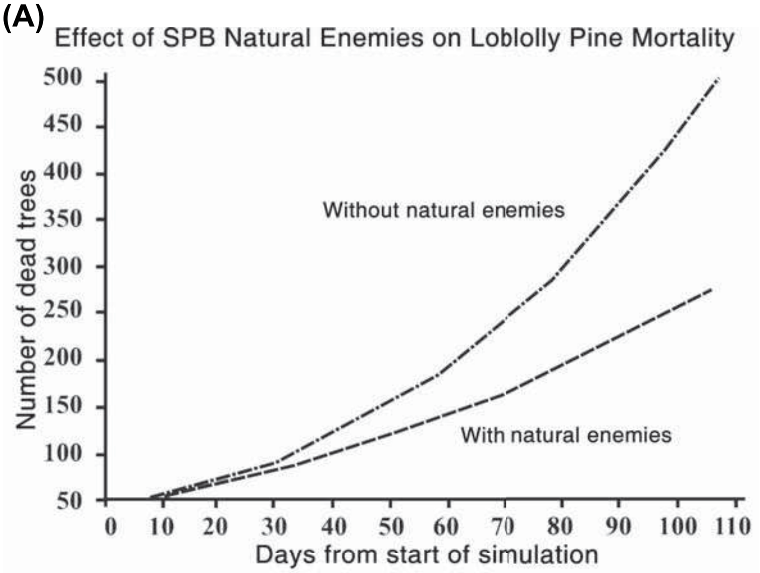
8.9. IMPACT OF PARASITOIDS ON SPB BROODS

Mortality of SPB broods caused by parasitoids and predators has been determined by excluding them from SPB-infested trees during specific periods of SPB brood development (Linit and Stephen 1983). More than half of the natural enemies, mostly predators, arrived during the first week of SPB development. Since predators are presumed to consume more than one host, highest SPB mortality probably occurrs due to their activities. Total mortality caused by parasitoids and predators during SPB brood development was estimated to be about 15 percent. However, parasitism of *Ips grandicollis* in Australia by *Roptrocerus xylophagorum* averaged 17 percent (Berisford and Dahlsten 1989), suggesting that individual species of parasitoids may be capable of parasitism rates higher than observed where they are in competition with other parasitoids and predators. Obviously, any evaluations of SPB population dynamics should consider the role and impact of parasitoids and predators.

Stephen and others (1989) developed SPB population dynamics models that allow testing of the role of natural enemies in the regulation of SPB populations. These models make it possible to simulate the impact of natural enemies on SPB population growth as affected by factors such as host tree species and season of the year. Figures 8.9A and B shows a simulation of SPB population growth in loblolly and shortleaf pine stands. The growth rate of SPB populations in the absence of natural enemies is rapid with either tree host, but substantially higher in shortleaf pine, which normally has thinner bark than loblolly pine. This suggests that parasitoids are likely to contribute more to SPB mortality on shortleaf pine since they are known to be more effective on trees with thin bark (Gargiullo and Berisford 1981). Simulations of SPB spot growth, starting at different times of the year, show that natural enemies are particularly important in regulating SPB spot growth in early summer (June). Natural enemies appear to be less effective in late summer and early fall, when simulated spot growth trends were similar with or without natural enemies.

8.10. ROLE OF PARASITOIDS IN SPB MANAGEMENT

Although natural enemies are presumed to regulate SPB populations at endemic levels, it is obvious that they cannot prevent periodic outbreaks in areas with large concentrations of highly susceptible trees, particularly overstocked plantations. Parasitoids may be less effective in dense pine plantations due to a lack of plant diversity, particularly flowering plants that provide nectar and pollen as energy sources for foraging adults (Stephen and others 1997). It may be possible to increase parasitoid impact on developing SPB broods by providing a nectar substitute (Stephen and Browne 2000). There is good experimental evidence that supplemental food can increase parasitoid adult longevity and egg production (Mathews and Stephen 1997). Future SPB management plans will likely acknowledge the contribution of hymenopterous parasitoids to SPB population regulation and attempt to conserve or perhaps augment this source of natural control.


(A) Effect of SPB Natural Enemies on Loblolly Pine Mortality

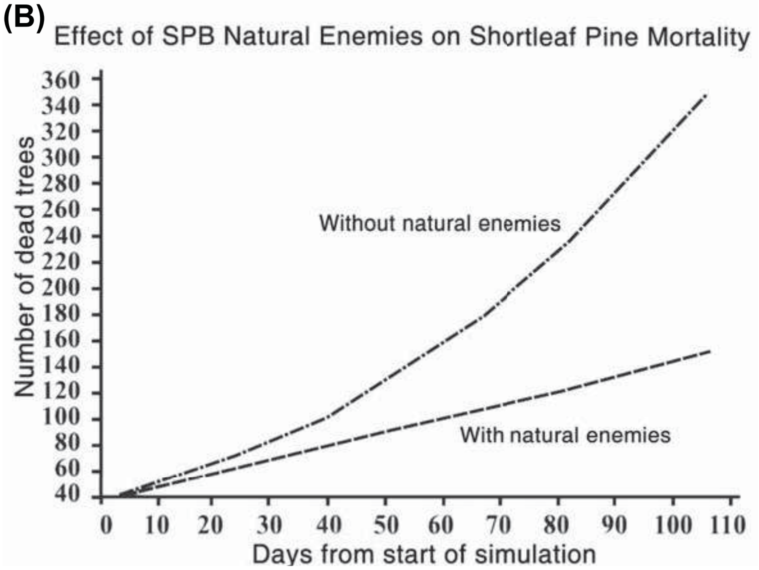

(B) Effect of SPB Natural Enemies on Shortleaf Pine Mortality

Figure 8.9—Predicted effect of SPB natural enemies on (A) loblolly and (B) shortleaf pine mortality. (redrawn from Berisford 1980)

9

From Attack to Emergence: Interactions between Southern Pine Beetle, Mites, Microbes, and Trees

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Abstract

Bark beetles are among the most ecologically and economically influential organisms in forest ecosystems worldwide. These important organisms are consistently associated in complex symbioses with fungi. Despite this, little is known of the net impacts of the fungi on their vectors, and mites are often completely overlooked. In this chapter, we will describe interactions involving the southern pine beetle (SPB), among the most economically damaging of North American forest insects. We examine SPB interactions with mites, fungi, and other microbes, following the natural temporal progression from beetle attack to offspring emergence from trees. Associations with fungi are universal within bark beetles. Many beetle species possess specialized structures, termed mycangia, for the transport of fungi. The SPB consistently carries three main fungi and numerous mites into the trees it attacks. One fungus, *Ophiostoma minus*, is carried phoretically on the SPB exoskeleton and by phoretic mites. The mycangium of each female SPB may contain a pure culture of either *Ceratocystiopsis ranaculosus* or *Entomocorticium* sp. A. The mycangial fungi are, by definition, transferred in a specific fashion. The SPB possesses two types of gland cells associated with the mycangium. The role of these cells and their products remains unknown. Preliminary studies have observed yeast-like fungal spores in the mycangium and several surrounding tubes that presumably carry secreted chemicals from gland cells (or bacteria) to the mycangium. The degree to which there is selective activity of the glandular chemical secretions remains to be seen. While *O. minus* may play some role in tree killing, none of these three fungi are highly virulent in their pine hosts. All three fungi grow within the phloem, sporulating heavily in beetle tunnels within which the SPB larvae graze. Though their ecological roles are complex and context-dependent, these three fungi can be divided into an antagonist (*O. minus*) and two mutualists (both mycangial fungi, though *Entomocorticium* sp. A appears to be of greater benefit to the beetles than *C. ranaculosus*). Naturally, all three of the fungi compete for access to uncolonized pine phloem. The results of these competitions can have significant impacts on their beetle and mite hosts, and ultimately on the population dynamics of this destructive pest.

Keywords

actinomycetes symbiosis
Dendroctonus frontalis
Ceratocystiopsis
Entomocorticiun
mycangium
Ophiostoma minus,

9.1. INTRODUCTION

Bark beetles (Coleoptera: Scolytidae, altern. Curculionidae: Scolytinae) are among the most ecologically and economically influential organisms in forest ecosystems worldwide. These important organisms are consistently associated in complex symbioses (from casual commensalisms to obligate mutualisms) with fungi (Harrington 2005, Paine and others 1997) and mites (Kinn 1971, Lindquist 1969, Moser and Roton 1971). Despite this, little is known of the net impacts of the fungi on their vectors, and mites are often completely overlooked. In this chapter, we will describe interactions involving the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), among the most economically damaging of North American forest insects (Price and others. 1998). We will examine SPB interactions with its associated mites and fungi, following the natural temporal progression from beetle attack to offspring emergence from trees.

9.1.1. Phoretic Mites

Mites (Chelicerata: Acariformes) are commonly associated with bark beetles and fungi (Kinn 1971). Although mites are often believed to be passive inhabitants of a community, they can have strong interactions with nonmite species (Hofstetter and others 2006a), are important indicators of disturbance (Schelvis 1990, Steiner 1995), impact natural and agricultural systems (Dicke and Sabelis 1988, Hill and Stone 1985, Lindquist 1986), and are major components of biological diversity (Walter and Proctor 1999). Details of the biology and ecology of this important group of organisms are handled in chapter 11. We focus here on their roles and activities within the beetle-tree interaction.

Dispersal and migration pose major challenges for mites living in discontinuous, ephemeral habitats (e.g., bark beetle-infested trees). Because mites are very small and wingless, movement between resources that are patchy in space and time requires assistance. The use of one organism by another for transport or phoresy, is common among mites, small insects, pseudoscorpions, nematodes, and microbes associated with bark beetles. Mites are especially adept at phoresy and often have highly modified phoretic stages (phoretomorphs) and appendages (Kinn 1971, Moser and Cross 1975). Phoretic individuals often go through a sequence of behaviors or morphological changes that are quite different from nonphoretic individuals of the same species. Many of these behaviors are analogous to those used by parasites to find their hosts (Athias-Binche and Morand 1993). In a sense, all phoresy can be considered an exploitation of the carrier, and therefore, parasitic. However, species interactions should be defined in terms of their ultimate effects on the fitness of the participants if they are to make ecological and evolutionary sense (Walter and Proctor 1999). Under most conditions, phoretic mites can be classified as commensal, in that they do not affect the carrier but the phoront benefits (Houck 1994). However, when mites are abundant they may interfere with carrier movement and reduce travel distances (Kinn 1971, Kinn and Witcosky 1978).

9.1.2. Phoretic Fungi

Associations with fungi are universal within bark beetles. Many beetle species possess specialized structures, termed mycangia, for the transport of fungi (Batra 1963, Klepzig and Six 2004, Levieux and others 1989, Paine and others 1997). Broadly defined, a mycangium is any structure that consistently transports fungi regardless of form (Beaver 1989, Farris and Funk 1965, Furniss and others 1987, Livingston and Berryman 1972). The mycangium may exist in a variety of forms, from simple pits to highly evolved integumental invaginations lined with glandularized cells (as in SPB).

Ophiostomatoid fungi are well adapted to dispersal on the exoskeletons of bark beetles and associated arthropods (Klepzig and Six 2004). Most of these fungi produce perithecia with necks that extrude sticky spores at heights where they are likely to be encountered by invertebrates. These spores are also shaped such that multiple contact points with the vector are likely, and easy removal is not. Asexual fruiting structures also produce mucilaginous masses of spores that readily adhere to insects (Malloch and Blackwell 1993). These adhesive coats of spores are easily dispersed in resin (though not in water) ensuring release only in the presence of an appropriate substrate (i.e., a new host tree) (Whitney and Blauel 1972).

9.2. THE SOUTHERN PINE BEETLE AND ITS SYMBIOTIC COMMUNITY

The SPB consistently carries three main fungi and numerous mites into the trees it attacks. One ophiostomatoid fungus, *Ophiostoma minus*, is carried phoretically on the SPB exoskeleton and by phoretic mites (Bridges and Moser 1983, Rumbold 1931). The phoretic transport of this fungus by SPB and its arthropod associates, especially mites, is the only means of access *O. minus* has to new host tissue (Dowding 1969). The mycangium of each female SPB (the structures are not found in males; Barras and Perry 1972, Happ and others 1971) may contain a pure culture of either *Ceratocystiopsis ranaculosus* (Barras and Taylor 1973, Jacobs and Kirisits 2003, Zipfel and others 2006) or *Entomocorticium* sp. A (aka, SJB122; Barras and Perry 1972, Happ and others 1976), an amber-colored basidiomycete (Hsiau 1996). A small percentage of beetles may not carry fungi in their mycangium. Only mycangial fungi, if present, are found in live beetles.

While *O. minus* may play some role in tree killing (see below), none of these three fungi are highly virulent in their pine hosts. All three fungi grow within the phloem, sporulating heavily in beetle tunnels within which the SPB larvae graze. Though their ecological roles are complex and context-dependent (also reviewed in greater detail below), these three fungi can be divided into an antagonist (*O. minus*) and two mutualists [both mycangial fungi, though *Entomocorticium* sp. A appears to be of greater benefit to the beetles than *C. ranaculosus* (Bridges 1985, Coppedge and others 1995, Goldhammer and others 1990, Klepzig and Wilkens 1997)]. Naturally, all three of the fungi compete for access to uncolonized pine phloem (Klepzig and Wilkens 1997). The results of these competitions can have significant impacts on their beetle and mite hosts. Interestingly, *O. minus* and *C. ranaculosus* spores are also carried by *Tarsonemus* mites (Acarina: Tarsonemidae) that can occur in high densities on SPB (Bridges and Moser 1983, Hofstetter and others 2006b, Moser 1985, Moser and Bridges 1986). *Tarsonemus* release fungal spores throughout newly excavated beetle galleries (Lombardero and others 2000c). Feedback between mites and *O. minus* (as well as *C. ranaculosus*) can affect SPB population dynamics and influence forest dynamics (Hofstetter and others 2006a; Lombardero and others 2000c, 2003).

9.2.1. Beetles in Flight

Mite Community

The mite community of the SPB is reviewed elsewhere in this volume (see chapter 11). The phoretic members of this assemblage are faced with a choice among a number of conspecific hosts, which may vary in quality as carriers. The best host is one that is predictable, available, and abundant. Southern pine beetles provide mites with the additional advantage of delivering their mite phoronts, such as *Tarsonemus krantzi*, to substrate suitable for their favored fungus (*O. minus*) (Hofstetter and others 2006a). Thus, *Tarsonemus* spp. occur frequently on SPB and have strong interactions with Ophiostomatoid fungi (Hofstetter and others 2006a, 2006b; Klepzig and others 2001a, 2001b; Lombardero and others 2000c, 2003) (Figure 9.1). Abundances of mite species vary with time of year, beetle density and emergence patterns, fungal abundance, and geographic location (Hofstetter and others 2006a, 2006b; Kinn 1971, 1982).

Fungal Community

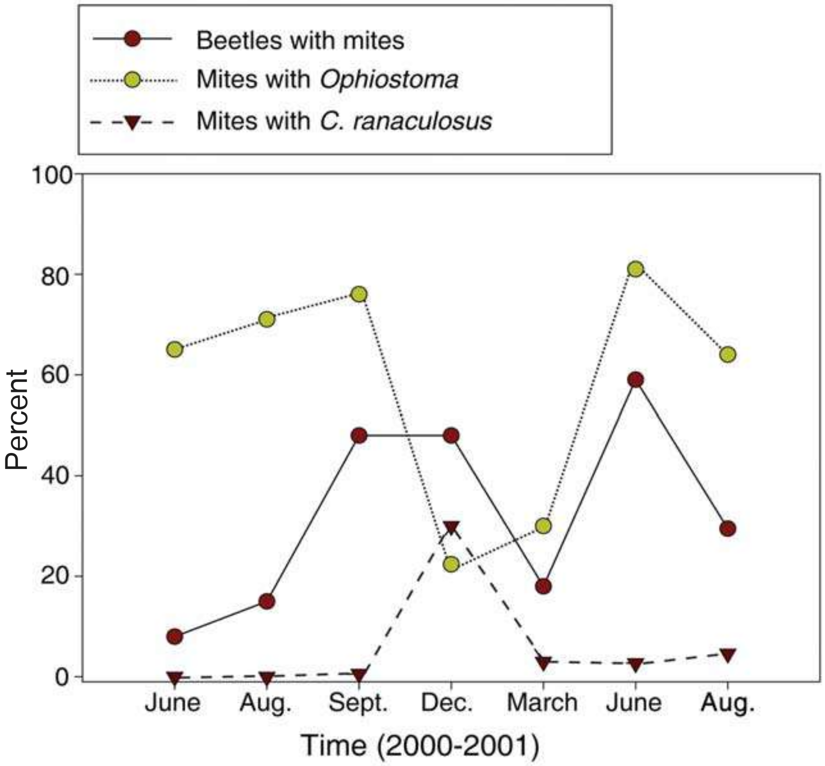
The relative abundance of each mycangial fungus within SPB populations varies with location and time of year (Harrington 2005, Hofstetter and others 2006b). Interestingly, 5-20 percent of females within a population have both mycangial fungi, one within each side their mycangium. A small percentage of SPB females within a population do not carry mycangial fungi (Hofstetter and others 2006b). Spores of *O. minus* (and *O. nigrocarpum*; Harrington 2005) are commonly found on the exoskeleton of SPB (Bridges and Moser 1983, Rumbold 1931). *O. minus* is the most abundant associate, but its abundance varies greatly among beetle populations and across regions (Harrington 2005).

9.2.2. Beetles on the Attack

Beetle Interactions with Highly Defended Host Trees

As beetles enter living/more or less healthy/well defended trees, they are met with an exudation of oleoresin (Hodges and others 1979). If sufficient oleoresin flows from each wound, and if that resin is viscous enough and crystallizes quickly enough, the SPB entomb or "pitch-out". Although SPB attack can be successfully resisted (Trapp and Croteau 2001), it is generally accepted that no potential host tree is immune to attack at high SPB densities (Strom and others 2002). Resistance by individual trees does vary, and environmental attributes that affect oleoresin production can have substantial impacts on the success of beetle attack. So far, it has not been possible to experiment with SPB effects on host trees in the absence of fungi and mites. It is also very

Figure 9.1—Percentage of beetles with *Tarsonemus* mites and percentage of *Tarsonemus* that have ≥ 1 spore of *Ophiostoma minus* or *Ceratocystis ranaculosus.* Each time period represents beetles from five infestations in Bankhead National Forest, Alabama. (data collected by R.W. Hofstetter)



difficult to artificially infest healthy trees with SPB (Cook and Hain 1987a,1987b). Most work on this insect-tree interaction has therefore been limited to artificial wounding and inoculation, without the direct inclusion of the insect itself. Fortunately, the fungal associates of SPB can be readily cultured on media and used as a practicable surrogate for SPB (Klepzig and Walkinshaw 2003).

Fungal Interactions with Highly Defended Host Trees

Ophiostoma minus

While the exact role of *O. minus* at this stage of the SPB life cycle continues to be debated, the insect-tree interaction is affected by and affects the fungus immediately. For example, SPB that have been exposed to tree resin carry dramatically reduced populations of viable fungal propagules on their exoskeleton (Veysey and others 2003). As SPB enter trees, the spores they carry may become detached and begin to germinate. This inoculation of *O. minus* into phloem begins the colonization process. While *O. minus* is not a primary pathogen within pine trees, it may work with the beetles to hasten tree death (Paine and others 1997). Studies examining the virulence of *O. minus* have varied in methodologies and results. Most investigators accept increased lesion size as an indication of greater growth within the host tissues. The relationship between growth *in situ* and degree of virulence is less clear. *Ophiostoma minus* is capable of growing some distance—and causing a relatively high degree of resinosis and necrosis—within well defended pine trees. In no case, however, have single point inoculations with *O. minus* been found to be capable of causing death of, or even external symptoms on, host trees. The spate of inoculation studies in the 1980s led to a change in thinking about the possible role of this fungus in the SPB life cycle. Contrary to initial investigations (Bramble and Holst 1940, Nelson 1934), *O. minus* was no longer seen as a virulent pathogen which killed the tree and allowed for development by its mutualistic insect vector, SPB. The observations of tree mortality attributed to SPB in the absence of *O. minus* (Bridges and others 1985, Hetrick 1949) added to this line of thinking.

A mass inoculation study, perhaps more closely reflecting the inoculation technique used by SPB, has cast a different light on the role of *O. minus* in the SPB attack process. Recognizing that previous work (Table 9.1) (Christiansen and others 1999; Cook and Hain 1986, 1987b; Guérard and others 2000; Horntvedt and others 1983; Krokene and Solheim 2001; Långström and others 2001; Lieutier 2002; Raffa and

Berryman 1983; Solheim and others 1993) in other systems had demonstrated the feasibility and utility of using mass inoculation to test host responses to beetles and vectored fungi, Klepzig and others (2005) tested whether mass inoculation with *O. minus* had lasting effects on resin defenses in loblolly pine. They quantified oleoresin production response to wounding alone, and wounding plus inoculation, relative to untreated controls. They also quantified a secondary defense of pines against *O. minus*, by measuring the extent to which this fungus colonized tree tissue. Finally, they tested the ability of loblolly pine to exhibit induced systemic resistance to fungi in response to mass inoculation, a phenomenon previously observed in Norway spruce (Krokene and others 1999), Scots pine (Krokene and others 2000), Monterey pine (Bonello and others 2001), and Austrian pine (Bonello and Blodgett 2003).

Trees mass inoculated with *O. minus* produced higher resin yields than control or wounded-only trees as soon as 15 days and as late as 105 days post-treatment. While fungal stimulation of resin flow was previously known (Hepting 1947, Popp and others 1991), it had never been studied in the context of a mass inoculation/simulated beetle attack context. Lieutier (2002) does caution against strong reliance on artificial inoculation studies in making conclusions about resistance to bark beetles. There are likely important differences between artificial inoculations and natural beetle attacks. For example, the percentage of SPB carrying *O. minus* varies significantly even within a population (Hofstetter and others 2006a, 2006b). However, in some cases there is close correspondence between results from artificial inoculations and natural attacks (Guérard and others 2000, Långström and others 2001). Klepzig and others (2005) did conclude that beetles attacking previously attacked trees—within the zone of the previous attack—would face a more extensive resinous response from their host than would beetles attacking unattacked trees. However, this effect does not appear to extend beyond a single season. While recently published studies have indicated that mass wounding might decrease tree resistance to SPB and *O. minus* (Tisdale and others 2003a, 2003b), these studies did not incorporate simultaneous impacts of wounding and fungal inoculation, as typically occurs in the natural SPB infestation process.

Klepzig and others (2005) did not observe signs of systemic induced resistance in loblolly pine. Lesions from inoculations outside the mass wounding/inoculation site did not differ between treatments. Fungal success, as measured by the area of host tissue colonized by the invading fungus before it was stopped by the host defensive response, was unaffected by prior fungal inoculation experience by the host. These results are in agreement with Krokene and others (1999) who, working with Norway spruce, only noted this phenomenon in the immediate vicinity of mass inoculations.

In this study, mass inoculations with *O. minus* did not result in the death of a single tree at either site. However, SPB likely inoculate *O. minus* at much higher rates (up to 1,900 m^2; Fargo and others 1978). While some bark beetle-associated fungi can kill trees (Krokene and Solheim 1998, Lieutier 2002, Solheim and

Table 9.1—Summary of inoculation studies using SPB associated fungi (literature summary by K.D. Klepzig)

Lesion size *(mm)*	Sampling time *(days)*	Wound *(mm)*	Inoculum type	Reference
42,68,62,69	7,14,21,28	13	Mycelia in broth	Cook and Hain 1985
100-150	14	13	Mycelia in broth	Cook and Hain 1986
103	14	13	Mycelia in broth	Cook and Hain 1987a
18,20,80,90	1,2,7,14	10	Mycelia in broth	Cook and Hain 1987b
74-97	14	13	Mycelia in broth	Cook and Hain 1988
65,49,85,87	21	3,6,12,24	Phloem disk	Paine and Stephen 1987b
111.5		48		
45	20	12	Phloem disk	Paine and Stephen 1987c
70-120	14	12	Phloem disk	Paine and others 1988
70,110,81	3,7,28	10	Cotton	Ross and others 1992
24	70	10	Malt extract agar	Nevill et al. 1995

others 1993), numerous inoculation studies have failed to demonstrate a similar role for *O. minus* (see Table above). Paine and others (1997) note that the long-held assumption that bark beetle-associated fungi kill trees is based primarily on the vector relationships, the association of staining with dead trees, and instances of artificial mass inoculation killing trees. However, Lieutier (2002) explains that this does not necessarily indicate involvement of phoretic ophiostomatoid fungi in tree death. Rather, the role of bark beetle associated fungi, e.g., *O. minus*, may be that of cofactors (Kopper and others 2004, Lieutier 2002)—biotic agents that are not pathogenic in and of themselves but do function in compromising host defenses (Beckage 1998).

In the SPB system, the primary role of *O. minus* may be to aid in exhausting tree defenses and allowing for beetle establishment. During the critical period that beetles first enter a tree and either succeed or fail to trigger aggregation, it appears that the host defensive response to fungal inoculation can dramatically reduce resin flow. The tree may be at this stage—and due to the fungus—more vulnerable to beetle infestation. Anything that contributes to depletion of the tree's ability to synthesize secondary metabolites during beetle aggregation improves the probability of successful beetle mass attack (Lieutier 2002). Subsequently, the ultimate death of the tree likely occurs from a combination of bark beetle and fungal effects (Lieutier 2002, Paine and others 1997). Via this mechanism and/or detoxification of host chemistry, *O. minus* appears to aid SPB in overcoming its tree host.

Mycangial fungi interactions with highly defended host trees

The early pine-SPB fungus interaction literature painted a contradictory picture of the relative virulence of these fungi. Some focused on the small resinous lesions formed by mycangial fungi within trees and inferred an avoidance of host defense, or greater virulence (Paine and Stephen 1987b, Paine and others 1988). Others concluded that a more extensive host response indicated a greater degree of fungal virulence (Cook and others 1986, Cook and Hain 1985, 1988). Cook and Hain (1988) noted that mechanical wounds alone produced shorter lesions than mycangial fungi, which produced shorter lesions than *O. minus*, concluding that "The more virulent invader appeared to evoke a stronger response… the less energy a tree uses in defending itself against less virulent attackers, the more energy it would have for future defensive responses." In general, mycangial fungi are now seen as weak pathogens of healthy trees (Paine and others 1997).

Mite Interactions with Highly Defended Host Trees

Little is know about how bark beetle-associated mites interact with trees during the attack stage, though it has been hypothesized that the heavy resin flow serves to scrub beetles clean of phoretic mites, at least to some extent. By comparing the number of mites on beetles that attack a tree (before entering the tree) with the number of mites on those same beetles when they reemerge from the tree, Hofstetter and others (unpublished) found that a majority (~90 percent) of phoretic mites leave their beetle host or are killed between the time a beetle lands on the tree and after it has mated and laid eggs. The trigger or cue that results in mites dismounting from a host beetle varies with the mite species and tree condition. In general, mites appear to leave host beetles when the host is in the appropriate habitat for the mite (Kinn 1971) or when the beetle is stressed (e.g., captured by a predator) or dying (e.g., old age) (Hofstetter, personal observation). Mites of most species are capable of surviving more than 30 days without food, indicating that phoretic mites can survive during the phoretic stage and through the early stages of bark beetle attack on trees (Kinn 1971). This extended survival allows time for fungi, nematodes, and beetle larvae to establish in trees.

9.2.3. Beetles in the Tree

Beetle Interactions with Poorly/Undefended Host Trees

Southern pine beetles must attack living trees for their offspring to develop properly, and do not attack dead or cut material. The SPB attack process transforms highly defended hosts into poorly defended hosts, which are good substrates for SPB larval and mycangial fungus development. However, new attacks by SPB on hosts that are already poorly defended are generally unsuccessful. These poorly defended hosts are often occupied by secondary bark beetles and saprophytic fungi that may be competitive and antagonistic towards SPB and its associated fungi. By the time defensive compounds in an attacked tree have diminished in quantity, most SPB larvae in that tree have moved through several developmental stages, and the mycangial fungi introduced by the mother beetle are well established in the surrounding phloem. Larvae may feed on a fungus that originates from an adjacent gallery of a conspecific or another arthropod. The fact that 20 percent of emerging SPB have two mycangial fungi suggests that this is not a rare occurrence (Hofstetter and others 2006b).

Fungus Interactions with Poorly/ Undefended Host Trees

Competitive interactions among SPB-associated fungi occur largely within trees that have succumbed to beetle attack. These poorly defended trees pose a different context to the interacting fungi and their insect vectors.

Ophiostoma minus

While the aggressiveness of *O. minus* within well defended trees may aid in stimulating and/or overcoming host defenses, this same aggression may make it a detriment to its beetle vector (Lieutier 2002). Highly pathogenic fungi that exhaust tree defenses and rapidly kill them are also very likely to invade the whole tree very rapidly, even before the beetle and its brood can became established. This makes these host tissues unsuitable for beetle development. This phenomenon has been well documented in the *O. minus*/SPB association in which the blue stain fungus is highly antagonistic to SPB mutualistic fungi (Klepzig and Wilkens 1997) and thus to larval development (Barras 1970). The moderately virulent habit of *O. minus* may be the best strategy for SPB. This allows SPB to successfully mass attack trees, but limits the extent to which the fungus can grow during beetle development (Lieutier 2002). By the time larvae begin developing within host tissues, *O. minus* becomes a competitor and antagonist of SPB (Barras 1970). The mechanism of this antagonism is likely due to, in large part, the interactions of SPB with its two other significant fungal associates. Areas fully colonized with *O. minus* are correlated with reduced developmental success in SPB —inhibited egg production, slower larval growth and development, even larval mortality (Barras 1970, Hofstetter and others 2006a). In addition, overall levels of *O. minus* within SPB infestations are negatively correlated with SPB population increase (Bridges 1985, Hofstetter and others 2006a, Lombardero and others 2000c).

Mycangial fungi

Most SPB infestations (from 1 to more than 100 colonized trees) have both mycangial fungi present (Bridges 1983, Coppedge and others 1995, Hofstetter and others 2005). This indicates the importance of both of these species to SPB and/or their phoretic mites. *Ophiostoma minus*, *Entomocorticium* sp. A, and *C. ranaculosus* compete for the uncolonized pine phloem (Klepzig and Wilkens 1997) and engage in primary resource capture, followed by direct interaction, which can lead to defense, and/or secondary resource capture. Competitive wins by mycangial fungi will result in successful development and emergence of fit adults. Wins by *O. minus* will likely result in poorly fed, weakened larvae and few, if any, emerging as adults. The most appropriate time to evaluate the role of the mycangial fungi is post-mass attack. Once the tree's resistance is overcome and the eggs hatch, early instar larvae begin feeding, constructing fine, sinuous galleries in the phloem as they develop and move (Payne 1983). Eventually, the larvae enlarge their feeding area into obovate feeding chambers that become lined with either of the two mycangial fungi. It appears extremely likely that larval SPB get most of their nutrition from the fungal growth within their feeding chambers rather than directly from the phloem itself. The mycangial fungi may, in fact, provide their most substantial benefits to SPB by concentrating dietary nitrogen for larvae (Ayres and others 2000). Beetles carrying *Entomocorticium* sp. A within their mycangia are more fecund and heavier, and have higher lipid contents than those containing *C. ranaculosus*. In turn, beetles containing *C. ranaculosus* tend to be more fit than those whose mycangia contain no fungi (Bridges 1985, Coppedge and others 1995, Goldhammer and others 1990). These interactions, however, are mediated by a variety of abiotic factors.

Differences in fungal tolerance to various tree compounds, for example, can have significance for fungal colonization, growth rate, and fungal-fungal competition. High levels of secondary metabolites (e.g., α-pinene) may favor the growth of one mycangial fungus over another. Seasonal variation in secondary metabolites can also lead to dynamic changes in mycangial fungi throughout the year. Phloem chemistry affects the nature of interactions between fungi by altering the production, diffusion, or volatilization of fungal-produced compounds (Boddy 2000). Differences in compound concentrations or lack of particular compounds and the abundance of *O. minus* within trees may influence the relative frequencies of mycangial fungi within beetle infestations. Because these fungi differ in their benefits to the beetle, allelochemical effects on competitive interactions can drastically affect beetle success. For example, *C. ranaculosus* is a better competitor with *O. minus* than *Entomocorticium* sp. A in the presence of α- or β-pinene. High levels of uric acid (a component of SPB frass) in growth media reduces *C. ranaculosus* and *O. minus* growth, but increases the growth rate of *Entomocorticium* sp. A (Goldhammer and others 1989). Uric acid also reduces *O. minus*' ability to capture resources previously captured by *Entomocorticium* sp. A (Hofstetter and others 2005). Uric acid levels likely increase in larval chambers as beetles develop, and thus become more important for competing fungi during the late larval or pupal stage. Differences in the tolerance of the two mycangial fungi to phloem chemistry, temperature, moisture, interactions with *O. minus*, or other species-specific organisms (e.g., nematodes associated with one of the fungal species) may have selected for two fungal mutualistic associates of SPB.

Competitive interactions among bark beetle-associated fungi are also potentially influenced by water potential, which undergoes marked changes over the course of beetle colonization of tree hosts. Soon after SPB attack, the phloem tissue the beetles inhabit rapidly dehydrates (Wagner and others 1979, Webb and Franklin 1978). Subsequent changes in water relations strongly affect the growth and competition of fungi (Klepzig and others 2004). At especially low water potentials, fungal growth is reduced to the extent that *C. ranaculosus* can equally compete with *O. minus*. This demonstrates the effects of an abiotic factor on fungal interactions and helps explain the success of mycangial fungi in SPB infested hosts, despite the nearly overwhelming competitive ability exhibited by *O. minus* in most cases (Klepzig and Wilkens 1997, Klepzig and others 2004).

Temperature also strongly affects the growth rates of all three fungi (Klepzig and others 2001b). *Entomocorticium* sp. A grows near maximum levels at cooler temperatures, suggesting that seasonal changes can alter relative fungal abundances within this community. In a study of several sites in northern Alabama, Hofstetter and others (2006b) observed that *Entomocorticium* sp. A became more abundant in winter and spring but tended to be supplanted by *C. ranaculosus* during the summer. Experimental manipulations of temperatures within infested logs were consistent with this seasonal pattern.

In summary, the variety of consistent SPB fungal associates may insulate SPB, to a degree, from the variety of abiotic conditions they face.

Mite Interactions with Poorly/ Undefended Host Trees

Tarsonemus mites are important in the propagation of *O. minus* between and within beetle-infested trees (Hofstetter and others 2006a, Lombardero and others 2003). Although ascospores of *O. minus* are abundant on the bodies of most mites within trees, only *Tarsonemus* spp. carry ascospores in the phoretic state (Moser 1985).

The feeding habits and interactions of mites underneath bark remain largely unknown. Food resources are readily available in undefended, infested host trees, and it is during this period that mites reproduce, feed, and propagate fungi throughout the inner bark. Mite populations are capable of staggering growth rates (Bruce and Wrensch 1990)—more than 300 fold in some cases (Lombardero and others 2000c) during this time.

Conditions within hosts can drastically worsen or improve for mites with time; phloem moisture changes, temperatures become more extreme, predator densities likely increase, microbial communities change, and pathogens may increase as the tree dies. Thus mite population growth rate and survival change as time progresses, depending upon the biology and trophic nature of the mite, insect, and microbial species present. For example, feeding by large woodborer larvae prior to beetle emergence may reduce fungal and mite levels under the bark. More specifically, *Tarsonemus* spp. and *O. minus* suffer direct loses from woodborer larval feeding and likely disrupt mite dispersal within bark (Hofstetter, unpublished).

Beetle Interactions with Fungi and Other Microbes in Poorly Defended Trees

By the time trees have succumbed to SPB attack, *O. minus* acts as an antagonist of the developing larvae. This negative effect is indirect: 1. there is strong asymmetric competition between mycangial fungi and *O. minus* (Klepzig 1998); 2. SPB larvae require mycangial fungi (Barras 1973); and 3. beetles without fungal mutualists are relatively less affected by phoretically vectored blue stain fungi (Klepzig and Six 2004, Yearian and others 1972). However, we cannot exclude direct effects from fungal compounds [(phenolics and isocoumarins (Hemingway and others 1977) or melanin (DeAngelis and others 1986)]. It is also possible that *O. minus* (or a colorless relative; e.g., Cartapip®) could be deployed as a biological control agent (Klepzig 1998).

Insects can harbor gut microbial communities that range from simple to complex (Cruden and Markovetz 1987, Handelsman and others 2005, Leadbetter and others 1999, Lilburn and others 2001). Little is known about gut symbionts of bark beetles. Previous studies have suggested a role in pheromone synthesis (Brand and others 1975, Conn and others 1984) and protection from gallery-invading fungi (Cardoza and others 2006). The importance of symbiotic fungi in the life cycles of bark beetles (Hofstetter and others 2006a, 2006b), the nutrient-poor substrate on which they feed, and the cellulolytic and nitrogen-fixing activities of some microbes associated with wood-boring insects (Bridges 1981, Delalibera and others 2006) suggest that gut symbionts could play important roles in the biology of bark beetles. Recently, Vasanthakumar and others (2006) found α- and γ-Proteobacteria and Firmicutes in SPB larvae. Adult SPB guts contained only γ-Proteobacteria. They concluded that the presence of *Bacillus* sp. and *Leuconostoc* sp. in larval but not adult guts indicated a role in growth and development for these bacteria. *Enterobacter* spp., *Rahnella aquatilis, Klebsiella* spp., and *Pantoea* spp. were all commonly found in SPB larvae, and are known to fix nitrogen in other environments (Behar and others 2005), indicating a possible role for these bacteria, together with some fungal associates, in nitrogen concentration for larvae (Ayres and others 2000, Bridges 1981, Klepzig and Six 2004). These microbes might also detoxify conifer defensive compounds (monoterpenes, diterpene acids, phenolics) (Lewinsohn and others 1991, Martin and others 1999, Raffa and others 2005, Yu and Mohn 1999). Neither Vasanthakumar and others (2006) nor Delalibera and others (2006) found cellulolytic bacteria with SPB. This important role is likely performed by other microbial associates. Recent work has identified yet another bacterial partner of SPB (Scott and others 2008). A new species of actinomycete bacterium occurs within the mycangium and larval galleries of SPB. Via a newly characterized antibiotic, mycangimycin, the bacterium strongly inhibits the fungal antagonist *O. minus*, but only weakly inhibits the mutualist, *Entomocorticium* sp. A. (Scott and others 2008).

Fungus Interactions with Fungi in Poorly/Undefended Host Trees

The fungi associated with SPB compete with one another and other fungi for host substrate and access to beetles and mites. While these competitions have been quantitatively characterized (Klepzig and Wilkens 1997), the mechanisms behind them remain poorly understood. One possible explanation for the observed antibiotic effects may lay with the molecules responsible for the common name of some ophiostomatoid fungi—stain fungi. Melanins are dark biological macromolecules that can protect fungi against irradiation, enzymatic lysis, temperature extremes, and desiccation (Butler and Day 1998). These secondary metabolites can also be toxic (Henson and others 1999), can act as virulence factors, and may account for as much as 30 percent of the dry weight of a cell (Butler and Day 1998). The role of melanins in the ecology and pathology of bark beetle-associated stain fungi remains unknown. Klepzig (2006) found that *Entomocorticium* sp. A was significantly inhibited by added melanin, though *C. ranaculosus* was not.

Fungus-Mite Interactions in Poorly/Undefended Host Trees

Mites and associated insects play a significant role in the dispersal of fungi within SPB-infested trees. Mite densities can be extremely high (> 100 individuals per cm^2 in phloem) in areas where food sources are plentiful. Food resource abundance and mite abundance are often interrelated, in that particular resources (e.g., a species of nematode or fungus) are closely associated with mite species (Lindquist 1986). For instance, there is strong evidence that *O. minus* abundance (number of distinct units) is strongly correlated with *Tarsonemus* abundance (Hofstetter and others 2006a, 2006b; Lombardero and others 2000c, 2003).

Mite-fungal interactions are dynamic and change as the tree decays or climatic conditions change. For example, in cool temperatures a larger proportion of *Tarsonemus* carry ascospores of *C. ranaculosus*. Presumably, hyperphoresy of *C. ranaculosus* on *Tarsonemus* tends to promote the extent of phloem that is colonized by *C. ranaculosus,* and therefore the proportion of SPB that later emerge carrying

C. ranaculosus (Hofstetter and others 2006b). Interestingly, changes in temperature and moisture might influence genetic variability in *C. ranaculosus* via effects on mite behavior. Temperature, or any other factor that influences the relative abundance of *C. ranaculosus* and *Entomocorticium* sp. A, would likely affect both the mite and beetle populations. Because *C. ranaculosus* represents an inferior nutritional resource for SPB (Bridges 1983; Coppedge and others 1995; Goldhammer and others 1990; Klepzig and others 2001a, 2001b) but a superior nutritional resource for *Tarsonemus* (Lombardero and others 2000c), seasonal changes in the ratio of mycangial fungi species could influence beetle and mite population dynamics in opposite directions. Field studies by Miller and Parresol (1992) and Bridges (1983) demonstrated increased reproduction in beetle populations when *Entomocorticium* sp. A was the dominant mycangial fungus. Likewise, Hofstetter and others (2006a, 2006b) recorded increased mite reproduction and decreased beetle reproduction during periods when *O. minus* and *C. ranaculosus* were particularly abundant. These results and interpretations predict that the abundance of *C. ranaculosus* relative to *Entomocorticium* sp. A would tend to be highest in the warmest climates where SPB occurs (for example, Florida and Mexico). Preliminary surveys of SPB mycangia in Mexico reveal that *Entomocorticium* sp. A is very uncommon (Hofstetter and others, unpublished).

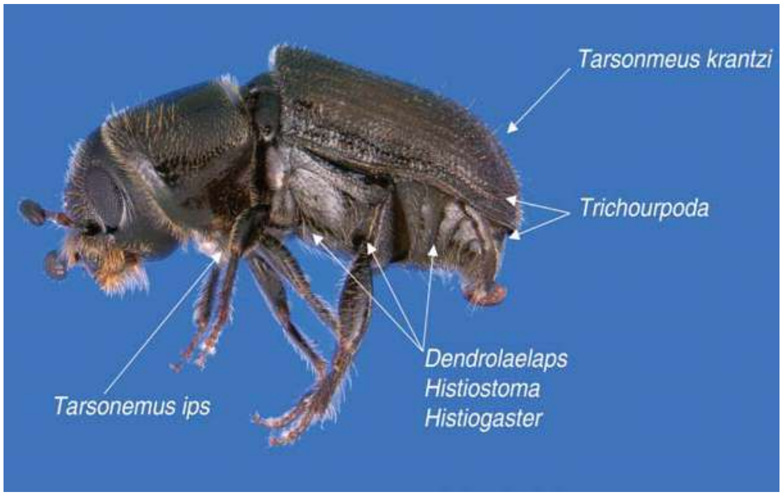


Figure 9.2—General locations of phoretic mite species on SPB during flight. (figure by R.W. Hofstetter)

9.2.4. Beetles Emerging

Acquisition of Mites during Emergence

Typically only one life history stage is phoretic in a given species. Most phoretic mites of many different taxa share similar morphologies: dorsoventral flattening, oval or circular bodies, and flanges covering all or some appendages (Athias-Binche and Morand 1993, Binns 1982, O'Conner 1994). This convergent morphology may serve to reduce loss of moisture when on the host and to present a smooth dorsal surface, making it difficult for the host to remove mites by grooming or rubbing (Figure 11.2 in chapter 11).

Mites may be attracted, or inhibited from attaching, to a given insect carrier via kairomonal secretions or acoustic emissions from the insect, the insect's fungal component or activity level (e.g., tunneling), as well as the condition, sex, and age of the insect. Abiotic factors, such as low moisture and high temperature within bark, can stimulate mites to search for phoretic hosts (Kinn 1971). Mites exhibit some site specificity, reminiscent of niche partitioning, in attaching to SPB adults (Figure 9.2). Interestingly, most SPB exiting a tree have just a few or even no mites (Hofstetter and others 2006a, 2006b; Kinn 1971).

Acquisition and Transport of Fungi

Many insects emerging from SPB-infested bark acquire *O. minus* while traveling through SPB galleries or stained phloem. Approximately 80 percent of SPB-associated species carry *O. minus*. Likewise, up to 80 percent of *Tarsonemus* may carry *O. minus* spores. No *O. minus* was observed on mite species phoretic on associated insects (Table 9.2). The mycangial fungi are, by definition, transferred in a much more specific fashion. Happ and others (1971) first described the mycangium of the SPB, identifying two types of gland cells associated with this structure. The role of these cells and their products remains unknown. In preliminary studies, Klepzig and others (unpublished) have observed yeast-like fungal spores in the mycangium and several surrounding tubes that presumably carry secreted chemicals from gland cells to the mycangium. The degree to which there is selective activity of the glandular chemical secretions remains to be seen.

Table 9.2 — The presence or absence of *O. minus* and mites on organisms captured in emergence traps on 36 SPB-infested *Pinus taeda* in Talladega National Forest, Alabama 2000 (Data collected by R.W. Hofstetter)

Insect	N	Percent insects with *Ophiostoma minus*	Percent insects with *Tarsonemus*	Percent insects with mites (all species)*
Crematogaster sp.	1	100.0	0	0
Aradus sp.	4	0	0	0
Aulonium sp.	2	100.0	0	50.0
Atanycolus comosifrons	2	100.0	0	0
Cossonus corticola	27	74.1	0	16.0
Corticius sp.	1	0	0	0
Crypturgus aleutaceus	4	0	0	0
Dendroctonus frontalis	247	59.1	35.1	49.2
D. valens	1	100.0	0	0
Gnathotricus materiarius	26	30.8	0	21.0
Platysoma sp.	2	100.0	0	50.0
Hylastes sp.	2	100.0	0	50.0
Ips avulses	1	100.0	100.0	100.0
I.grandicolus	1	100.0	0	0
Leptacinus sp.	1	100.0	0	0
Lyctocoris sp.	5	80.0	0	0
Platysoma attenuata	11	72.7	0	0
P. parallelum	22	72.7	0	46.0
Plegaderus sp.	1	100.0	0	0
Roptroceris sp.	1	100.0	0	0
Silvanus bidentatus	3	66.7	0	0
Tenebroides collaris	1	0	0	0
Thanasimus dubius	1	100.0	0	0
Temnochila sp.	2	0	0	50.0
Tenebroides collaris	2	50.0	0	50.0
Tenebroides marginatus	1	0	0	100.0
Xyleborus sp.	5	60.0	0	25.0

9.3. CONCLUSIONS AND EVOLUTIONARY CONSIDERATIONS

The SPB creates ephemeral habitats that are occupied by a large community of insects, mites, and fungi. These organisms interact with each other and the host tree in ways that modify the phloem resource on which they all depend. Some of the stronger interactions, such as those between the mycangial fungi, *O. minus*, SPB, and *Tarsonemus,* have been thoroughly covered in this chapter. Long-term evolutionary changes in these symbiotic associations may have resulted in specialized behaviors and dependencies. Closely related taxa that exhibit a variety of ecological relationships allow the testing of hypotheses about the direction of evolution (e.g., phoresy leads to parasitism) and about forces behind such changes and associations. Mites and fungi associated with bark beetles provide numerous clear examples of switches in lifestyle that encompass parasitism, antagonism, commensalism, and mutualism. More studies are needed to evaluate how these interactions and others change over geographic space and evolutionary time, and how bark beetle communities influence beetle dynamics and beetle-tree interactions.

Factors that affect the evolution of obligate associations or promote the virulence of mites and microbes are important topics relating to disease dynamics and species preservation. How important are neutral symbionts (e.g., commensal mites) in promoting pathogens and diseases? Do microbes transmitted vertically (mites or fungi transmitted from parent beetle to offspring) produce greater effects on host dynamics than those transmitted horizontally between unrelated beetles within the tree? How would global climate change affect the stability of organisms within a tight community or the dynamics of an outbreak species? How do cheaters (e.g., *C. ranaculosus*) join and persist within communities? These are some questions that can be addressed through studies of interactions between bark beetles and their associated organisms.

10

Predators of the Southern Pine Beetle

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Keywords

delayed density-dependence
Medetera bistriata
predators
Thanasimus dubius
woodpeckers

Abstract

This chapter of the Southern Pine Beetle II reviews the overall influence of predators on southern pine beetle (SPB) population dynamics, as well as recent research on specific predators such as the clerid beetle *Thanasimus dubius*. Several lines of evidence suggest that predators and other natural enemies generate significant SPB mortality that contributes to outbreak collapse, likely operating with a time delay and so causing delayed density-dependence. The predators that seem most likely to significantly impact SPB are *T. dubius*, the dolichopodid fly *Medetera bistriata*, and several woodpecker species. The chemical ecology of both *T. dubius* and *M. bistriata* indicates they are well synchronized with mass attack by SPB. The prolonged development of *T. dubius* under field conditions, however, suggests it is a component of the delayed density-dependence seen in SPB. It is recommended that trees vacated by SPB be left intact during control operations because these often contain immature *T. dubius* 1-2 years after SPB attack, and also provide foraging and nesting opportunities for woodpeckers. Current research is exploring methods for mass-rearing *T. dubius* using an artificial diet, for potential use as a control tactic.

10.1. INTRODUCTION

Predators and other natural enemies are important factors in the population dynamics of many insect pests, and southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is no exception. In this chapter of the Southern Pine Beetle II, I review evidence of the overall impact of predators on SPB and their potential effects on SPB population dynamics. For several common predators, I also summarize recent research on their life histories, chemical ecology, mortality inflicted on SPB, and dispersal behavior. For the majority of predator species, however, there is little information beyond that provided in a previous review (Berisford 1980).

10.2. IMPACT OF PREDATORS ON SPB

There are several lines of evidence suggesting that natural enemies, including predators, have a role in SPB dynamics and population regulation. One is that time-series analysis suggests that delayed density-dependence is an important factor in SPB population dynamics. In particular, Turchin and others (1991) analyzed a 30-year record of SPB activity in East Texas and found evidence for delayed density-dependence in SPB population growth. More recent analyses incorporating additional data also detected delayed density-dependence (Reeve and Turchin 2002) as well as a temperature effect (Friedenberg and others 2008). Because natural enemies often affect prey populations with a time delay, this provides circumstantial evidence that natural enemies affect SPB dynamics. In addition, a commonly used forecasting method employs a predator/prey ratio to predict SPB population trends, in particular the ratio of the clerid beetle *Thanasimus dubius* (see below) to SPB in trap catches (Billings 1988), further implying a role for natural enemies in SPB dynamics.

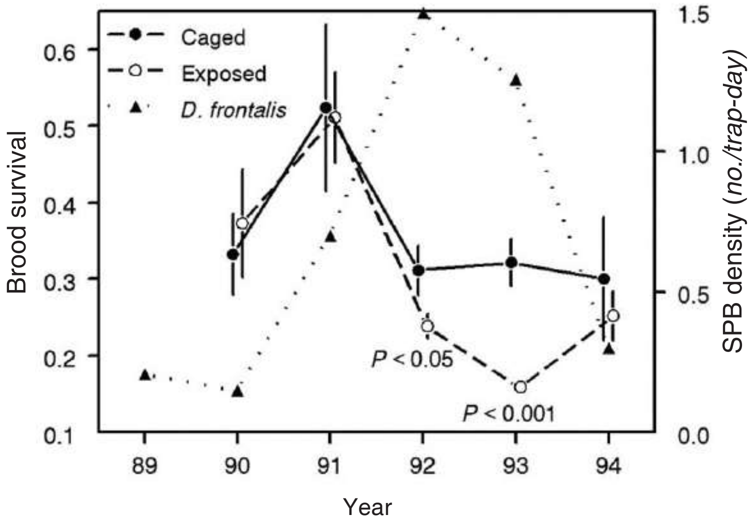

Figure 10.1—Survival of SPB brood (emerging adult density/egg density) for caged vs. exposed trees, during the course of an SPB outbreak. SPB densities were estimated using traps baited with frontalin and turpentine. A two-sample *t*-test was used to compare survival rates in caged vs. exposed trees.

More direct evidence for the effect of natural enemies comes from exclusion studies. Linit and Stephen (1983) excluded natural enemies at various times after SPB attack using cages, and found that natural enemies arriving early in the attack (which would typically be predators) caused the greatest amount of mortality. Turchin and others (1999b) compared the survival rates of SPB brood in caged and uncaged trees during the course of an SPB outbreak. They observed a highly significant difference in survival rates 1 year after SPB populations reached peak levels, with brood survival approximately two times higher in the caged vs. exposed trees (Figure 10.1). This pattern suggests that natural enemies could be a component of the delayed density-dependence found in the time-series analyses, but does not identify the type of natural enemy, such as predators or parasitoids, much less the actual species involved. The most likely candidate appears to be *T. dubius*, however, because of its lengthy development time and probably substantial impact on SPB.

10.3. SPECIFIC PREDATORS

This section summarizes information on the life histories, chemical ecology, dispersal behavior, and impact on SPB of selected predators, where such information is available. Predator species were chosen based on a known response to SPB pheromones, a significant impact on SPB or other bark beetles, and recent attention in the literature. One group excluded by these criteria was histerid beetles; although they appear to be important natural enemies of *Ips* bark beetles (Aukema and others 2004; Aukema and Raffa 2002, 2004), they do not respond to the SPB pheromone frontalin (Aukema and Raffa 2005). Many other predator species are listed for SPB (Berisford 1980, Moser and others 1971, Overgaard 1968), but little new information has been published.

10.3.1. *Thanasimus dubius* (Coleoptera: Cleridae)

Life History

The natural history of *Thanasimus dubius* (Coleoptera: Cleridae) has received the most attention among predators of SPB. Adult *T. dubius* locate trees undergoing mass attack by responding to the semiochemicals emitted by SPB and the host tree (see Chemical Ecology below). Adult *T. dubius* attack and consume the adult SPB (Figure 10.2) arriving on the bark surface during mass attack (Thatcher and Pickard 1966), although they have also been reported on trees where SPB brood adults are emerging (Clarke and Menard 2006). Oviposition occurs in crevices in the bark. The eggs hatch within a few days, and the larvae enter the tree, where they attack the immature stages of SPB within the phloem layer (Thatcher and Pickard 1966). The larvae make use of SPB galleries to move about and can also construct their own tunnels. They have also been observed crawling on the bark surface (Dix and Franklin 1977), presumably traveling between SPB galleries. The larvae reach a nonfeeding prepupal stage (Figure 10.3) at approximately the same time as SPB complete development, and then construct an oval chamber lined with a silvery-white material in the outer bark (Thatcher and Pickard 1966). Most of these chambers are located toward the base of the tree, 2-5 m above ground level (Mizell and Nebeker 1981). The combined prepupal and pupal stage is longer in duration than the egg and larval stages, with most of the time spent in the prepupal stage (Lawson and Morgan 1992, Nebeker and Purser 1980). For example, Lawson and Morgan (1992) reported mean durations of 7.2 ± 0.1 (SE) days for eggs, 41.9 ± 0.6 for larvae, 56.4 ± 1.0 for prepupae and pupae combined, and 50.1 ± 7.1 for adults, when reared at room temperature. However, the length of the prepupal period is extremely variable under field conditions. Reeve (2000) found that there were often several adult emergence periods for an infested tree, with most individuals emerging in spring or fall (Figure 10.4). The maximum adult emergence time observed was approximately 2 years after SPB attack. The pattern of emergence suggests that *T. dubius* has approximately two generations per year in the southern portion of its range, with some individuals taking much longer to complete development (Reeve 2000). Given that SPB has approximately six generations per year (Ungerer and others 1999), this implies a long time delay in the numerical response of *T. dubius* to fluctuations in SPB density, potentially making it a source of the delayed density-dependence found in SPB dynamics. A simple predator-prey model incorporating the life histories of SPB and *T. dubius*, including extended development times and a spring-fall

Figure 10.2—Adult *T. dubius* attacking an adult SPB on the bark surface. (photographer unknown)

Figure 10.3—Prepupal *T. dubius* larva lying within a cell excavated in the outer bark. (photograph by Erich G. Vallery)

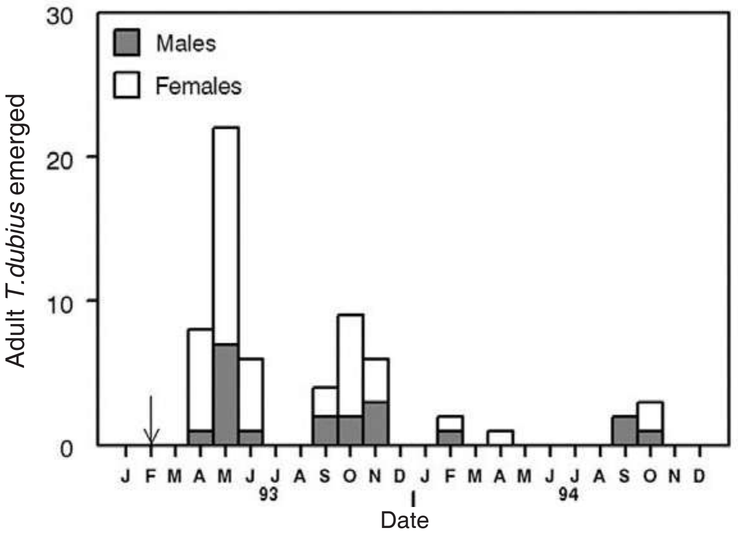

Figure 10.4—Numbers of emerging adult *T. dubius* from a host tree for which SPB emergence was complete in February 1993 (see arrow). The base of the tree was enclosed in a 1.5 m long emergence trap.

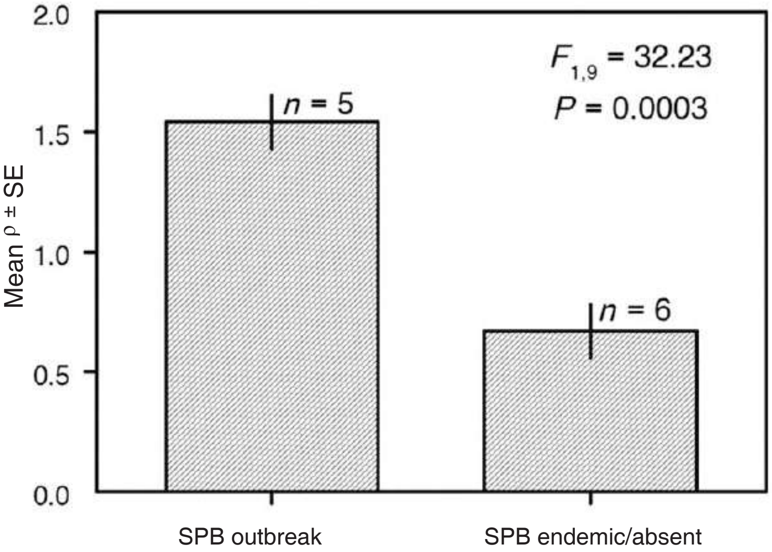

Figure 10.5—Mean values of the preference index ρ (± SE) comparing the response to frontalin vs. ipsdienol and ipsenol, for SPB outbreak sites vs. sites where SPB was endemic or absent. One-way ANOVA was used to test for differences in ρ across the two site types.

pattern of emergence, produced cycles similar in period to those sometimes observed in SPB (Reeve and Turchin 2002).

Chemical Ecology

It has long been recognized that adult *T. dubius* are attracted to trees undergoing mass attack by SPB, arriving shortly after the first attacks are initiated and continuing for several days thereafter in a pattern that matches arrival by SPB (Camors and Payne 1973, Dixon and Payne 1979a). This close synchronization occurs because *T. dubius* is strongly attracted to the SPB pheromone frontalin, with the response synergized by host tree volatiles such as -pinene that are generated by beetle damage (Billings 1985, Dixon and Payne 1980, Payne and others 1984, Vité and Williamson 1970). This predator is also attracted to the pheromones emitted by *Ips* bark beetles, such as ipsdienol and ipsenol, although the response to frontalin generally appears to be stronger (Aukema and Raffa 2005, Billings and Cameron 1984, Erbilgin and Raffa 2001, Haberkern and Raffa 2003, Herms and others 1991, Mizell and others 1984, Raffa 2001, Raffa and Klepzig 1989). Trapping studies have shown this predator is also sensitive to visual cues, with fewer insects trapped in white or yellow traps vs. black traps, similar to the pattern observed for SPB (Strom and Goyer 2001, Strom and others 1999).

This predator also shows a change in its preference for SPB vs. *Ips* pheromones as a function of SPB density, in a pattern that suggests switching in prey preference (Murdoch 1969, Murdoch and Oaten 1975). In particular, *T. dubius* shows a strong response to frontalin vs. ipsdienol and ipsenol at SPB outbreak sites, while the response is more even at sites where SPB are endemic or absent (Billings and Cameron 1984, Reeve and others 2009). This pattern was especially obvious in an analysis that combined the results from four studies that compared trap catches for frontalin vs. ipsdienol and ipsenol (Aukema and Raffa 2005, Billings 1985, Billings and Cameron 1984, Reeve and others 2009). For each site in the four studies, Reeve and others (2009) calculated a preference index of the form

$$\rho = \log_{10}(\overline{Y}_{FR}) - \log_{10}([\overline{Y}_{IS}+\overline{Y}_{ID}]/2) \qquad (1)$$

where $\overline{Y}_{FR}$, $\overline{Y}_{ID}$ and $\overline{Y}_{IS}$ are the mean trap catches for treatments using frontalin, ipsdienol, and ipsenol. This metric is similar in form to the log response ratio used in meta-analysis (Hedges and others 1999). One-way ANOVA was used to compare this index between SPB outbreak sites vs. sites where SPB were either endemic or absent (Figure 10.5). There was a highly significant difference in preference between the two site types, with the preference for frontalin much higher at SPB outbreak sites. This corresponded to a 34.7 to 1 ratio of predators trapped with frontalin vs. ipsdienol and ipsenol at SPB outbreak sites, while the ratio was only 4.7 to 1 at endemic or absent sites. This switching behavior should enhance the persistence of *T. dubius* populations when SPB are low, because their attraction to alternative prey would be higher under these conditions.

Impact on SPB

Both adult and larval *T. dubius* appear to cause appreciable mortality of SPB. Thatcher and Pickard (1966) first observed that *T. dubius* adults could reduce the number of adult SPB successfully attacking cut green logs in a laboratory setting. Reeve (1997) estimated the density of adult *T. dubius* on pines undergoing mass attack by SPB, then used similar densities in a laboratory study where adult SPB were added to caged green logs. The proportion of SPB successfully entering the logs was significantly reduced by *T. dubius* predation (Figure 10.6), although some SPB always escaped predation and entered the logs. Adult *T. dubius* also appear to have a ratio-dependent functional response (Arditi and Ginzburg 1989), implying that the predation rate depends on the SPB/*T. dubius* ratio rather than on the separate densities of predator and prey.

More results are available for interactions between *T. dubius* and various *Ips* species, because *Ips* are easier to rear and otherwise manipulate using cut logs, whereas SPB often develop poorly under these conditions. A significant impact on *Ips* survival and reproduction was found by Aukema and Raffa (2002, 2004), Mignot (1966), and Mignot and Anderson (1969). However, these studies were not designed to separate the effects of larval vs. adult *T. dubius* on *Ips*. Reeve and Turchin (2002) examined the effect of larval *T. dubius* on the survival and reproduction of *I. grandicollis*, seeding infested logs with different densities of *T. dubius* eggs, chosen using field densities of adult predators and daily oviposition rates. There was a highly significant effect of egg density on the ratio of increase for *I. grandicollis* (Figure 10.7), but the initial density of adult *Ips* also had an effect, presumably because of intraspecific competition.

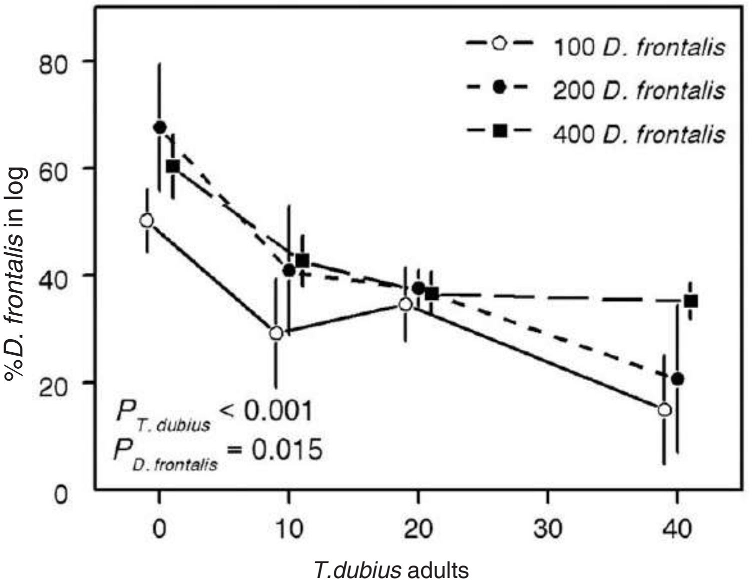

Figure 10.6—Effect of predation by adult *T. dubius* on the percent of adult SPB successfully attacking a green log, as a function of predator and SPB density. *P*-values indicate the effect of predator and SPB densities on the percent attacking, tested by fitting general linear models. (from Reeve 1997, Reeve and Turchin 2002)

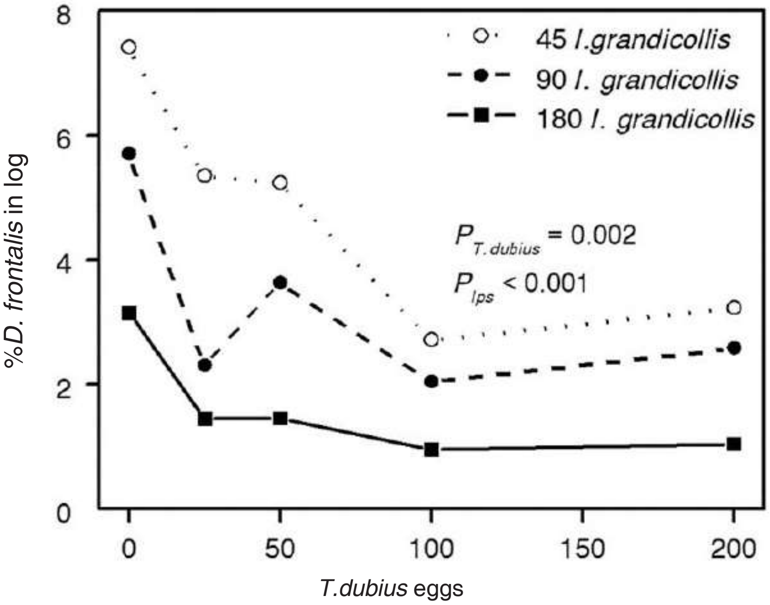

Figure 10.7—Effect of predation by larval *T. dubius* on the ratio of increase for *I. grandicollis* as a function of the density of predator eggs and initial densities of adult *I. grandicollis*. *P*-values indicate the effect of predator and *I. grandicollis* densities on the ratio of increase (emerging adults/attacking adults) for *I. grandicollis*, tested by fitting general linear models. (from Reeve and Turchin 2002)

Dispersal Behavior

Dispersal behavior has been studied in both SPB and *T. dubius*, directly using mark-recapture experiments as well as indirectly with genetic markers. Turchin and Thoeny (1993) fitted a diffusion model to the data from SPB mark-recapture experiments and estimated that the median dispersal distance for SPB was 0.69 km. Cronin and others (2000) estimated that the median dispersal distance for *T. dubius* was approximately 1.25 km, with some individuals moving several times this distance (Table 10.1).

Table 10.1 — Estimated dispersal quantiles (radius of a circle in km enclosing a given proportion of dispersers) with 95 percent confidence intervals for *T. dubius* and SPB (from Cronin and others 2000)

Dispersal quantiles	*T. dubius*	SPB
50%	1.24 (0.74, 4.48)	0.69 (0.45, 0.92)
75%	2.02 (1.30, 6.73)	0.99 (0.65, 1.34)
95%	5.10 (3.56, 15.89)	2.27 (1.48, 3.05)

Thus, *T. dubius* can apparently disperse farther than SPB, likely enabling it to track changes in SPB abundance in space. Less is known about the effects of habitat fragmentation and isolation on dispersal behavior. Ryall and Fahrig (2005) showed that densities of *I. pini* were higher in isolated red pine patches than nonisolated ones, while *T. dubius* densities were unaffected, leading to a significantly lower predator-to-prey ratio in isolated patches. This suggests little or no effect of isolation for *T. dubius*, at least at the spatial scale of the patches used in this study.

Studies using genetic markers indicate both predator and prey are capable of considerable long-range dispersal, with *T. dubius* again showing higher dispersal rates than SPB. Schrey and others (2005) used a mitochondrial DNA marker to examine the population genetic structure of *T. dubius* throughout the Eastern United States. There was significant structuring between northern and southern populations, roughly corresponding to portions of its range with and without SPB. No structure was detected among southern populations, suggesting considerable gene flow occurs among predator populations within the range of SPB. Schrey and others (2008) examined the genetic structure of SPB within a single State (Mississippi) using microsatellite markers, and found that on this scale SPB populations were quite homogeneous. Previous work using isozymes showed significant structure among sites in different states, however, implying that gene flow is reduced at larger scales (Anderson and others 1979, Namkoong and others 1979, Roberds and others 1987). The overall pattern for SPB suggests gene flow among forests within States, but reduced flow at higher spatial levels, whereas *T. dubius* populations could be mixing even at these higher levels.

10.3.2. *Medetera bistriata* (Diptera: Dolichopodidae)

Life History

Adult *M. bistriata* (Figure 10.8) arrive on the host tree shortly after the initiation of SPB attack (Dixon and Payne 1979b). The adults of *M. dendrobaena* have been reported to feed on collembolans and thrips on the bark surface as well as *Drosophila melanogaster* in the laboratory (Nicolai 1995), and one would expect *M. bistriata* to forage on insects of similar size, but not adult SPB. Oviposition

Figure 10.8—*Medetera* spp. adult. (photograph by Gerald J. Lenhard, www.forestryimages.org).

likely occurs close to SPB attack holes to facilitate entry by the larvae, similar to the behavior observed in *M. aldrichii* (Fitzgerald and Nagel 1972). The larvae (Figure 10.9) then attack the immature stages of SPB, likely paralyzing them with a venom delivered using their tentorial rods (Aukema and Raffa 2004, Nagel and Fitzgerald 1975). Pupation occurs on the bark surface in *M. dendrobaena* (Nicolai 1995), and *M. bistriata* is probably similar.

Chemical Ecology

It has been shown that adult *M. bistriata* are attracted to logs infested with SPB and *Ips*, as well as pheromone components including frontalin and host volatiles (Dixon and Payne 1980, Goyer and others 2004, Williamson 1971). Goyer and others (2004) found that the number of *M. bistriata* attracted to *Ips*-infested logs was affected by log color (fewer were trapped on white vs. black or natural color logs), suggesting visual cues are also important in prey location. Newly hatched larvae *M. aldrichii* are attracted to α-pinene, a behavior that presumably helps them locate attack holes (Fitzgerald and Nagel 1972).

Impact on SPB

No studies were found that directly examined the impact of *M. bistriata* on SPB, but findings from other systems give indications it could be significant. Aukema and Raffa (2004) observed an effect of larval predator density on the number of dead *I. pini* immatures in laboratory studies using bark sandwiches. Nicolai (1995) observed up to 45 percent mortality in the larvae of *Pityogenes chalcographus* (a European bark beetle species) generated by *M. dendrobaena* using infested logs. Based on prey consumption rates for larval *M. dendrobaena*, Dippel and others (1997) projected similar mortality values for *P. chalcographus*.

10.3.3. Woodpeckers (*Picidae* spp.)

Impact on SPB

A few studies have considered the impact of woodpeckers on SPB brood within infested trees (Figure 10.10). Kroll and Fleet (1979) found that woodpecker foraging had a significant impact on the densities of SPB pupae and adults at mid-bole (but apparently not the upper and lower bole), in a comparison of infested trees with and without woodpecker exclusion cages. The species commonly associated with SPB infestations are the downy, hairy, and pileated woodpeckers (*Picoides pubescens*, *P. villosus*, and *Dryocopus pileatus*, respectively) (Kroll and Fleet 1979, Kroll and others 1980). These species also showed elevated densities in an infested vs. uninfested stand, a pattern that has been observed in other woodpecker-bark beetle systems (Fayt and others 2005, Morrissey and others 2008). This increase in density may represent a short-term aggregative response to increases in prey density, but Kroll and others (1980) also observed an increase in overall

Figure 10.9—*Medetera* spp. larva. (photograph by Gerald J. Lenhard, www.forestryimages.org)

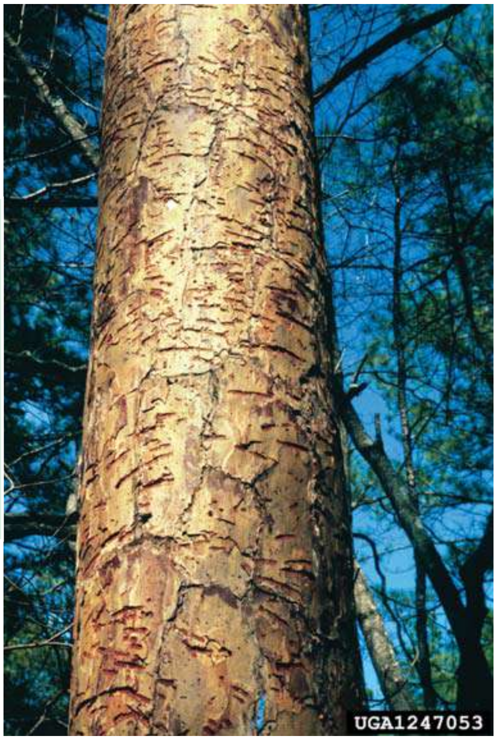

Figure 10.10—Evidence of woodpecker feeding on SPB brood. When attacking SPB, woodpeckers first flake off the loose outer bark and then cut grooves into the cork-like inner bark to extract late-stage SPB brood. (photograph by Terry Price, www.forestryimages.org)

woodpecker densities with the number of SPB infestations over a 10-year period, possibly indicating a true numerical response to changes in SPB density. Given these results, it seems likely that woodpeckers exert some effect on SPB dynamics, but the overall magnitude of the effect and whether it generates density-dependence in SPB growth remains unknown. Fayt and others (2005) hypothesized that woodpeckers associated with bark beetles attacking spruce in North America likely exert their greatest effect in locations where outbreaks are just beginning, before their response becomes saturated by high beetle populations, and this scenario also seems plausible for SPB.

Although this review has focused on predator-prey relationships, there is one woodpecker species for which the relationship is more ambiguous: the endangered red-cockaded woodpecker (*P. borealis*). Attacks by SPB are a major source of cavity tree mortality (Conner and others 1991, 2001b; Conner and Rudolph 1995), although SPB brood are also a food source for red-cockaded woodpecker (Schaefer and others 2004).

10.4. CONSERVATION AND BIOLOGICAL CONTROL

Given the apparent impact of predators and other natural enemies on SPB, it seems logical that control methods for SPB should attempt to minimize their impact on natural enemy populations. It is commonly recommended that cut-and-remove or salvage operations leave trees vacated by SPB in place, to spare the natural enemies remaining behind (Mizell and Nebeker 1981, Swain and Remion 1981, Thatcher and Pickard 1966). This is especially the case for *T. dubius* because some individuals remain in the tree years after initial colonization by SPB. Such trees also provide foraging and nesting opportunities for woodpeckers (Kroll and others 1980).

In addition to conservation, it may eventually be possible to use laboratory-reared predators to augment natural populations within an infestation, as a control method (augmentative biological control). An artificial diet for rearing *T. dubius* larvae has been developed with this purpose in mind (Reeve and others 2003). It is also possible to feed adult *T. dubius* using cowpea weevils, *Callosobruchus maculatus* (Mizell and others 1982, Nebeker and others 1980), meaning that no bark beetles are required to complete the life cycle. This predator has been successfully reared for many generations in the laboratory, producing adults of similar quality (size and fecundity) to wild adults that also retain their preference for natural prey (Reeve and others 2003). Current research is focused on extending the time between predator feedings by adding a preservative to the artificial diet (A. Costa and J. D. Reeve, unpublished data). However, the overall rearing process remains time consuming and thus expensive because the cannibalistic larvae must be separately confined and fed. Another unsolved problem concerns the method of deployment in SPB infestations. Is it better to release adults within an infestation, even though they could easily disperse from the release point, or place eggs or larvae on infested trees? Laboratory studies indicate that eggs and larvae placed on the bark surface will enter infested logs and attack the developing brood (Reeve and Turchin 2002), but this method has not been tested under field conditions. At present, our rearing methods can provide sufficient predators for research purposes but will require significant improvements to make augmentative biological control of SPB feasible.

11

Mutualists and Phoronts of the Southern Pine Beetle

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Keywords

mite
mutualist
mycangia
nematode
phoretic
predator

Abstract

The large numbers of invertebrates and microbes that exist only within dying and decayed pines killed by the southern pine beetle (SPB) make this system ideal for the study of species interactions, including mutualism and phorecy. The associated organisms comprise an entire functioning community that includes fungivores, herbivores, detritovores, scavengers, parasitoids, and predators. Because the SPB causes physical state changes in biotic materials and creates a stable supply of resources for an extensive assemblage of species, it can be considered a keystone species, ecosystem engineer, or foundation species. Within the SPB community, species interactions range from mutualistic to commensalistic to antagonistic, depending on the species composition, environmental conditions, and quality of available resources. These species often use SPB adults to access and disperse among trees and can affect the population dynamics, behavior, and evolution of the SPB. In addition, interactions among the community can impact bark beetle-fungal associations and thus, beetle fitness. In this chapter, I provide an overview of the known associations with the SPB, both mutualistic and phoretic, and discuss how these associations impact the SPB and the evolution and ecology within this community.

11.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) can be considered a keystone species (Holling 1992), ecosystem engineer (Jones and others 1994), or foundation species (Dayton 1972) in that it causes physical state changes in biotic materials and creates a stable supply of resources for an extensive assemblage of species. Large numbers of invertebrates exist only within dying and decayed pines killed by the SPB, such as nematodes (as high as 90 percent of beetles infested; Atkinson and Wilkinson 1979), bacteria (> 21 species; Vasanthakumar and others 2006), fungi (Whitney 1982), and mites (> 96 species; Moser and Roton 1971). This collection of organisms comprises an entire functioning community that includes fungivores, herbivores, detritovores, scavengers, parasitoids, and predators.

11.1.1. Mutualistic Associations

Among these SPB associates, there are several species that benefit the beetle and receive benefits in return. The benefit of this reciprocal gain to both species, termed mutualism, can be of one or more types, namely, energetic, nutritional, protective, and transport (Morin 1999), and associations have the potential to be obligate or facultative, tight or diffuse, and direct or indirect (Addicott 1995, Morin 1999). In many cases, these associations may be facilitative interactions (i.e., commensalism) in that one of the participants benefits but neither is harmed. The impact and comprehensiveness of positive interactions on the evolution, behavior, and ecology of the SPB is difficult to assess given all the possible combinations of species, interaction types and strengths, and outcomes of trophic organizations within the SPB community. However, some of the best known and best understood positive interactions among the SPB community are described in this chapter. For instance, some benefits to the SPB include the production or enhancement of aggregating pheromones (Brand and others 1976, 1977), alteration and improvement of phloem by altering plant defenses (Paine and others 1997), direct nutritional services (Goldhammer and others 1990), and enhanced defense in the form of protection from disease, predators, and parasites.

11.1.2. Phoretic Associations

Dispersal and migration pose major challenges for many organisms living in a discontinuous, ephemeral habitat such as that of SPB-infested trees. These microorganisms are wind-dispersed, travel under their own power, or attach to another organism for dispersal to trees. Those species that attach to other organisms, called phoronts, are highly adapted for phorecy and often have highly modified phoretic stages, morphs, appendages, or parts. Phoronts often go through behavioral changes such as cessation of feeding or morphological changes that are quite different from nonphoretic individuals of the same species. Many of these behaviors are analogous to those used by parasites to find their hosts (Athias-Binche and Morand 1993).

Phorecy could be considered an exploitation of the carrier and therefore, parasitic. However, species interactions should be defined in terms of their ultimate effects on the fitness of the participants if they are to make ecological and evolutionary sense (Walter and Proctor 1999). Under most conditions, phoretic organisms can be classified as commensal or facilitative, in that they do not harm the carrier but the phoront benefits (Houck 1994). However, when phoronts are abundant they may interfere with carrier movement, reduce travel distances, and be energetically costly (Kinn 1971, Kinn and Witcosky 1978). Alternatively, phoronts may provide direct or indirect benefits to their carrier. Thus, phoretic relationships may be mutually beneficial to the phoront and the phoretic host, neutral (e.g., commensal – benefiting the phoront), or antagonistic, resulting in a loss of fitness to the carrier.

11.2. ASSOCIATED TAXA

Standing deadwood and trees attacked by SPB are home to a large variety of microorganisms that invade beetle-infested trees by associating with SPB or other colonizing arthropods. Many of these microorganisms, such as bacteria and nematodes that travel on the body of SPB, are covered in other chapters of this book and will only be briefly discussed here. This chapter will primarily focus on the robust diversity of fungi and mites phoretic on SPB that live around and within SPB galleries.

11.2.1. Nematodes

Nematodes are common associates of the SPB (Atkinson and Wilkinson 1979, Joye and Perry 1976, Massey 1974) and interact as parasites (antagonists), commensals, and mutualists of SPB adults, larvae, or eggs. Most nematodes are endoparasitic and travel between trees within adult beetle bodies. However, several species are ectoparasitic and form cocoon-like structures usually under the elytra of beetles (Figure 11.1). Several nematode species may prey upon parasitic nematodes of beetles and thus have a mutualistic relationship with the SPB. However, we know very little about these species. Nematodes may be important factors regulating populations of the SPB (Moore 1971, Sikorowski and others 1979) and have been reported to reduce fertility and fecundity of SPB (Kinn 1980). Studies by MacGuidwin (1979) showed that SPB females infected with the endoparasitic nematode *Contortylenchus brevicomi* (Massey) Ruhm produced fewer eggs and constructed shorter galleries than healthy females during the 3-week period after attack. Parasitism of either male or female SPB by *C. brevicomi* did not affect survival of progeny, even though the number of eggs was reduced.

11.2.2. Fungi and Bacteria

There are several fungi that are obligate mutualists with the SPB. Female SPBs possess a prothoracic mycangia that consists of paired invaginations of the exoskeleton, each of which has one pore-like ventral opening and contains two types of secretory cells (Barras and Perry 1972, Happ and others 1971). Within each side of the mycangium, each individual female maintains a pure culture of either *Ceratocystiopsis ranaculosus* Bridges & Perry (Barras and Taylor 1973) or *Entomocorticium* sp. A Hsiau & Harrington (Barras and Perry 1972, Happ and others 1976, Hsiau 1996) (Figure 11.2). Each female carries either one of the two fungi or no fungi in each of the mycangial pouches (Bridges 1985). The relative abundance of each mycangial fungus within SPB populations varies with geographic location and time of year (Harrington 2005, Hofstetter and others 2006b). Interestingly, 5-20 percent of females within a population carry both mycangial fungi, one within each mycangial pouch. As the female oviposits within the tree, she may inoculate the area immediately surrounding the eggs with the contents of her mycangium. Early instar larvae feed within short galleries that quickly enlarge into ovate feeding chambers (Payne 1983), within which can be found abundant growth of either of the two mycangial fungi. The larvae likely then feed on fungal hyphae and reproductive structures, receiving the majority of their nutrition (especially nitrogen and lipids) from the fungi and substantially benefit from the presence of these fungi (Ayres and others 2000, Bridges 1985, Coppedge and others 1995, Goldhammer and others 1990).

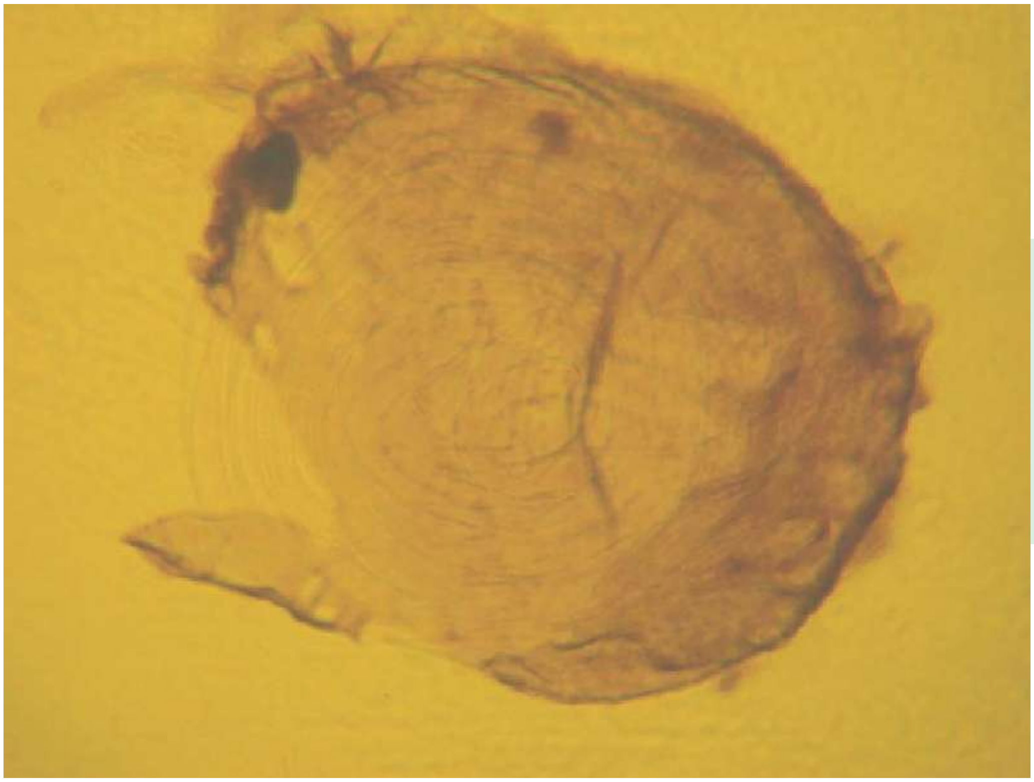


Figure 11.1—Cocoon-like structure (< 1 mm in diameter) created by phoretic nematode. Structure was removed from under the elytra of an SPB caught in a flight trap. Note that the nematode is still within structure. (photograph by R.W. Hofstetter)

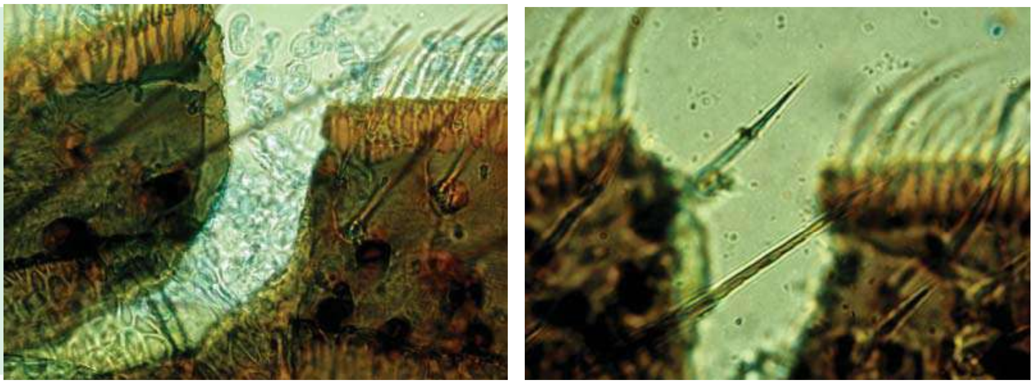


Figure 11.2—Close-up of stained mycangial fungi coming out of the mycangia of a female adult SPB. Left: *Entomocorticium* sp. A; Right: *Ceratocystiopsis ranaculosus*. Note that *C. ranaculosus* cells are much smaller than *Entomocorticium* sp. A. (images taken by R.W. Hofstetter)

Bridges and Perry (1985) found that in the laboratory, SPBs without mycangial fungi produce much shorter galleries and fewer progeny than beetles with mycangial fungi. The same pattern continued through a second generation, suggesting that populations of SPB without mycangial fungi cannot survive for long. Brand and others (1975, 1976) isolated a mycangial fungal culture that was able to convert α-pinene to *cis-* and *trans*-verbenol, and *trans*-verbenol to verbenone. Verbenone is believed to terminate beetle attack (Brand and others 1976) and thus reduce intraspecific competition among beetles (Byers 1989a). The mycangial fungi receive protected, selective transport to the next available resource (Happ and others 1971). The symbiosis between these organisms is clearly mutualistic (Klepzig and others 2001a, 2001b) .

Spores of *Ophiostoma* species (*O. minus* Hedge and *O. nigrocarpum* (Davidson) De Hoog (Harrington 2005)) are commonly found on the exoskeleton of SPB (Bridges and Moser 1983, Rumbold 1931), associated insects (Hofstetter 2004), and on phoretic mites (Moser 1985). *Ophiostoma minus* is the most abundant non-mycangial fungal associate, but its abundance varies greatly among beetle populations and across regions (Harrington 2005; Hofstetter and others 2006a, 2006b). *Ophiostoma minus* is an ascomycetous fungus which causes "blue stain" within infected wood. While this fungus may aid the SPB in killing trees (Mathre 1964, Nelson 1934, however see Klepzig and others 2005), it is not required for tree death to occur (Bridges 1985, Bridges and Perry 1985, Bridges and others 1985, Hetrick 1949). Colonization by *O. minus* may, however, cause tree death to occur more quickly or at least differently than it would in the absence of the fungus (Paine and others 1997). Because of this and because the fungus benefits by receiving transport to new host tissue (Dowding 1969), the SPB-*O. minus* relationship at the early stages of attack may be defined as a mutualistic association. However, as beetle eggs hatch, the introduced fungi grow and colonize the phloem. When colonization by *O. minus* overlaps areas of larval feeding, reduced developmental success—inhibited egg production, slower larval growth and development, and increased mortality—may occur (Barras 1970, Franklin 1970a), and higher levels of *O. minus* thus correlate with lowered SPB reproductive success (Hofstetter and others 2006a, Lombardero and others 2000c) . This antagonism between *O. minus* and SPB larvae is due to interference by the fungus with interactions between the beetle and its two mutualistic mycangial fungi (Klepzig and others 2001a, 2001b) .

Most bacteria associated with the SPB are found within the guts and alimentary canal of adults and larvae (Moore 1972, Vasanthakumar and others 2006), and within the mycangia of adult females (observations by R.W. Hofstetter; Scott and others 2008). In addition, a suite of bacteria is likely passively picked up on the exoskeleton of beetles and transferred into new host trees. Bacteria and yeasts associated with other bark beetles (e.g., *D. rufipennis* Kirby) are known to inhibit the growth of antagonistic fungi (Cardoza and others 2006) and may influence interactions among beetles and mycangial fungi (Scott and others 2008). Scott and others (2008) identified actinomycete bacteria from the mycangia and the galleries in the presence of mycangia fungus *Entomocorticium* sp. A. Interestingly, the bacteria produces an antibiotic that selectively suppresses the antagonistic fungus, *O. minus*. This indicates that the SPB engages in additional mutualisms with bacteria to regulate fungus-fungus interactions. The functions that most bacteria play in SPB development, host exploitation, reproduction, and interactions with associated organisms remain largely unknown.

11.2.3. Mites

Mites (Chelicerata: Acariformes) are commonly associated with bark beetles (Kinn 1971, Moser and Roton 1971). Approximately 111 species of mites are phoretic on SPB or found within trees killed by the SPB (Figure 11.3). Although mites are often believed to be passive inhabitants of bark beetle communities, we now know that they can have strong interactions with nonmite species, are major components of biological diversity, and can impact bark beetle population dynamics and fungal interactions (Hofstetter and others 2006a, 2006b). Details of the biology and ecology of this important group of organisms are discussed later in this chapter.

11.2.4. Other Phoretic Organisms

Species of pseudoscorpions (Figure 11.4) and other small arthropods, such as fungivorous dipterans and coleopterans, are periodically phoretic on the SPB. Many of these species are also found on predators and competitors associated with the SPB.

11.3. INTERACTIONS WITH SPB

Many of the phoronts associated with SPB have little direct effects on SPB adults, larvae, and eggs. Furthermore, it is likely that many of the phoronts affect the SPB only indirectly by interacting with other species within trees. However, several of the species are direct predators, parasitoids, or pathogens of the SPB. In laboratory tests, Moser (1975) found that 32 of 51 species of mites were predaceous on one or more SPB life stages. Currently, of the 111 known mite species associated with the SPB, 35 percent are likely predaceous on SPB eggs or larvae as well as on other mites or nematodes. Of the remaining 70 mite species, 15 percent are believed to feed on fungi and other microbes, while the remaining 50 percent have unknown feeding preferences and behaviors.

11.3.1. Impacts on Health and Vigor of Beetle Larvae

As stated previously, phoronts can affect beetles in a variety of ways that range from beneficial to antagonistic (Table 11.1). These effects are often context-dependent, in that the interaction can change depending on time of year, host tree condition, local species community within the tree, and so on. Here are several examples of mutualistic interactions among SPB and phoronts. Nematophagous mites (e.g., *Dendrolaelaps neodisetus* (Hurlbutt)) may benefit SPB larvae by preying on nematodes which are endoparasitic on bark beetles (e.g., nematode *Contorylenchus brevicomi*) (Kinn 1980). Many nematophagous mites and generalist predatory mites attack and kill other mites (Kinn 1983). Some examples include: the eggs and larvae of *Dendrolaelaps quadristus* (Berlese) are preyed upon by *Cercoleipus coelonotus* Kinn; *Histiogaster arborignis* Woodring is fed on by *Mexecheles* spp., *Proctolaelaps dendroctoni* Lindquist and Hunter, and *Hypoapsis* spp.; *Macrocheles boudreauxi* Krantz and *Eugamasus lyriformis* Mcgraw and Farrier nymphs and adults eat *Dendrolaelaps* spp., cheyletids (Prostigmata) and uropodid mites. Fungivorous mites increase fungal inoculation loads and thus could benefit the SPB if the fungi are mycangial fungi, or harm beetle larvae by introducing antagonistic fungi (discussed below) during colonization and gallery production. For additional information, see chapter 9 of this book.

11.3.2. Impacts on Fungal-Beetle Associations

Trophic interactions among mites, fungi, and the SPB are covered in chapter 9 and are well documented for particular mite-fungal interactions (Bridges and Moser 1983, 1986; Hofstetter and others 2006a, 2006b; Klepzig and others 2001a, 2001b; Lombardero and others 2000c, 2003). *Tarsonemus* mites significantly affect the abundance of and interactions between mycangial and *Ophiostoma* fungi associated with the SPB. *Tarsonemus* possess specialized, flap-like structures of the integument, called C-flaps or sporothecae, which frequently contain *O. minus* and *C. ranaculosus* ascospores (Bridges and Moser 1983, Moser 1985, Moser and others 1995) (Figure 11.5). The collection and inoculation of *C. ranaculosus* ascospores by *Tarsonemus* spp. within SPB-infested trees provide the primary mechanism for which sexual spores of *C. ranaculosus* are transported. This may be one of many cases of pseudopollination between fungi and mites found within bark beetle communities. The transports of fungal spores likely have important consequences for this beetle-mycangial fungal relationship and the maintenance of high genetic variation and cross-fertilization of fungi.

The presence of *O. minus* in phloem negatively affects SPB larvae (Bridges 1983, Bridges and Perry 1985, Goldhammer and others 1990,

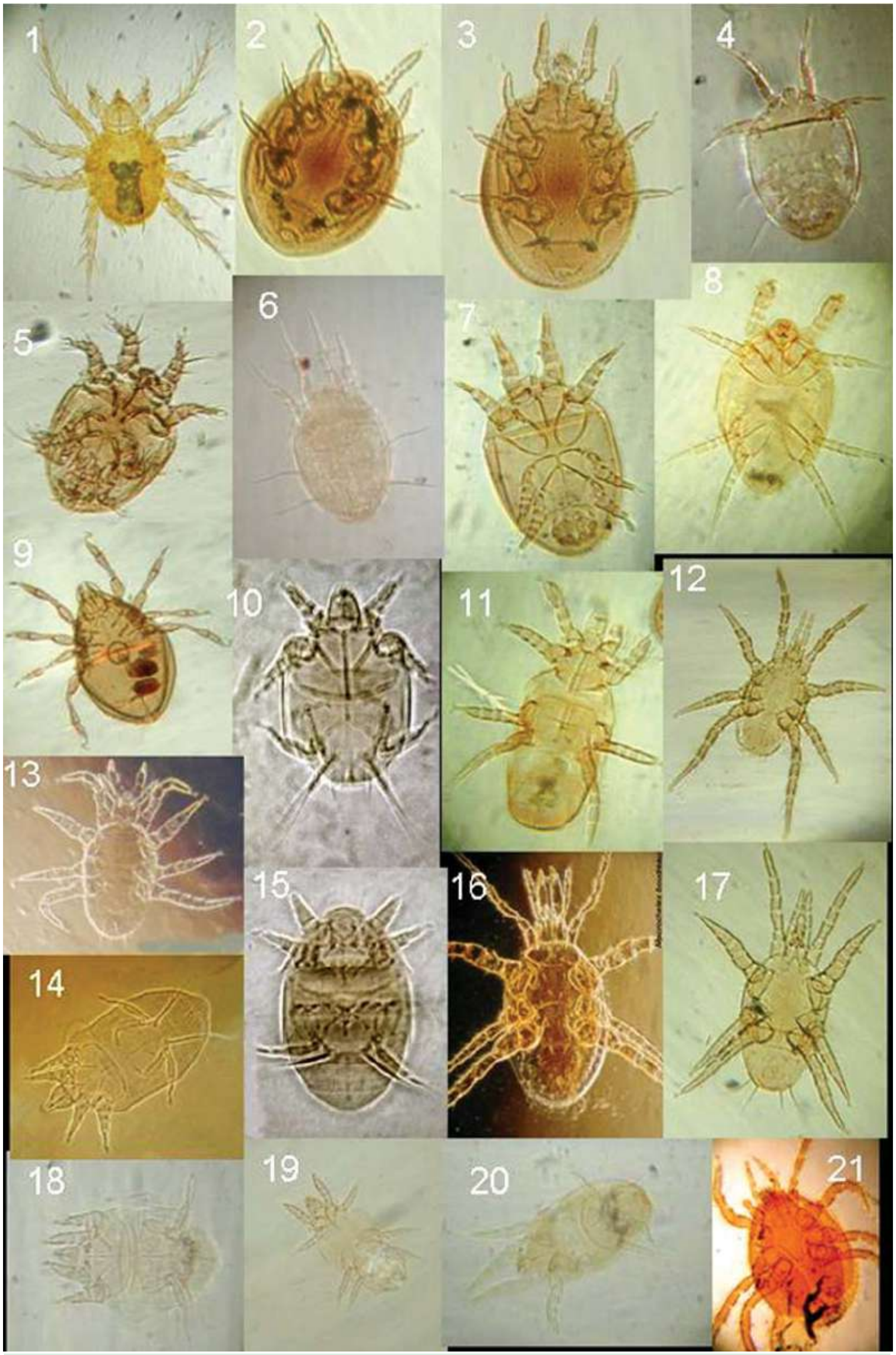


Figure 11.3—Images of common mites associated with bark beetles. Not all mites pictured here are phoretic on the SPB. (1) *Mexecheles virginiensis* Baker, (2) *Uroobovella orri* Hirschmann, (3) *Trichouropoda* sp., (4) *Histiostoma* sp., (5) *Histiogaster anops* Woodring, (6) *Bonomia* sp., (7) *Schwiebia* sp., (8) *Paracarophaenax* sp., (9) *Paraleius* sp., 10) *Iponemus truncatus* Lindquist, (11) *Elattoma* sp., (12) *Lasioseius safroi* Ewing, (13) *Proctolaelaps* sp., (14) *Tarsonemus ips* Lindquist, (15) *Heterotarsonemus* sp., (16) *Macrocheles* sp., (17) *Dendrolaelaps quadrisetus* (Berlese), (18) *Tarsonemus krantzi* Smiley and Moser, (19) *Pyemotes* sp., (20) *Parawinterschmidtia* sp., and (21) *Cerocoleius* sp. (images by Elisabeth Alden, R.W. Hofstetter, and J. Khai Tran)

Figure 11.4 — Pseudoscorpion removed from SPB in Arizona. (photograph by R.W. Hofstetter)

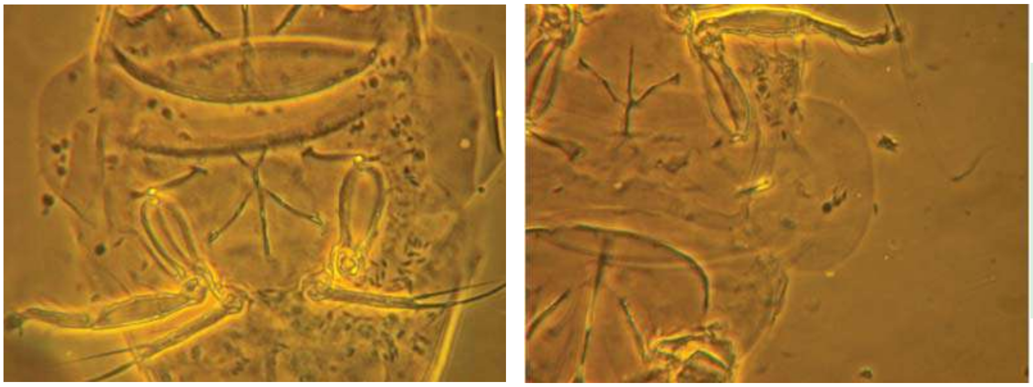


Figure 11.5 — *Tarsonemus krantzi* with fungal spores within sporothecae, also called C-flaps. Mites removed from SPB collected in flight traps in Alabama 2001. (images by R.W. Hofstetter)

Table 11.1—Description of phoretic interactions between SPB and phoront(s)

Impact on SPB	Impact on Phoront	Interaction type	Examples
+	+	Mutualism	Mycangial fungi, *Tarsenomus ips* carrying mycangial fungi; mite predators (eg., *Dendrolaelaps* spp.) of parasitic nematodes
-	+	Antagonism	*Ophiostoma minus*, mite predators/ parasitoids of SPB; pathogenic fungi
0	+	Commensalism, Facilitative	Most fungi and phoretic mites

Combinations in which the impacts on the phoront is – or 0 are unlikely, in that the phoront should benefit (+) from transportation by SPB, thus having an overall positive effect on fitness. However, theoretically the phoront can be harmed or depredated by SPB, in which case the SPB benefits and the phoront is harmed. Situations in which the impact is negative (-) or there is no impact (0) on the phoront would not likely persist over time.

Hofstetter and others 2006a, Lombardero and others 2000c). Variance in abundance of *Tarsonemus* spp. appears to be a meaningful driver in SPB population dynamics and *O. minus* abundance in infested trees (Goldhammer and others 1990; Hofstetter and others 2006a, 2006b; Lombardero and others 2003). Several mite genera other than *Tarsonemus* may be partially or wholly mycetophagous and affect beetle-fungal associations; these include *Elattoma*, *Heterotarsonemus, Histiogaster, Histiostoma, Parawinterschmidtia, Schwiebia,* and *Tyrophagous* (Moser and Roton 1971).

11.3.3. Impacts on Beetle Population Dynamics

Because the fungus *Ceratocystiopsis ranaculosus* represents an inferior nutritional resource for the SPB (Bridges 1983; Coppedge and others 1995; Goldhammer and others 1990; Klepzig and others 2001a, 2001b) but a superior nutritional resource for *Tarsonemus* mites (Lombardero and others 2000c), seasonal changes in the ratio of the beetle-mutualistic fungi (due to temperature; Hofstetter and others 2007) could influence beetle and mite population dynamics in opposite directions. Field studies by Miller and Parresol (1992) and Bridges (1983) demonstrated increased reproduction in beetle populations when *Entomocorticium* sp. A was the dominant mycangial fungus. Likewise, Hofstetter and others (2006a, 2006b) recorded increased mite reproduction and decreased beetle reproduction during periods when *O. minus* and *C. ranaculosus* were particularly abundant within bark. Hofstetter and others (2007) predicted that the abundance of *C. ranaculosus* relative to *Entomocorticium* sp. A would tend to be highest in the warmest climates where the SPB occurs (for example, Florida and Mexico). Surveys of the SPB mycangia in Mexico and Arizona reveal that *Entomocorticium* sp. A is very uncommon but present (Hofstetter and others, unpublished; Davis and Hofstetter 2009) .

Variation in *O. minus* (i.e., blue stain within trees) abundance among and across SPB infestations appears to be driven by the association between *O. minus* and phoretic mites, while the association between *O. minus* and the SPB has little affect on total blue stain within infested trees (Hofstetter and others 2006a, 2006b). Even with large experimental additions of *O. minus* spores to beetles, *O. minus* in the absence of *Tarsonemus* spp. do not reach levels observed in natural infestations (Hofstetter and others 2006a). Field surveys, in combination with experimental manipulation of *Tarsonemus* on beetles, suggest that *Tarsonemus* is a key factor for *O. minus* abundance and may be necessary for *O. minus* to reach levels high enough (> 45 percent of phloem) to curtail beetle population growth (Hofstetter and others 2006a, Lombardero and others 2003). Apparently, *Tarsonemus* spp. propagate *O. minus* both by transporting ascospores into newly attacked trees (69 percent of phoretic mites carried an average of 18 ascospores per mite in natural infestations; Hofstetter and others 2006b) and by dispersing existing *O. minus* within the phloem of attacked trees (Lombardero and others 2003). *Tarsonemus* spp. presumably propagates *O. minus* because it feeds on it (Lombardero and others 2000c). Because *Tarsonemus* spp. feeds on *O. minus*, it is logical that the addition of *O. minus* leads to an increase in mites, and those infestations with high *O. minus* abundances have high mite densities within phloem. In any case, *Tarsonemus* spp., *O. minus* and beetle reproduction covary in a manner consistent with a system of strong direct and indirect interactions (Figure 11.6). Consequently, while environmental factors can cause short-term fluctuations in SPB abundances, species interactions act as a filter through which short-term environmental effects are translated into long-term population variability (Ives and Gross 1999).

The community of fungi and mites associated with the SPB likely transforms with seasonal temperatures as well as large scale changes in climate. Changes in the relative abundances of these organisms result from direct effects on reproduction, growth, behavior, and mortality, and from indirect effects through symbiotic species. Such variability in species responses suggests that there is flexibility within this community but species loss will likely occur. Increases in average temperature (as predicted with global climate change) will likely lead to a shift or reduction in community richness and a predominance of a few species. However, increased variability in temperatures could further promote multiple symbionts and associations within this community.

11.4. NATURAL HISTORY OF PHORETIC MITES

Mites are common phoronts of the SPB and impact the ecology and behavior of the SPB. There are many unanswered questions related

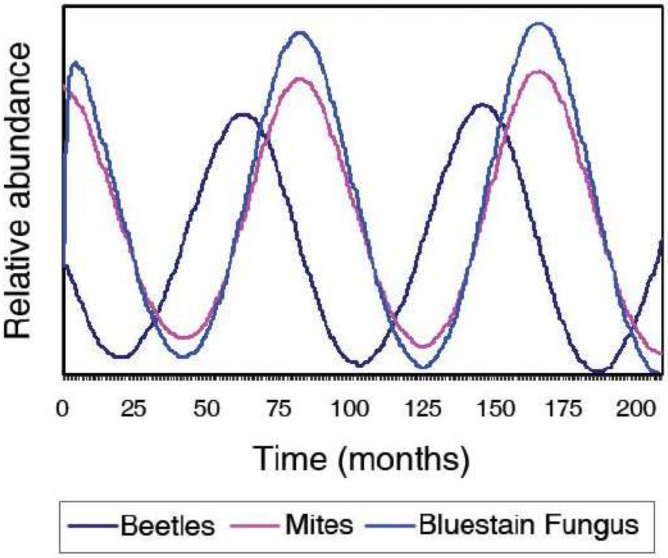


Figure 11.6—Model of SPB, mites, and blue stain fungi abundances through time. The pattern is similar to predator-prey dynamics proposed in other systems. (created by R.W. Hofstetter)

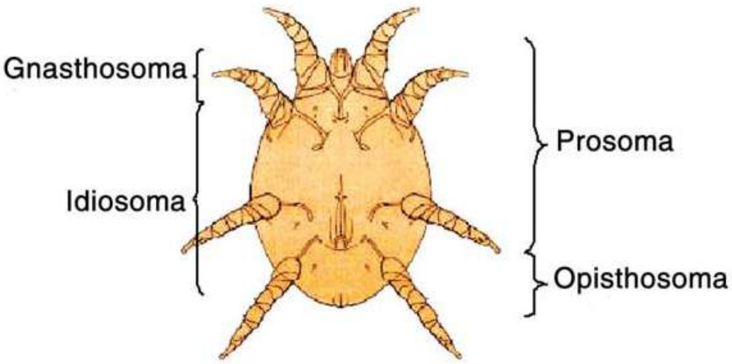
to phoretic mite abundance and behavior. For instance, does the frequency of a mite species on SPB adults indicate preference for the SPB? How do phoretic mite abundances correlate with mite populations within trees? What is the relationship between frequency of phoretic mites on beetles and the numbers of mites per beetle, and how do these two measurements vary? Do beetles actively remove phoronts or discourage mites from attaching to them? What cues do mites use to locate beetle hosts? What effects do environmental factors have on phoretic mite patterns? How have mites affected the evolution of beetle-microbial associations?

11.4.1. Taxonomy

Mites are in the phylum Arthropoda, which encompasses the insects, myriapods, spiders, scorpions, crustaceans, and ticks. Arthropods are characterized by jointed legs and a chitinous exoskeleton. Mites are in the Subphylum Chelicerata, which is characterized by having two body regions, the prosoma (front body) and the opisthosoma (hind body), which excludes the insects (Figure 11.7). Antennae, mandibles, and maxillae, which are common on other arthropods, are absent in the Chelicerata. Instead, the prosoma contains a head region which has two pairs of pincer-like mouthparts called the chelicerae and the subcapitulum, and a region with four pairs of legs. The posterior body region, the opisthosoma, contains organs for digestion, gas exchange, and reproduction. Mites are in the Class Arachnida, which is comprised of Chelicerata that may possess simple eyes and are primarily terrestrial, including such groups as the scorpions, spiders, harvestmen, ticks, and mites. The mite Subclass, Acari, contains organisms in which segmentation is generally inconspicuous or absent, unlike the Araneae (the spiders).

Most mites associated with the SPB are in the Orders Astigmata and Prostigmata within the Superorder Acariformes and the Order Mesostigmata within Superorder Parasitiformes (Kinn 1971, Moser and Roton 1971). The Acariformes are the most diverse and abundant of the three mite Superorders (Opilioacariformes, Parasitiformes and Acariformes; Krantz 1978), with more than 30,000 described species. Acariformes mites occur in most habitats and regions of the world and are common phoronts of the SPB. Opilioacarans have not been found in bark beetle-killed trees, but it is possible that they live in decayed wood. About 11,000 species have been described within

Figure 11.7—Morphological regions of a mite.



the Parasitiformes, which includes the Orders Ixodida (ticks) and the Mesostigmata. Many Mesostigmata, including several of the genera associated with decaying fungi, are phoretic on beetles (Kinn 1971, Lindquist 1975, McGraw and Farrier 1973), and are prominent predators of nematodes and mites or mycetophagous on bark beetle fungi (Kinn 1971, Lindquist 1975, Lindquist and Wu 1991, Moser and Roton 1971). Table 11.2 shows the mite species known to travel on adult SPBs in the Southeastern and Southwestern United States. Many of the mite species are unique to either the Eastern or Western United States, but genera are often found in both geographic areas.

11.4.2. Morphology

Although the majority of mites are minute, adult body lengths can vary greatly from 50 µm (plant parasites) to 3 cm (engorged ticks). In general, mites associated with the SPB range from 60 µm (Iponemus sp.) to 0.5 mm (*Mexecheles* sp.).

Mites have an anterior section resembling a tiny head. This region, the gnathosoma, is comprised of the chelicera, subcapitulum, and palps. The chelicerae, which are primarily used for capturing, tasting, and ingesting food, may be highly modified with various structures, such as Trägårdh's organ, spermatodactyl, and stylophores. Chelicerae may also be used for nonfeeding behavior, such as holding on to the host during phoretic migration (Walter and Proctor 1999).

Adult mites have four pairs of legs, with the first pair of legs often being slender, elongated, and lacking well-developed claws. This first pair (Leg I) is used like antennae. A cluster of sensory setae may be located near the tips of Leg I, and are used for sizing up a potential sexual partner or prey by using tentative tapping movements (Walter and Proctor 1999). Sometimes the first two pairs of legs are used in conjunction with the palps and chelicerae to capture prey. Leg pairs II, III, and IV are the primary organs of locomotion.

The remainder of the body is fused into a sac-like idiosoma that contains organs for digestion, excretion, and reproduction. Digestion in mites is very primitive. The parasitiform and trombidiform mites only ingest fluids, sucking liquids through filtering structures. However, the sarcoptiform and opilioacariform mites use a different feeding method, cutting off pieces of food that they then move into their mouths. Food fragments form into a food bolus at the base of the esophagus. Entire spores of fungi can be seen within the hindgut of some mycetophagous mites. The food bolus is expelled as a fecal pellet through a relatively large anal opening covered by a pair of trapdoor-like valves (Walter and Proctor 1999).

11.4.3. Reproduction

Mites have extremely diverse mating habits and reproductive biology/strategies. Variation in reproductive mode can occur within families, genera, and species (Norton and others 1993). Direct transfer of sperm via genitalia is relatively uncommon. In males, appendages are modified for sperm transfer. Spermatodactyls on chelicerae of males are sometimes used to channel sperm into the female's genital opening. In some parasitiform species, the male picks up a spermatophore (sperm packet) and places it into the female's genitalia.

Although there is an extensive body of literature on the sex ratio biology of mites (Proctor 1996, Wrensch and Ebbert 1993), knowledge of sex determination of offspring and oviposition behavior of mites associated with bark beetles is sparse. For most species, the mode of reproduction (haploid or diploid) and the genetic system (e.g., arrhenotoky, parahaploidy, thelytoky, and amphitoky) remain unknown. Several species of Tarsonemidae are arrhenotokous, theyletokous, or amphitokous (Karl 1965, Schaarschmidt 1959). In general, mite species that are haplodiploid and dependent on beetles for dispersal have relatively high sex ratios in favor of females (Lindquist 1969, Mitchell 1970). The patchiness and discrete time periodicity of bark beetle habitat allow for tests of evolutionary stable sex allocation strategies (for example, local mate competition; Hamilton 1967), founder effects (e.g., haystack model; Nagelkerke and Sabelis 1996), exploitation and competition, and island biogeography theory (Sanchez and Parmenter 2002, Terborgh and others 2001) .

11.4.4. Growth and Development

Mites associated with the SPB generally have many generations within each host tree. Development rates vary greatly across mite taxa and are strongly affected by temperature, humidity, and food quality. The most rapidly developing acariforms are in the Tarsonemidae, which can complete development in 3-10 days at moderate temperatures. Mite longevity also is highly variable across species, with some

Table 11.2—The distribution and feeding behavior of mite species phoretic on the SPB in the United States. Generalist = feeds on multiple fungi, nematodes, and dead invertebrates. Mycetophagous = feeds on specific fungi, often transports and disperses reproductive structures of fungi. I categorize phoretic mites abundance on beetles as rare (< 1 percent of beetles have this species), infrequent (1-5 percent), common (5-20 percent), and frequent (>20 percent). Surveys of SPB populations by R.W. Hofstetter in Arizona, Mississippi, and Alabama, and by J.C. Moser throughout Southeast United States. Mites identified by J.C. Moser and stored as voucher specimens by R.W. Hofstetter at Northern Arizona University and J. Moser at Southern Research Station.

		Dist. on SPB		
Phoretic mite species	Mite family[a]	S.E. U.S.[b]	S.W. U.S.[c]	Phoretic abundance
Dendrolaelaps (Longoseius) cuniculus	Digamasellidae[P]	X	X	Infrequent
D. neocornutus	Digamasellidae[P]	X		Infrequent
D. neodisetus	Digamasellidae[P]	X	X	Common
D. quadrasetus	Digamasellidae[P]		X	Infrequent
D. varipunctatus	Digamasellidae[P]	X	X	Rare
Elattoma spp.	Pyemotidae[A]	X	X	Infrequent
E. bennetti	Pyemotidae[A]	X		Common
Ereynetes scutulis	Ereynetidae[A]	X	X	Rare
Ereynetes spp.	Ereynetidae[A]	X	X	Rare
Eugamasus lyriformis		X		Rare
Heterotarsonemus lindquisti	Tarsonemidae[A]	X	X	Rare
Histiogaster anops	Acaridae[A]		X	Common
H. arborsignus	Acaridae[A]	X		Common
Histiostoma varia	Histiostomatidae[A]	X	X	Common
Iponemus truncatus	Tarsonemidae[A]	X	X	Rare
Licnocephalus reticulatus	Oribatidae[A]		X	Infrequent
Macrocheles boudreauxi	Macrochelidae[P]	X	X	Rare
Mexecheles virginiensis	Cheyletidae[A]	X	X	Rare
Nanacarus sp.	Hemisarcoptidae[A]		X	Rare
Nentaria sp.	Uropodidae[P]		X	Rare
Paracarophanax sp.	Pyemotidae[A]		X	Rare
Paraleius leontonychus	Oribatidae[A]	X		Rare
Paraleius sp.	Oribatidae[A]		X	Rare
Parawinterschmidtia furnissi	Wintershniditiidae[A]		X	Infrequent
Proctogastrolaelaps libris	Ascidae[P]	X		Rare
Proctolaelaps dendroctoni	Ascidae[P]	X	X	Rare
P. hystrix	Ascidae[P]	X		Common
Pyemotes parviscolyti	Pyemotidae[A]	X		Rare
Pyemotes n. sp.	Pyemotidae[A]		X	Rare
Schwiebia sp.	Acaridae[A]		X	Infrequent
Tarsonemus fuseri	Tarsonemidae[A]	X		Rare
T. ips	Tarsonemidae[A]	X	X	Common
T. krantzii	Tarsonemidae[A]	X	X	Frequent
T. subcorticallis	Tarsonemidae[A]	X	X	Rare
Trichouropoda australis	Uropodidae[P]	X	X	Common
T. hirsuta	Uropodidae[P]	X	X	Common
Uroobovella orri	Uropodidae[P]	X	X	Infrequent

[a] Mite family: [A] Order Acariformes; [P]Order Parasitiformes.

[b] SPB populations in Louisiana, Mississippi, and Alabama, U.S.

[c] SPB populations in Coronado and Coconino National Forests, Arizona, U.S.

adults living only weeks while others live for several months or possibly a year.

The basic acarine development sequence is egg, prelarva, larva, protonymph, deutonymph, tritonymph, and adult (Krantz 1978). Suppression of one or more nymphal instars and accelerated development are common in many species. Several lineages are characterized by terminal truncation of nymphal instars and rapid developmental rates (e.g., some Parasitiformes and Acariformes). Some species of Heterostigmata give birth to fully formed, mated adult offspring. Eggs are usually laid individually on the substrate and not protected by the parent, although some eggs may be carried by adults. Eggs are also quite large, almost half the size of an adult mite in some species. The typical acarine larva is hexapod and completes its development with little or no change in initial form other than slight increases in girth. Larvae of some species pass into an inactive, turgid state before becoming a nymph or adult (e.g., Tarsonemidae; Lindquist 1986). Males (Figure 11.8B) of several species carry virgin females while they are in this quiescent state. Two or three nymph states usually appear between the larval and adult stage. These nymphs usually have four pairs of legs, although the fourth pair may not be complete and may lack claws (Figure 11.8A). The first nymph or protonymph is free-living and does not always feed. The second nymphal stage or deutonymph assumes the general nonsexual characteristics of the adult, differing from it only in size and in sclerotization pattern. In many species, phorecy occurs in the deutonymph stage rather than as mature adults.

11.4.5. Food and Host Specificity

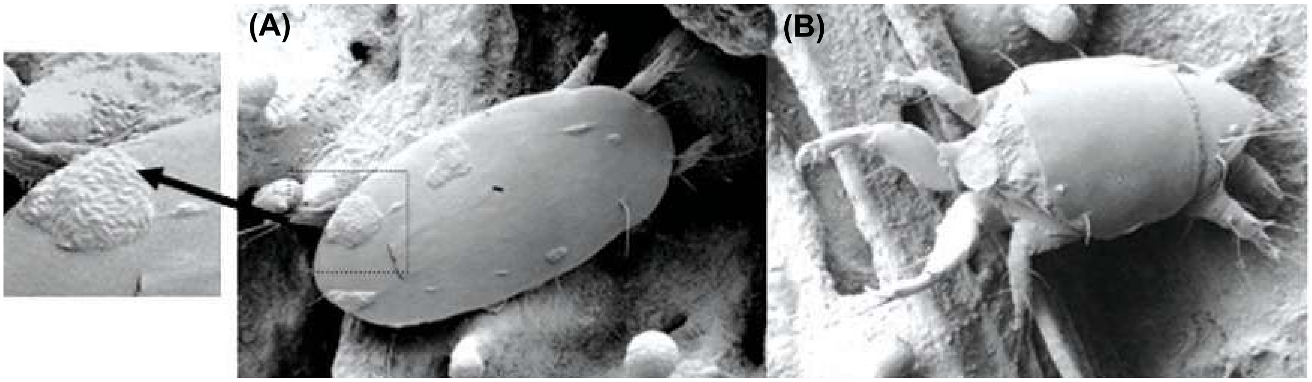
The eating habits and food preference of mites associated with the SPB are well understood compared to other bark beetle communities (Tables 11.2 and 11.3). Most mites associated with bark beetles are predators on nematodes and other small arthropods including SPB larvae and eggs (Table 11.3). Mycetophagous species vary from highly specific, feeding on and carrying spores of one fungus (e.g., *Tarsonemus krantz* on *Ophiostoma minus*; Figures 11.8 and 11.9) to generalists, feeding on several fungi (e.g., *Histiogaster* spp.).

11.4.6. Movement and Dispersal

Typically, only one life history stage is phoretic in a given species. In the Astigmata the phoretic stage is the deutonymph, while in the Prostigmata it may be the fertilized adult female (Zhang and Sanderson 1993). Heteromorphic deutonymphs in the Uropodina attach to their arthropod hosts with a stalk secreted from the anus called a pedicel (Figure 11.10), although other mites use caudal suckers, claws, or chelicerae. Phoretic morphs in many different taxa share similar morphologies: dorsoventral flattening, oval or circular bodies, and glanges covering all or some appendages (Athias-Binche 1991, Binns 1982, Norton and others 1993). This convergent morphology may serve to reduce loss of moisture when on the host and to present a smooth dorsal surface, making it difficult for the host to remove mites by grooming or rubbing.

In the case of Tarsonemidae and some other families, mite species are phoretic on specific insect species (such as the SPB), genera, or families associated with SPB-killed trees. Some phoretic mite species may disperse as groups rather than individual mites, which ensures that

Figure 11.8—SEM photograph of (A) female and (B) male *Tarsonemus ips* in bark. Ascospores of *O. minus* can be seen on their cuticle. Note the modified IV legs of the male for grasping pharate females. (photographs by Eric Erbe, Ronald Ochoa, and K.D. Klepzig)



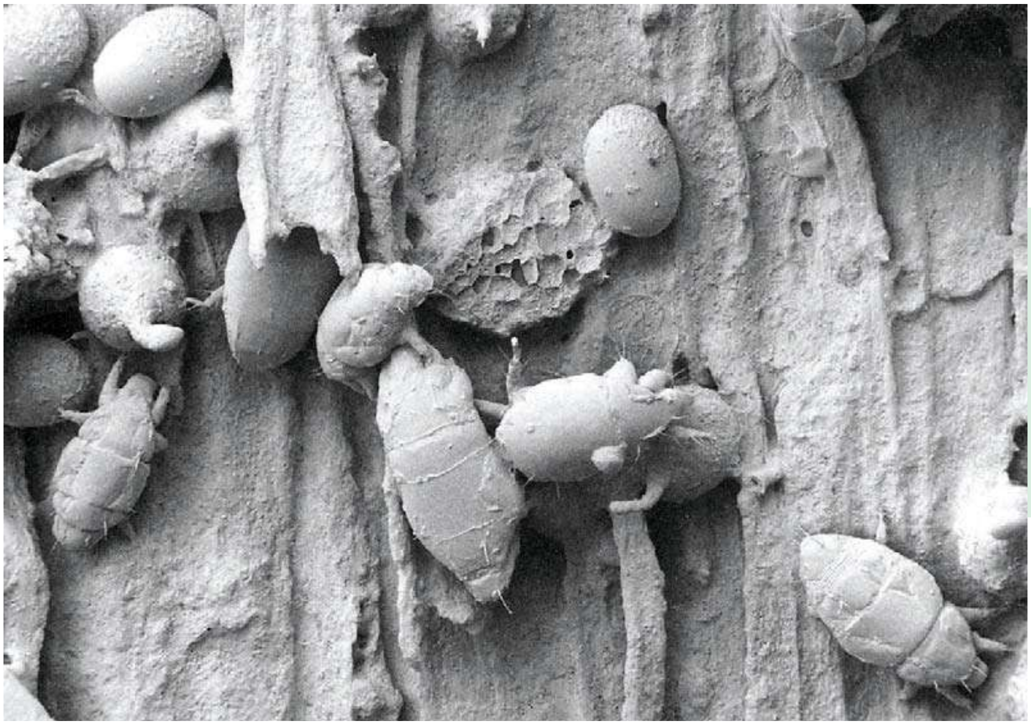


Figure 11.9—SEM photograph of adult and immature *Tarsonemus* mites that feed on *Ophiostoma minus*. Perithecia of *O. minus* and *Tarsonemus* eggs are covered with minute ascospores. (photograph by Eric Erbe, Ronald Ochoa, and K.D. Klepzig)

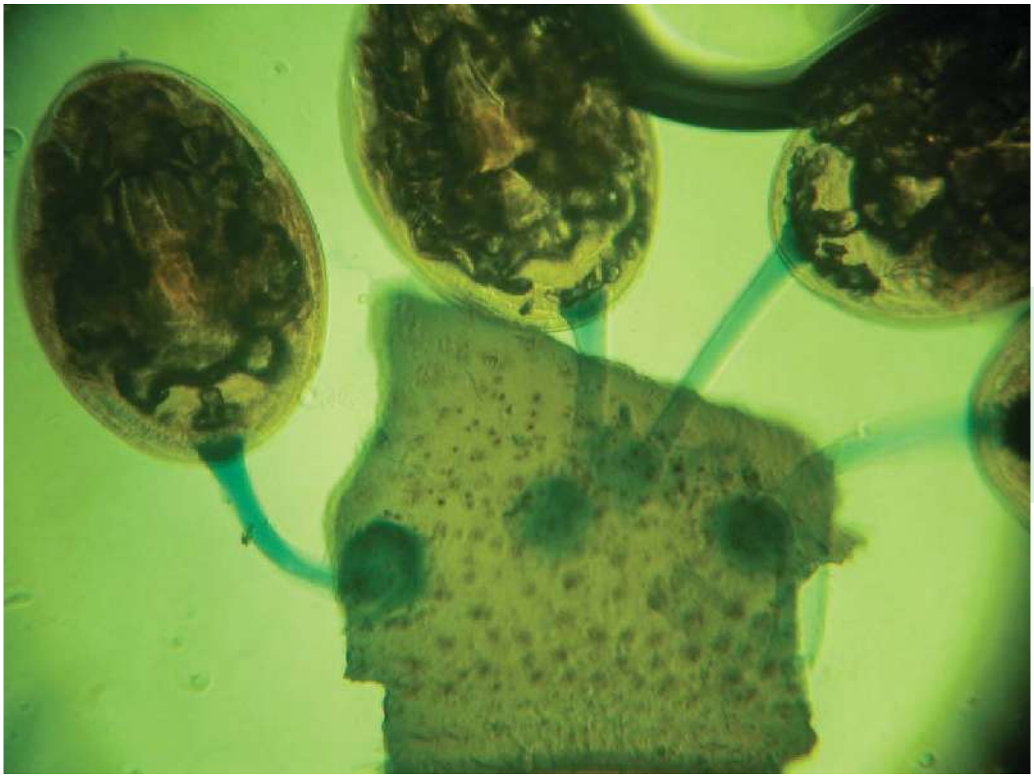


Figure 11.10— Uropodina mites attached to the exoskeleton of SPB. Note the anal glue stalks, termed pedicels (stained blue). (photograph by R.W. Hofstetter)

unmated mites find mates at their new location. This behavior likely occurs in species that do not exhibit parthenogenesis, or if the likelihood of mating prior to dispersal is small.

The attachment pattern of phoretic species on the SPB is reminiscent of niche partitioning that reduces interspecific competition and predation. Several species appear to attach to specific locations on beetle hosts (Figure 11.11),

Table 11.3—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini,* and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m^2 bark; low = 1-5 mites/m^2 bark; Moderate = 6-50 mites/m^2 bark; high = > 50 mites/m^2 bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
1	*Acrocheyla impolita* Smiley and Moser	Mite predator	Low	61%	Moser and Roton 1971
2	*A. virginiensis* (Baker)	Generalist predator	Rare	10%	Moser and Roton 1971
3	*Amblyseius guatemalensis* (Chant)	?	Rare	13%	Moser and Roton 1971
4	*Ameroseius longitrichus* Hirschmann	?	Low	6%	Moser and Roton 1971, Moser 1975
5	*Androlaelaps casalis* (Berlese)	Egg, mite predator	Rare	3%	Moser and Roton 1971, Moser 1975
6	*Histiostoma (Anoetus) conjuncta* Woodring and Moser	?	Rare	6%	Moser and Roton 1971
7	*H. insolita* Woodring and Moser	?	Rare	10%	Moser and Roton 1971, Moser 1975
8	*H. media* Woodring and Moser	?	Rare	10%	Moser and Roton 1971
9	*H. sordida* Woodring and Moser	?	Low	29%	Moser and Roton 1971, Moser 1975
10	*Bakerdania sellnicki* (Krczal)	?	Low	3%	Moser and Roton 1971
11	*Blattisocius keegani* Fox	Egg/mite predator	Rare	6%	Moser and Roton 1971
12	*Bryobia* sp. (*praetiosa* complex)	Phytophagus	Rare	2%	Moser and Roton 1971
13	*Cercoleipus coelonotus* Kinn	Nematode, mite, egg/larval predator	Rare	19%	Moser and Roton 1971, Moser 1975, Kinn 1971
14	*Cryptograthus barrasi* Smiley and Moser	?	Rare	1%	Moser and Roton 1971
15	*C. capreolus* (Berlese)	?	Rare	2%	Moser and Roton 1971
16	*C. taurus* (Kramer)	?	Rare	6%	Moser and Roton 1971
17	*Cunaxoides andrei* Baker and Hoffmann	?	Rare	4%	Moser and Roton 1971
18	*Cyta latirostris* (Hermann)	?	Rare	1%	Moser and Roton 1971
19	*Dendrolaelaps brachypoda* (Hurlbutt)	?	Rare	3%	Moser and Roton 1971
20	*D. (Longoseius) cuniculus* (Chant)	?	Low	2-60%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
21	*D. isodentatus* (Hurlbutt)	Egg/larval predator	Moderate	0-35%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
22	*D. neocornutus* (Hurlbutt)	Egg/larval predator	Moderate	5-35%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
23	*D. neodisetus* (Hurlbutt)	Larval/Nematode predator	High	74-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
24	*D. quadrisetus* (Berlese)	Nematode predator	Low-Moderate	25-100%	Moser and Roton 1971, Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini,* and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m² bark; low = 1-5 mites/m² bark; Moderate = 6-50 mites/m² bark; high = > 50 mites/m² bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
25	*D. quadrisetosimilis* (Hirschmann)	?	Rare	1%	Moser and Roton 1971
26	*D. quadritorus* Robillard	?	Rare	1%	Moser and Roton 1971
27	*D. rotoni* (Hurlbutt)	Egg/larval predator	Rare	6%	Moser and Roton 1971, Moser 1975
28	*D. varipunctatus* (Hurlbutt)	Larval predator	Low	13%	Moser and Roton 1971
29	*Elattoma (Pygmephorellus) bennetti* (Cross and Moser)	Mycetophagous[3]	Low	17-42%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
30	*Ereynetoides scutulis* Hunter	?	Moderate	11-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
31	*Eugamasus (Vulgarogamsus) lyriformis* McGraw and Farrier	Larval/pupal predator	Moderate	1-80%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
32	*Eupelops* sp.	?	Rare	3%	Moser and Roton 1971
33	*Eupodes* sp.	?	Rare	3%	Moser and Roton 1971
34	*Eutogenes vicinus* Summers and Price	Mite predator	Rare	1%	Moser and Roton 1971
35	*Gamasellodes rectiventris* Lindquist	?	Rare	6%	Moser and Roton 1971
36	*Gamasiphis* sp.	?	Rare	3%	Moser and Roton 1971
37	*Gamasolaelaps subcorticalis* McGraw and Farrier	Larval predator	Rare	0-13%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
38	*Glycyphagus* n. sp.	?	Rare	3%	Moser and Roton 1971
39	G*ymnolaelaps* sp.	?	Rare	1%	Moser 1975
40	*Heterotarsonemus lindquisti* Smiley	Mycetophagous	Low	0-48%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
41	*Histiogaster anops* Woodring	Generalist[4]	Low	1-25%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
42	*H. arborsignis* Woodring	Generalist predator; mycetophagus	Moderate	23-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
43	*H. rotundus* Woodring	Generalist predator; mycetophagus	Low	29%	Moser and Roton 1971, Moser 1975
44	*Histiostoma (Anoetus) varia* Woodring	Filter feeder	Low-Moderate	13-70%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
45	*Hoplocheylus pickardi* Smiley and Moser	?	Rare	1%	Moser and Roton 1971
46	*Hypoaspis disjuncta* Hunter and Yeh	Mycetophagus	Rare	3%	Moser and Roton 1971, Moser 1975
47	*H. krantzi* Hunter	?	Rare	0-3%	Stephen and Kinn 1980, Moser and Roton 1971

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini,* and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m^2 bark; low = 1-5 mites/m^2 bark; Moderate = 6-50 mites/m^2 bark; high = > 50 mites/m^2 bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
48	*H.* sp. nr. *praesternalis* Willman	Egg predator	Rare	1%	Moser 1975
49	*H. vitzthumi* (Womersley)	Larval predator	Rare	1%	Moser 1975
50	*Iponemus calligraphi calligraphi* Lindquist	Egg parasitoid	Rare	3%	Moser and Roton 1971, Moser 1975
51	*I. confusus oriens* Lindquist	Egg parasitoid	Rare	10%	Moser and Roton 1971, Moser 1975
52	*I. truncatus* Lindquist	Egg parasitoid	Rare	1%	Moser and Roton 1971, Moser 1975
53	*Kleemannia* sp.	?	Rare	1%	Moser 1975
54	*Lasioseius corticeus* Lindquist	Egg/larval predator	Low	32%	Moser and Roton 1971
55	*L. dentatus* (Fox)	Egg predator	Rare	3%	Moser and Roton 1971, Moser 1975
56	*L. epicriodopsis* DeLeon	Larval predator	Rare	1%	Moser and Roton 1971, Moser 1975
57	*L. neometes* McGraw and Farrier	?	Rare	3%	Moser and Roton 1971
58	*L. tubiculiger* (Berlese)	Egg predator	Rare	1%	Moser 1975
59	*Ledermulleria segnis* Koch	?	Rare	3%	Moser and Roton 1971
60	*Leptus* n. sp.	Predator	Rare	9%	Moser and Roton 1971
61	*Licnocephelus reticulates*	?	Rare	1%	Moser, pers. comm.
62	*Liodes* sp.	?	Rare	2%	Moser and Roton 1971
63	*Macrocheles boudreauxi* Krantz	Predator	Low	11-80%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
64	*M. mammifer* Berlese	Predator	Rare	1%	Moser 1975
65	*Melichares monochami* (Lindquist)	?	Rare	2%	Moser and Roton 1971
66	*Mesotritia* sp.	?	Rare	2%	Moser and Roton 1971, Moser 1975
67	*Mexecheles virginiensis* Baker	Predator	Low	1-10%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
68	*Microtydeus* n. sp.	?	Rare	1%	Moser and Roton 1971
69	*Nanacarus* sp.	?	Rare		Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
70	N*enteria* sp.	?	Rare	1%	Moser and Roton 1971
71	N*eophyllobius lorioi* Smiley and Moser	?	Rare	3%	Moser and Roton 1971
72	*Neoraphignathus howei* Smiley and Moser	?	Rare	1%	Moser and Roton 1971
73	*Neotrombidium* n. sp.	?	Rare	2%	Moser and Roton 1971
74	*Oodinychus* sp.	?	Rare	1%	Moser and Roton 1971

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini,* and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m^2 bark; low = 1-5 mites/m^2 bark; Moderate = 6-50 mites/m^2 bark; high = > 50 mites/m^2 bark (continued)

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
75	*Paracarophenax* sp.	Egg parasitoid	Rare	1%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
76	*Paracheyletia wellsi* (Baker)	Mite predator	Rare	4%	Moser and Roton 1971
77	*Paraleius leontonychus* Berlese	?	Rare	1-5%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
78	*Paraleius* sp.	?	Rare	3%	Moser and Roton 1971
79	*Paraupalopis hodgesi* Smiley and Moser	?	Rare	1%	Moser and Roton 1971
80	*Parawinterschmidtia furnissi*	?	Low-Moderate	5-20%	Collections by R.W. Hofstetter in Arizona 2005-2006, unpublished
81	*Peloribates* sp.	?	Rare	5%	Moser and Roton 1971
82	*Pleuronectocelaeno drymoecetes* Kinn	Egg/larval predator	Rare	0-32%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
83	*Podocinum pacificum* Berlese	?	Rare	3%	Moser and Roton 1971
84	*Proctogastrolaelaps libris* McGraw and Farrier	?	Low	6-80%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
85	*Proctolaelaps bickleyi* (Bram)	Larval/nematode predator	Low	1-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
86	*P. dendroctoni* Lindquist and Hunter	Larval/pupa/mite predator	Moderate	87%	Moser and Roton 1971, Moser 1975
87	*P. fiseri* Samsinak	Larval predator	Low	13%	Moser and Roton 1971, Moser 1975
88	*P. hystricoides* Lindquist and Hunter	Larval predator	Low	39%	Moser and Roton 1971, Moser 1975
89	*P. hystrix* (Vitzthum)	Larval predator	Low	10%	Moser and Roton 1971, Moser 1975
90	*P. xyloteri* Samsinak	?	Rare	2%	Moser and Roton 1971
91	*Prosocheyla acanthus* Smiley and Moser	?	Rare	4%	Moser and Roton 1971
92	*Pseudoparasitus thatcheri* Hunter and Moser	Egg/larval predator	Low	19%	Moser and Roton 1971, Moser 1975
93	*Pyemotes parviscolyti* Cross and Moser	Egg/larval predator	Low	30%	Moser and Roton 1971, Moser 1975
94	*Scapheremaeus palustris* (Sellnick)	?	Rare	9%	Moser and Roton 1971
95	*Scheloribates* sp.	?	Rare	3%	Moser and Roton 1971
96	*Schwiebia* sp.	Generalist	Moderate-High	0-80%	Stephen and Kinn 1980
97	*Spinibdella depressa* (Ewing)	?	Rare	1%	Moser and Roton 1971
98	*Tarsonemus fuseri*	Mycetophagous[4]	Rare	1%	Moser and Roton 1971

continued

Table 11.3 (continued)—Mites found within the bark of SPB-infested trees. Additional information on feeding behavior and relative abundance of each species within bark is included. It is important to note that some of the bark-inhabiting mite species were likely introduced by beetle species other than SPB, such as *Ips pini,* and are not directly associated with SPB. Relative abundance scale: Rare = < 1.0 mites/m^2 bark; low = 1-5 mites/m^2 bark; Moderate = 6-50 mites/m^2 bark; high = > 50 mites/m^2 bark

#	Mite species found in SPB-infested bark	Feeding guild	Relative abundance	Frequency in samples	References
99	*T. ips* Lindquist	Mycetophagous[4]	Moderate	26-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
100	*T. krantzi* Smiley and Moser	Mycetophagous[4]	High	54-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
101	*T. subcorticalis* Lindquist	Mycetophagous	Low	77%	Moser and Roton 1971
102	*Trichogalumna* sp.	?	Rare	1%	Moser and Roton 1971
103	*Trichoribates* sp.	?	Rare	1%	Moser and Roton 1971
104	*Trichouropoda australis* Hirschmann	Generalist	High	77-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
105	*T. hirsuta* Hirschmann	Generalist	Low-High	8-100%	Stephen and Kinn 1980, Moser and Roton 1971, Moser 1975
106	*T. lamellosa* Hirschmann	Nematode/ larval predator	Low-High	58%	Moser and Roton 1971, Moser 1975, Kinn 1987
107	*Tydeus* n. sp.	?	Rare	1%	Moser and Roton 1971
108	*Tyrophagus putrescentiae* (Schrank)	Mycetophagus	Low	58%	Moser and Roton 1971, Moser 1975
109	*Uroobovella americana* Hirschmann	Larval predator	Rare	23%	Moser and Roton 1971, Moser 1975
110	*U. laciniata* Berlese	?	Rare	3%	Moser and Roton 1971
111	*U. orri* Hirschmann	?	Low	32%	Moser and Roton 1971, Moser 1975

while others may attach anywhere on the body. Whether species compete or exclude other individuals or species from particular locations is not known. Species may have adaptations that allow them to hold on to specific structures and locations on the beetle body. Why some species select particular locations on the beetle body is unknown. Presumably, attachment sites vary in their exposure and difficultly to hold fast. How do attachment location patterns on SPB compare to other phoretic systems?

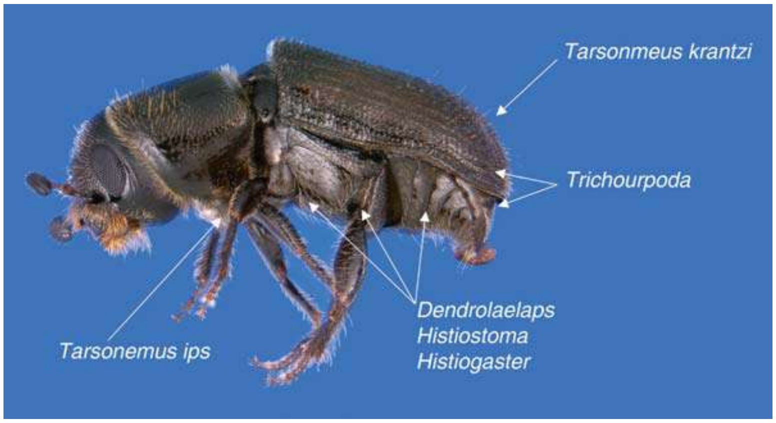


Figure 11.11—General locations of some phoretic mite species and genera on SPB during flight. (photograph by Erich G. Vallery, USDA Forest Service, SRS-4552, www.forestryimages.org).

Anywhere from 10 to 90 percent of flying SPB within a population carry phoretic mites (Hofstetter and others 2006a, 2006b; Moser 1976b), but this number can vary seasonally. For example, *Proctolaelaps dendroctoni, Longoseius cuniculus*, and *Macrocheles boudreauxi* are most common in early summer. During midsummer, *Dendrolaelaps neodisetus*, *Eugamasus lyriformis*, and *Trichouropoda australis* are most abundant, and *Tarsonemus krantz* and *T. ips* increase in numbers from spring through early fall (Hofstetter and others 2007). Hofstetter and others (2006b) and Evans and others (in review) exposed sections of SPB-infested trees from Mississippi and Alabama and observed significant effects of temperature on phoretic mite species abundances on emerging beetle progeny. In general, *Trichouropoda* spp. and *Dendrolaelaps* spp. abundances increased with temperature (up to 32 °C), while *Tarsonemus* spp. were most abundant at cooler temperatures (between 22 and 26 °C).

Mite abundances and distributions within trees can vary with height of the tree and season. Stephen and Kinn (1980) found more mite species in the upper boles of SPB-infested trees than in the lower boles. More mites in the upper bole are likely due to higher numbers of attacking bark beetles and beetle species in that portion of the bole. *Trichouropoda australis* and *Dendrolaelaps neodisetus* were more abundant in the lower bole, while *Pygmephorellus bennetti* and *Tarsonemus ips* were most abundant in the upper bole. The distribution of *Tarsonemus krantz* was somewhat uniform over the entire bole. *Trichouropoda* spp. and *Dendrolaelaps* spp. mites are much larger than *Tarsonemus* spp. and *Pygmephorellus* spp., giving support to the hypothesis that the flight ability of beetles can be impacted by mite loads. Flying SPB can carry at least 20 percent of their weight in mites (Moser 1976a, 1967b) .

Predators and competitors of the SPB are potential phoretic hosts for many species (Table 11.4) (Kinn 1983). Predators and competitors are often large in size, mobile, and excellent fliers, and thus make good phoretic hosts. The disadvantages of using these hosts are that they may not be common or predictable within trees. Interestingly, these phoretic hosts may provide a way for phoronts to switch habitats, even between coniferous- and hardwood-beetle communities. Surveys of predators of bark beetles in the Southern United States reveal that the most frequent phoretic mites are in the genera *Histiostoma, Parawinterschmidtia, Dendrolaelaps*, *Trichouropoda,* and *Saproglyphus*, many of which are believed to be generalist feeders or predators and are common associates in other bark beetle communities. The mycetophagous mites that are phoretic on predators and competitors of the SPB probably feed on late-successional fungi. However, the feeding habits of many mites associated with large woodboring beetles (i.e., Cerambycidae, Buprestidae) and predators remain largely unknown. Woodborers create extensive habitat within trees and are phoretic hosts for many mite species. For example, a single sawyer beetle was found to have 1,816 phoretic *Dendrolaelaps fukikoae* on its body (Enda and Tamura 1980).

11.4.7. Mortality Factors

Few observations have been reported on the predators and natural enemies of mites associated with the SPB. Many mite species are likely subject to predation by small insects and predatory mites or accidental feeding by invertebrate larvae. Mortality rates suffered during phorecy have not been documented but may be high. Phoretic mites quickly climb off the beetles that are attacked by predators. Whether these mites climb onto the attacker likely varies with the length of the attack and the species attacking. Mites appear to be susceptible to entomopathogenic fungi (Schabel 1982). However, the greatest mortality is suffered by mites that remain within habitats after phoretic hosts have left (Hofstetter 2004).

11.5. EVOLUTION OF MUTUALISMS AND ITS IMPLICATIONS ON SPB

Although mutualisms occur in virtually all ecosystems (Boza and Scheuring 2004), there is great variation in the way positive species interactions likely evolve. It is commonly thought that environmental heterogeneity and harsh conditions facilitate mutualistic tendencies (Bertness and Callaway 1994, Boza and Scheuring 2004, Morin 1999, Tewksbury and Lloyd 2001). For instance, mutualisms may allow for the exploitation of resources in marginal environments (Addicott 1995, Davidson and Morton 1981). Habitat amelioration is a common mutualist process that promotes the exploitation of harsh environments (Morin 1999). In this way, mutualism(s) between tree-killing bark beetles and microbes may allow beetles and their associates to utilize resources within a habitat that would be inaccessible without each other. To put another way, the mutualism(s) between SPB and their symbiotic fungi enable SPB to persist across a broad host range, host condition, and physical environment that would not be possible in the absence of these mutualists. In fact, in most mutualisms, the niche or physical space occupied by a species in the presence of interspecific interactions is actually greater than that occupied when the species lives alone (Bruno and others 2003). In addition, many mutualisms begin to evolve between beetles and phoronts under more benign conditions (i.e., within a colonized tree) that entail benefits of protection, defense, and nutrition, and eventually dispersal for the phoront.

Table 11.4—Phoretic mites of predators and competitors of bark beetles collected in baited flight traps during summer 2005 in Coconino National Forest, Arizona. Mites identified by J.C. Moser and stored as voucher specimens by R.W. Hofstetter at Northern Arizona University

Mite species	Mite family[a]	*Enoclerus sphegus* (N=176)	*Temnochilla chloridia* (N=201)	*Platysoma* species (N=35)	*Cortecius* species (N=23)	*Elacatis* species (N=25)	Cerambycidae & Buprestidae (N=16)
Anoetidae sp.	Anoetidae[A]	X					
Bonomia sp.	Histiostomatidae[A]	X	X	X		X	
Dendrolaelaps cuniculus	Digamasellidae[P]		X				X
Dendrolaelaps neodisetus	Digamasellidae[P]	X	X	X	X		X
Dendrol. varipunctatus	Digamasellidae[P]			X			
Dendrolaelaps sp.	Digamasellidae[P]			X			
Elattoma sp.	Pyemotidae[A]	X	X		X		
Gamasina sp.	Ascidae[P]		X				
Heterotarsonemus lindquisti	Tarsonemidae[A]				X		X
Histiostoma sp.	Histiostomatidae[A]	X	X	X			
Histiostoma medea	Histiostomatidae[A]			X	X		
Histiostoma varia	Histiostomatidae[A]			X	X		
Histiostoma sordida	Histiostomatidae[A]		X	X			
Histiogaster anops	Acaridae[A]	X					
Histiogaster arborsignis	Acaridae[A]	X	X				X
Histiogaster sp.	Acaridae[A]			X			
Nanacarus sp.	Hemisarcoptidae[A]	X	X				
Pachylaelapidae sp.	Pachylaelapidae[P]		X				
Parawinterschmidtia sp.	Winterschmidita[A]	X	X			X	X
Proctolaelaps dendroctoni	Ascidae[P]				X		
Proctolaelaps fiseri	Ascidae[P]		X				
Proctolaelaps hystrix	Ascidae[P]	X					
Proctolaelaps subcorticalis	Ascidae[P]		X		X		
Pyemotes sp.	Pyemotidae[A]				X		
Saproglyphus sp.	Saproglyphidae[P]	X	X			X	X
Schwiebia sp.	Acaridae[A]	X	X	X			X
Schizostethus lyriformis	Parasitidae[P]				X		
Tarsonemus ips	Tarsonemidae[A]	X					X
Tarsonemus krantzi	Tarsonemidae[A]		X				
Trichouropoda sp.	Uropodidae[P]		X		X		X
Trichouropoda denticulata	Uropodidae[P]						X
Trichouropoda hirsuta	Uropodidae[P]		X				X
Trichouropoda lamellosa	Uropodidae[P]						X
Uroobovella neoamericana	Uropodidae[P]		X				
Uroobovella orri	Uropodidae[P]		X	X	X		X

[a] Mite family: [A] Order Acariformes; [P]Order Parasitiformes

The strength and reliability of mutualisms greatly influence SPB dynamics. Palmer and others (2003) outlined three general factors that influence mutualism strength or specificity: 1. variability in the quality of alternative partner species, 2. the reliability/dependence of mutualist species, and 3. the effectiveness of partner selections. Thus, consistency is a key element of long-term mutualist associations, and mycangial fungi and the SPB is a good example (Klepzig and Six 2004). It is thought that the relative strength and importance of most mutualisms vary temporally and spatially with respect to the extent that they confer reciprocal benefit (Bronstein 2001). This implies that some level of context dependency is inherent in many mutualisms (Bronstein 1994), and in fact many species interactions in the SPB community range from mutualistic to commensalic to antagonistic, given varying sets of environmental conditions, resource quality, and presence of particular species (Klepzig and Six 2004). The relationship between the SPB and phoretic *Tarsonemus* provides an example: Tarsonemids phoretic on bark beetles carry weakly pathogenic fungi (*Ophiostoma* sp.) that are introduced to host trees during colonization by beetles. Fungi may aid beetles in overcoming tree defenses; however, they are generally antagonistic to beetle larvae and are actively avoided by the larvae and adults (Lombardero and others 2000c). In addition, context dependency is relevant to interactions between sympatric bark beetle species with a shared resource (e.g., *Ips avulsus* and SPB; Klepzig and others 2001a, 2001b), as interactions between species can also shift from mutualistic to antagonistic under varying conditions.

The classical view that mutualisms exist independently of other species and are bound by tightly evolved species interactions is being overturned in favor of the idea that many mutualist pairs act indirectly upon one another (Stanton 2003) and are influenced exogenously (e.g., temperature). Positive-species interactions are not always equally reciprocal (Bronstein 1994), and consequently, localized variations in fitness and fecundity for individual species potentially alter mutualism effects and ecological functionality. The relative ubiquity of mutualisms has consequences on SPB dynamics and resource capture, and speculation has arisen that mutualistic interactions play an equal role in shaping community structures, as do predation and competition (Berlow and others 2004, Hofstetter and others 2006a). The diversity and abundance of positive species interactions in the SPB community can facilitate complex interactions due to multiple mutualistic associations. Phoretic species and mutualists competing for access to the SPB is likely a very dynamic process that changes over both ecological and evolutionary time and at multiple spatial scales (Hofstetter and others 2006a, 2006b; Palmer and others 2003).

11.6. ACKNOWLEDGMENTS

This chapter is dedicated with gratitude to Dr. John C. Moser, whose extraordinary work with mites and other associates of bark beetles over his entire career has both driven and enriched the field of phoretic biology and bark beetle ecology.

12

Southern Pine Beetle Competitors

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Abstract

When southern pine beetles mass attack a living pine tree, if colonization is successful the tree dies and its phloem becomes immediately available to a complex of other bark beetles and long-horned beetles, all of which, in order to reproduce, compete for the new resource. In southern pines the phloem-inhabiting guild is composed of the southern pine beetle *Dendroctonus frontalis*; plus bark beetles in the genus *Ips*, *(I. avulsus*, *I. grandicollis*, and *I. calligraphus)*, as well as the black turpentine beetle, *D. terebrans*. In addition to these scolytid beetles, long-horned (cerambycid) beetles of several species, the most important being the pine sawyers (*Monochamus* species), also compete for their larval feeding sites in this temporarily available community. Because aggregation pheromones are the signal used by most of the bark beetles to locate and exploit the limited food source comprised by this newly found tree, it is likely that both intra- and interspecific competition among those arriving individuals will develop. As competition can negatively affect the fitness of all individuals, mechanisms to avoid or minimize competition will evolve. For the bark beetles these mechanisms include their systems of chemical communication (expressed through differences in timing and rate of arrival), variation in body size (and hence ability to use thicker and thinner phloem), gallery structure, oviposition, and larval feeding habits. When bark beetle and *Monochamus* larvae compete, the competition is highly asymmetric, meaning that *Monochamus* is not affected by the presence of the bark beetles, which can be greatly disadvantaged by the feeding of the much larger cerambycid larvae. Despite considerable research to document the existence of competition throughout the processes of attack, reemergence, oviposition, and larval development, the larger question of how competition influences southern pine beetle population dynamics remains uncertain.

Keywords

bark beetles
Cerambycidae
competition
population dynamics
Scolytidae

12.1. INTRODUCTION

The intent of this chapter is to describe the interactions among the complex of bark beetles and cerambycid beetles that are potential competitors for the transient resource of phloem tissue in beetle-killed southern pines. The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), may have to compete with members of its own kind, with other bark beetles, and with long-horned wood-boring beetle larvae (Cerambycidae), all of which require nutrition from a common resource, the newly available phloem in beetle-killed trees (Figures 12.1 and 12.2). The process of competition begins when adult SPB respond to a combination of host volatiles plus male and female SPB-produced pheromones and fly to the surface of a potential host pine. Mass attack, with resulting aggregation of thousands of male and female SPB at the surface of potential host trees, occurs over a period of 2-4 days (Coster and others 1977a). Females locate a site at which to begin boring through the bark, while males search for a fresh pitch tube leading to a gallery containing a female to join with and mate (Bunt and others 1980). Females then create galleries in phloem tissue and oviposit eggs that hatch and develop as larvae by feeding in phloem tissues. Additional species of bark beetles, primarily three *Ips* species, soon aggregate and also attempt to colonize the phloem, as do long-horned beetles in the genus *Monochamus*.

Southern pine beetles are called primary bark beetles because to successfully reproduce, adults must attack and colonize living pine trees (Coulson 1979). This requires that they overcome constitutive and induced tree defenses in order to kill those trees (Berryman 1972). They then create galleries in the healthy phloem tissue in which their eggs are laid and larval broods will develop. The colonization process is mediated by blends of pheromones that initially attract beetles but later discourage further colonization by additional members of their own species on successfully attacked trees and act to move attacking adults to new hosts (Raffa 2001, Wood 1982b). This process of regulating their own density on host trees is also important as a means to avoid competition with others of their own kind, for as Berryman and Pienaar (1973) suggest, bark beetles are especially subject to intraspecific competition because the adults produce aggregation pheromones to draw in large quantities of beetles to overcome resistance of host trees.

Competition, in the strict sense, is defined as occurring "when a number of animals… utilize common resources the supply of which is short; or if the resources are not in short supply competition occurs when the animals seeking that resource nevertheless harm one or another in the process" (Birch 1957). A more complete definition, adapted from Begon and others (2006) and Speight and others (2008), is that competition is an interaction among individuals having a shared requirement for a limited resource that leads to a reduction in survival, growth, and/or reproduction of the competing individuals, or through emigration or immigration causes their movement from the resource in question. The process of competition is often separated by whether the interactions occur among individuals of the same or different species. Competition among members of the same species is referred to as *intra*specific competition, and competition for resources with individuals from other species is termed *inter*specific competition. Competition among individuals can be further separated by the outcome of competing for limited resources. There are two extremes as to how this works: in one example food is in short supply; if you are first to arrive at the food, your presence will keep any others arriving at that food supply from becoming established and they won't be able to begin feeding. You will get all of the food you need to develop and reproduce, and those others will not get any. You win! At the other extreme there is a limited supply of food, and as individuals arrive and they all begin feeding, food becomes increasingly scarce as all grow and continue to feed. Few, if any, grow to full size, and many die before they can reproduce, and all suffer during this scramble for the limited food resource. The first example is termed "contest" or "interference" competition, and the second example is called "scramble" or "exploitation" competition (Begon and others 2006, Nicholson 1954).

Intraspecific competition among developing bark beetle larvae has been reported for multiple species in the genera *Dendroctonus* (Coulson and others 1976b, McMullen and Atkins 1961, Safranyik and Linton 1985), *Ips* (Anderbrant and others 1985, Light and others 1983), *Scolytus* (Beaver 1974, Berryman and Pienaar 1973), and *Tomicus* (Beaver 1974). Because density-dependent competition can result in lower brood weight and increased brood mortality, selective mechanisms to minimize such competition have also evolved (Byers 1989a, Raffa 2001).

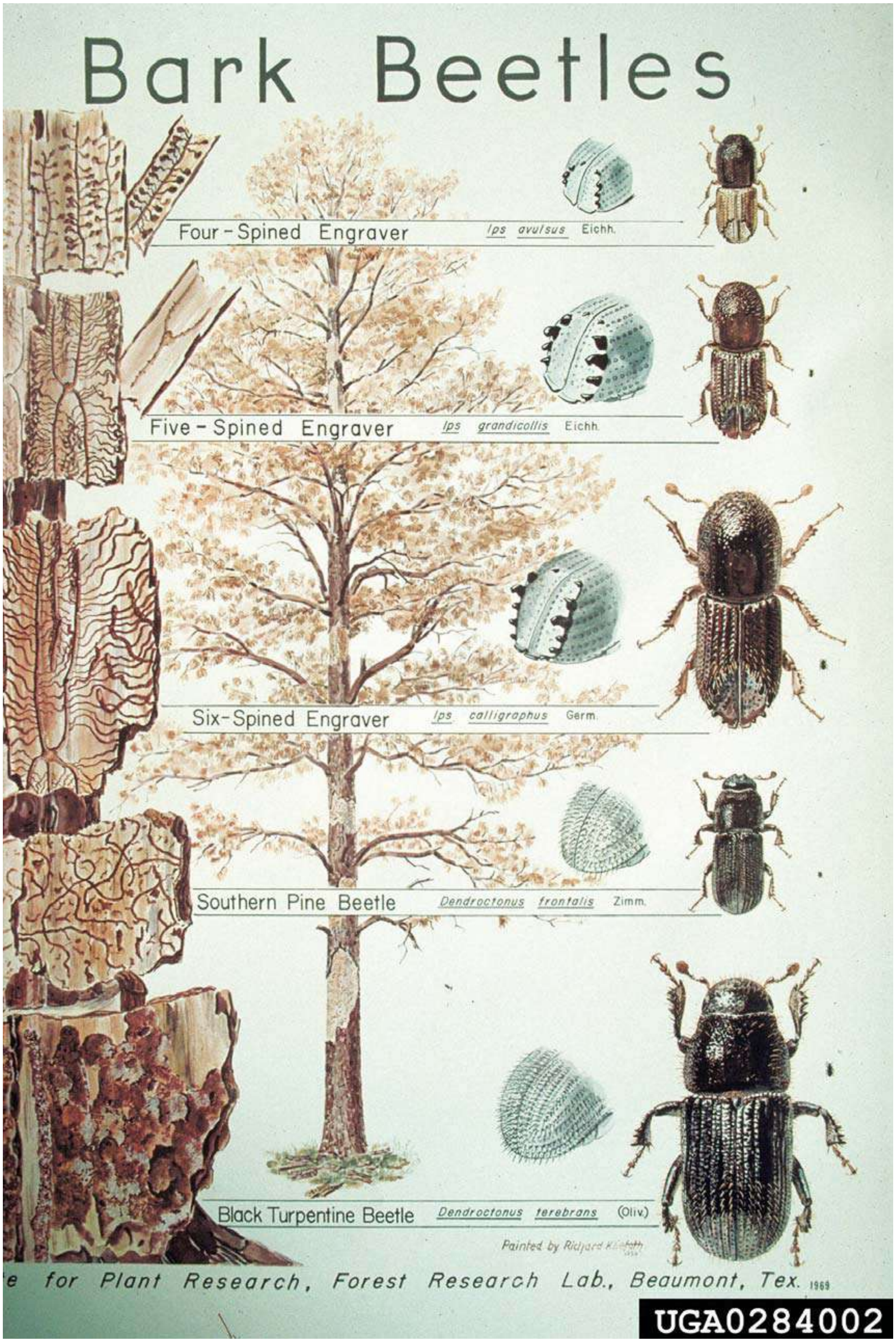

Figure 12.1—Classic painting, by Richard Kleifoth; Southern Forest Research Institute, of the southern pine bark beetle guild showing spatial preferences within trees, gallery patterns under bark, relative size, and elytral characteristics. (photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

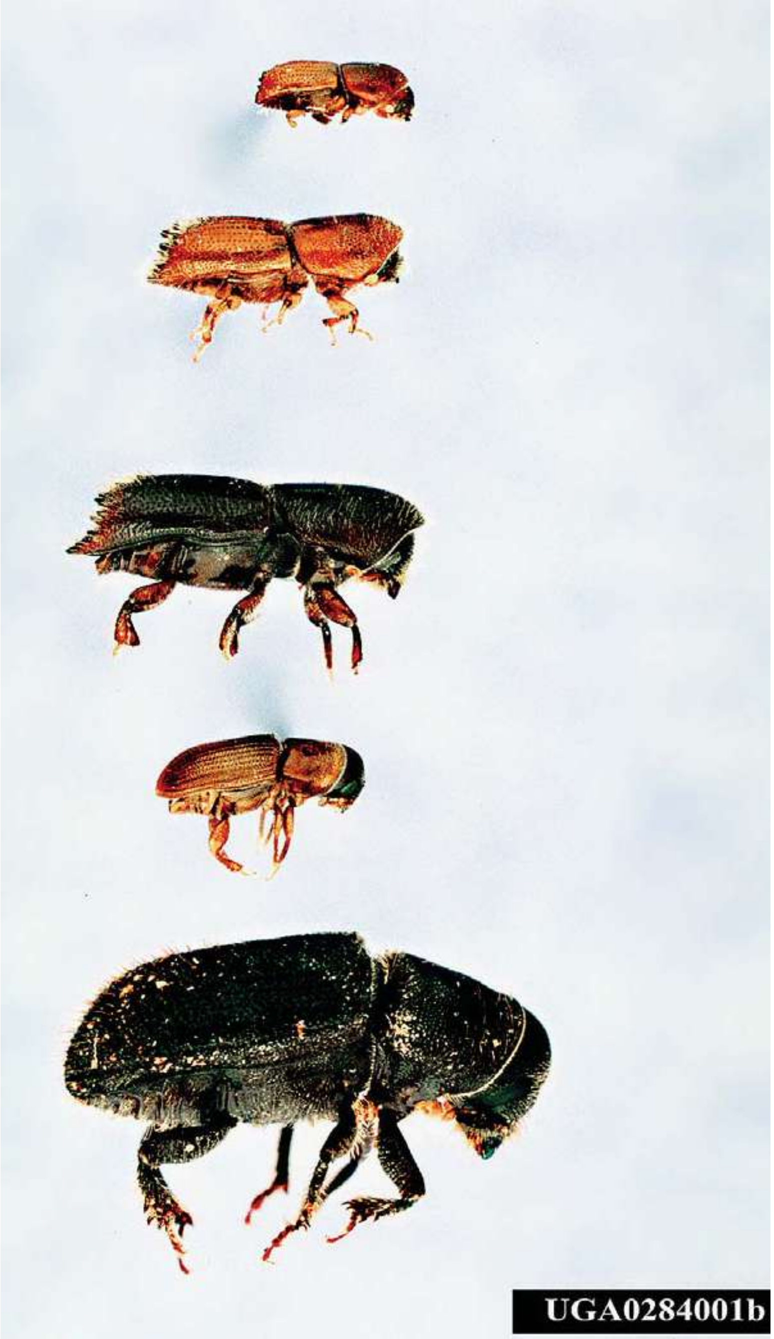

Figure 12.2—Adults of three species of southern pine engravers (top to bottom), *Ips avulsus*, *Ips grandicollis*, *Ips calligraphus*, plus the southern pine beetle, *Dendroctonus frontalis,* and the black turpentine beetle, *Dendroctonus terebrans*. Note relative size differences of each species, and the rounded elytral wing covers for the two *Dendroctonus* species. (photograph by Gerald J. Lenhard, www.forestryimages.org)

One interesting characteristic of competition for the phloem resource in bark beetle-killed pine trees is the fact that it exists not only as a fragmented landscape (Tscharntke and Brandl 2004), but also that the habitat is exceptionally transient. It exists only for a brief period in time and is continually degrading during that time. Within each generation bark beetles must accomplish several basic things that help to explain the selection pressures they face during host colonization. They must attract mates, colonize host phloem, minimize intraspecific and interspecific competition, and avoid natural enemies (Raffa 2001). Individual success depends on how well beetles are able to accomplish this. The process of mass attack and beetle aggregation results in important tradeoffs. If attacking adults do not arrive in adequate numbers, in a sufficiently short time, to overcome resistance of the host tree, the tree will survive and the attacking beetles will die in the process or be forced to abandon the attack and seek another host. However, as beetle aggregation densities become greater, and as more colonizers oviposit, their developing offspring will face greater and greater intraspecific competition. The most successful beetles, in terms of fitness, are those that colonize during the peak of mass attack (Pureswaran and others 2006), emphasizing the need for synchronous mass attacks on trees. Wagner and others (1985) speculate that although there is much potential for intense scramble competition among the bark beetle guild in southern pines, it is often not realized. They further suggest that the mechanisms that enable avoidance of competition are their systems of chemical communication (expressed through differences in timing and rate of arrival), variation in body size (and hence ability to use thicker and thinner phloem), and gallery structure, oviposition, and larval feeding habits. Southern pine beetle and *I. avulsus* are more similar in biology and resource utilization than the other two *Ips* species.

12.2. HOST COLONIZATION AND THE PHLOEM INHABITING GUILD ASSOCIATED WITH SOUTHERN PINE BEETLE

Southern pine beetle mass attack is the trigger for all species that follow (Figures 12.2 and 12.3). Dixon and Payne (1979b) found that 97 percent of SPB adults arrived within a 9-day period, with most arriving on the second (Bunt and others 1980) or third day (Coster and others 1977a). The colonization process is not uniform along the bole of the tree (Fargo and others 1978). Attacks by SPB begin about 3.5 m up the bole (Coster and others 1977a) and spread up and down from that height. Attack densities are highest in the mid-bole of the tree

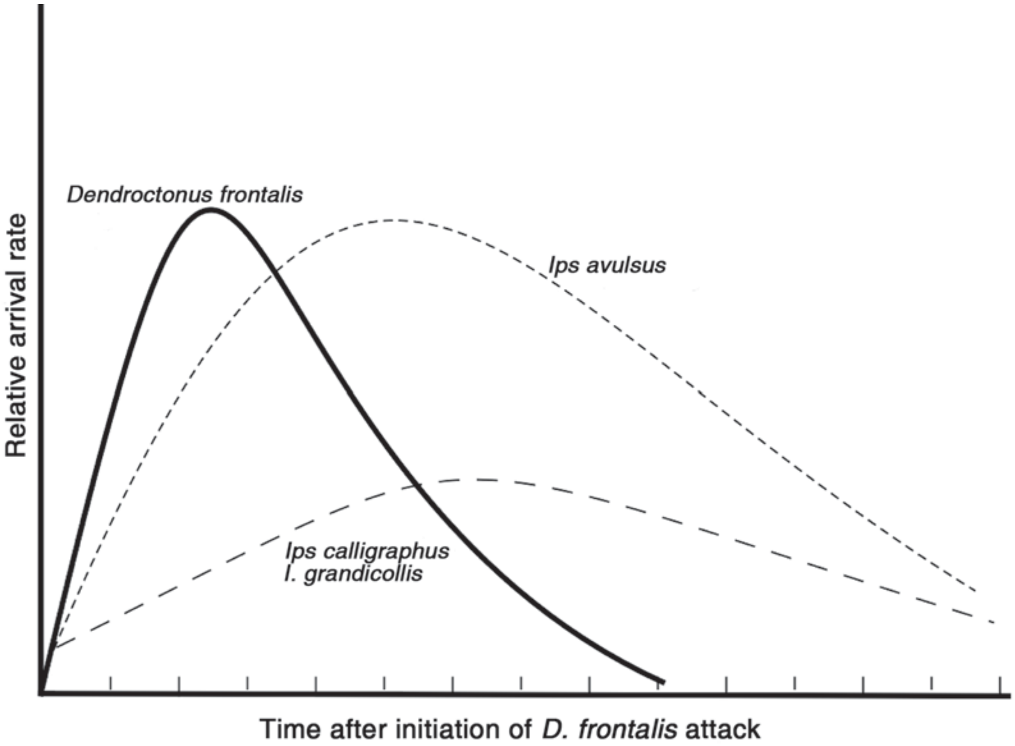

Figure 12.3—Generalized temporal patterns of arrival of *D. frontalis* and the southern pine engraver complex. (adapted from Berisford and Franklin 1971, Coster and others 1977a, Fargo and others 1978, Wagner and others 1985, Flamm and others 1987b, Stephen and others 1993)

and lower toward the top of infestation (Fargo and others 1978). Variation in SPB attack density is considerable, with average number of about 5 attacks/dm^2 (Stephen and Taha 1979b), but ranging from about 2 to 9 (Reeve and others 1998) or more (Lih and Stephen 1996, Stephen and Taha 1979b).

When bark beetles successfully overcome resistance of their pine host and begin the process of colonization, they initiate arrival, at the new host resource, of a procession of insect species that is predictable in time and space (Camors and Payne 1973, Dixon and Payne 1980, Stephen and Dahlsten 1976, Stephen and others 1993). This complex includes predators and parasitoids of the colonizing bark beetles, plus phytophagous competitors for the newly available phloem resource and a rich variety of other species that are scavengers, detritivores, and secondary natural enemies. Southern pine beetle will be followed in a short time by well over 100 insect species (Dixon and Payne 1979b), and a significant number of these may compete for phloem with the newly established SPB larvae. The competitors are primarily found in two groups: other bark beetle larvae,—the Scolytidae, and long-horned wood-boring beetle larvae—the Cerambycidae (Dodds and Stephen 2002, Flamm and others 1989, Paine and others 1981, Stephen and others 1993, Wagner and others 1985).

Birch and others (1980) demonstrated that olfactory communication occurred among SPB and the three *Ips* species of the southern pine bark beetle guild. The most aggressive of the species, SPB does not respond to the pheromones of the *Ips* complex, but at varying levels all of the *Ips* species do exhibit interspecific response to the pheromones of their guild members, and *I. grandicollis* can also respond to SPB pheromones (Figure 12.4). These olfactory interactions are important in enabling full exploitation of beetle-killed trees in a transitory habitat, and undoubtedly are important in defining competition among the species.

12.2.1. Scolytidae

Southern pines attacked and killed by SPB may be colonized by up to 16 additional bark beetle species (Dixon and Payne 1979b). A guild of five species is most likely to share and at times compete for the phloem required by all for successful development (Berisford 1980, Paine and others 1981). Three southern pine engravers, species in the genus *Ips* De Geer, frequently arrive shortly after SPB attacks (Figure 12.2). Both *I. avulsus* (Eichhoff) and *I. grandicollis* (Eichhoff) were trapped during SPB mass attack, but the peak arrival of the two species was 12 and 18 days, respectively, after the initiation of mass attack (Dixon and

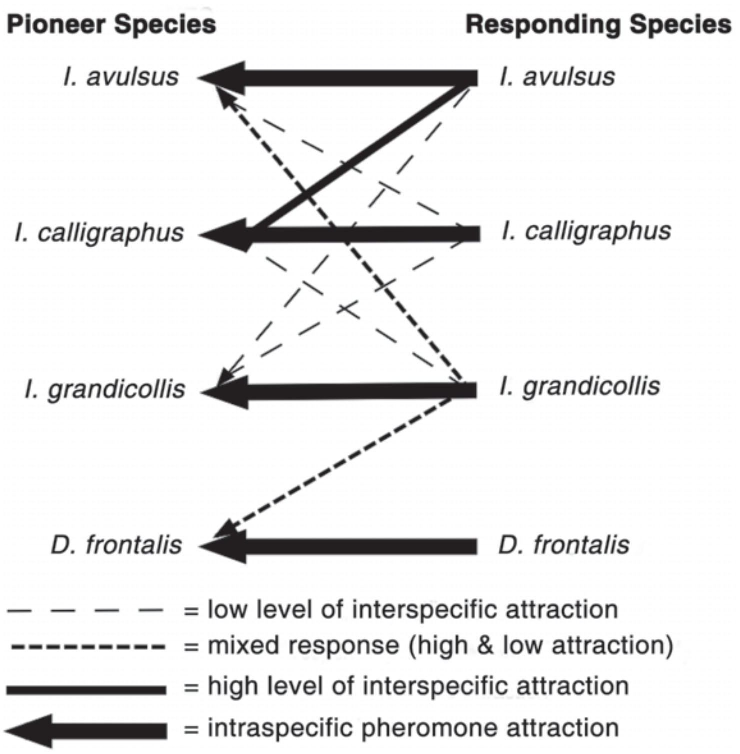

Figure 12.4—Summary of interspecific attraction within the southern pine engraver guild and SPB. A pioneer species produces pheromones as individuals of that species arrive at host resource. A responding species may respond to pheromones of one or more of the pioneer species. (abstracted from data in Table 9, Birch and others 1980, and Figure 8, Byers 1989a)

Payne 1979b). *Ips calligraphus* (Germar) was also observed on trees at the time of mass attack, but greatest abundance was about 3 weeks following initial SPB attack (Dixon and Payne 1979b). The southern pine engravers are considered secondary bark beetles, and although they are less aggressive than SPB, when trees are damaged or stressed and when pine engraver populations are sufficiently high, they have been implicated in killing trees (Conner and Wilkinson 1983, Hetrick 1942). It is uncommon for any of these species to attack healthy undamaged pines, but once host resistance has been overcome by SPB mass attack, *Ips* arrive quickly to compete for the available phloem. All three species will successfully develop in just about any species of southern pine (Conner and Wilkinson 1983), and unlike SPB, the *Ips* complex will colonize and can produce high populations in wind-thrown trees, logging slash, and logs stored in pulpwood or sawmill yards (Hetrick 1942).

Where do background populations of beetles arise? Coulson and others (1986) have shown the importance of lightning in the ecology of SPB, and it is evident that lightning-struck trees are an important resource not only for SPB, but also for *Ips* species. These trees also remain as potential hosts for relatively long periods of time (Flamm and others 1993). Logging operations and thinning of stands can injure trees and provide slash in which *Ips* populations can build (Hetrick 1942), but little in the way of quantitative or predictive information exists that relates such conditions to changes in abundance of bark beetle populations or their competitors. In comparisons of epidemic and endemic SPB infestations, Hain and McClelland (1979) found higher *Ips* and *Monochamus* populations in nonexpanding SPB plots in the North Carolina Piedmont. They further suggest that *Ips* are more closely associated with SPB in these endemic plots. *Ips* frequently attacked trees first in these small infestations, and the infestations quickly died out.

Southern Pine Beetle

Intraspecific competition among SPB individuals can occur at different times in their life cycle. Adults arriving during mass attack must 1. locate suitable sites on bark to initiate attack, 2. attract a mate, and 3. create maternal galleries in which to oviposit and then frequently reemerge to colonize new trees. Larvae feed and develop through four instars in phloem, a potentially limited resource.

The chemical communication system of SPB enables mass aggregation of males and females at trees that are initially attacked by pioneer beetles. The chemicals involved and the sequence of events are described in detail by Payne (1980) among others, and Sullivan and others (2007b). A blend of beetle-produced pheromones, in combination with *alpha*-pinene released by the host tree, attracts both sexes of the beetles in numbers sufficient to overcome tree resistance (Sullivan and others 2007b). Thus adult SPB cooperate to kill the tree, but since the tree's phloem resource is limited, competition between developing brood will become intense if beetle density is too high. Following successful colonization and as densities of attacks begin to mount, male beetles produce verbenone and *endo*-brevicomin, which function as antiaggregation compounds and terminate the mass attack on that specific host (Sullivan and others 2007b), thus providing a mechanism to minimize competition (Byers 1989b). Those beetles that arrive early in the attack process encounter more of the tree's defenses but more rapidly gain access to the phloem resource, while those arriving later in the attack sequence encounter fewer defenses but greater intraspecific competition. Those that arrive during the peak of mass attack, neither too early nor too late, appear to maximize fitness of their offspring (Pureswaran and others 2006, Raffa 2001).

Bark beetles can be classified into two fundamentally different models of life history strategy related to their colonization of hosts (Raffa 2001). Under the first strategy, cooperation and competition, such species as SPB attack healthy trees with resin defenses that are capable of killing entering beetles, and thus require cooperative efforts via mass attack with many conspecifics to overcome host tree resistance. However, beyond some optimal colonization density, competition occurs. For the second strategy, competition only, species such as the southern pine engravers (*Ips* spp.) colonize dead or dying hosts that cannot resist invading beetles. Under this scenario increasing colonization density results in decreased fitness for the average female. The competitive interactions related to colonization density, and expressed as a measure of beetle fitness, are adapted from Raffa (2001) and illustrated in Figure 12.5.

The process of adult SPB constructing galleries and ovipositing eggs also is related to the density of the attacking population. Coulson and others (1976b) found that the total gallery per unit of phloem area was independent of the density of attacking beetles, while Reeve and others (1998) reported that total gallery and egg density per unit of phloem area is positively related to increased attack density. However, both of these studies reported that as SPB attack density per unit area increased, the amount of gallery constructed and numbers of eggs per female decreased (Coulson and others 1976b, Reeve and others 1998). However, effects of temperature may influence numbers of eggs per female produced at different densities, as Wagner and others (1981a) found that beetles emerging in February showed a greater tendency to an exponential decrease in eggs per female with increasing density than did females who emerged between May and September. Female beetles turn their galleries as density increases, thus dispersing galleries more evenly in the phloem resource and avoiding interaction with other females (Wagner and others 1981a). These adaptations can be interpreted as means to minimize intraspecific competition.

Reemergence of parent adults is common with many bark beetle species and may be of

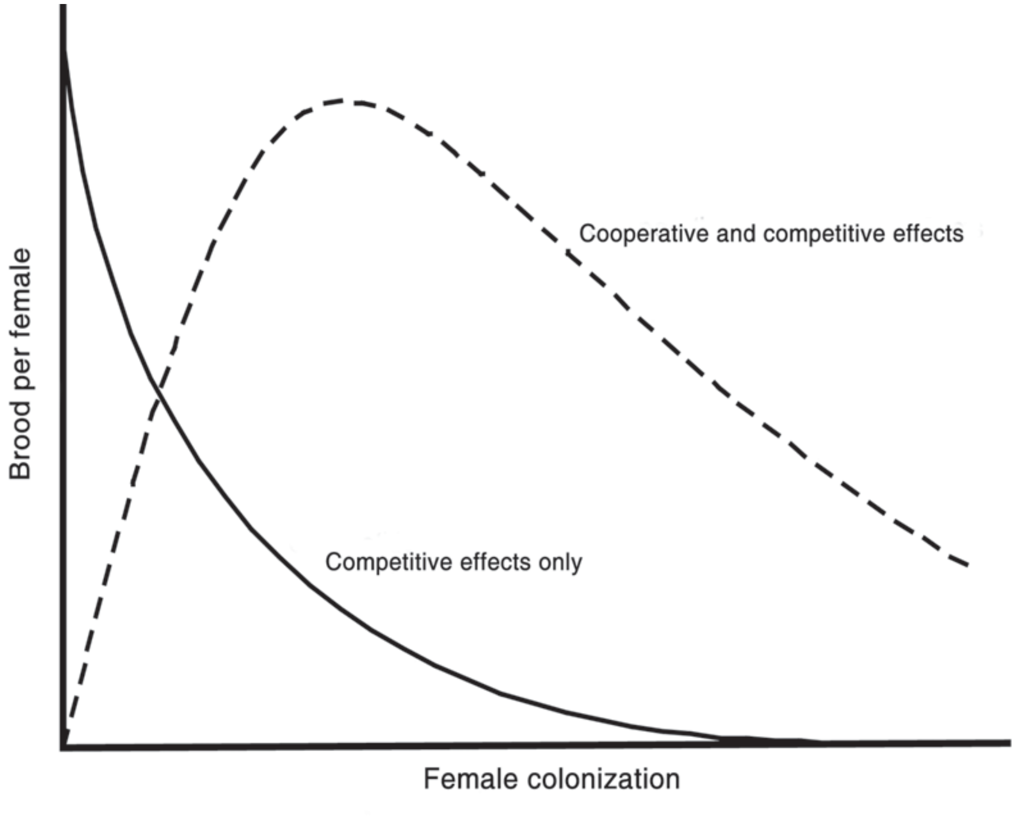

Figure 12.5—Proposed model of the effects of aggregation on individual beetle fitness, adapted from Raffa (2001). The solid line illustrates the hypothetical effects on numbers of females produced per female with bark beetle species such as the complex (*Ips avulsus*, *I. grandicollis* and *I. calligraphus*) in which, when dead hosts are colonized, only competition for a limited substrate exists. The dashed line is proposed as a model for species such as *D. frontalis* in which some competitive effect exists across all densities and beetle aggregation is required to kill a living host, but beyond that threshold density, increasing colonization results in increased competition for the available phloem resource.

special importance in the population dynamics of SPB (Coulson and others 1978). In addition to providing more adults to the pool of beetles that attack and colonize new trees, they can be responsible for contributing to pheromone production that keep beetles within the confines of a "spot" and focuses new attacks on adjacent trees in rapidly expanding infestations (Coulson and others 1978). It is clear that variation in reemergence does occur. Cooper and Stephen (1978) sampled beetles during 6 months of the year and found an average of 65 percent reemerging beetles (range of 9.3-83.0 percent), while Coulson and others (1978) reported more than 90 percent reemergence of parent beetles. Although studied in considerable detail, this process remains not fully understood (Coulson 1979). Variation in density of the attacking adult population does influence the rate of reemergence, as Coulson and others (1978) report that reemergence will be faster at high densities than at low densities because females complete oviposition sooner at high densities, in that they lay fewer eggs and thus leave the tree faster. This could be a component of the overall mechanisms to avoid intraspecific competition through effective resource utilization (Coulson and others 1976b).

The importance of intraspecific competition in relation to larval development and survival has been discounted (Coulson 1979) owing to the process of females regulating their egg density as a function of attacking adult density, thus optimizing use of the available resource. Reeve and others (1998), however, based on data from a study in East Texas, suggest that in naturally attacked trees strong intraspecific scramble competition can exist during brood development, and results in significant decreases in brood survival and the ratio of increase. They conclude that attack densities above six per 100 cm^2 (occurring about 23 percent of the time in their study) will result in increased brood mortality from intraspecific competition. The mechanism for this increased mortality was not determined, and no data were collected on causes of mortality, but they did suggest a possible impact from high levels of blue stain fungi (*Ophiostoma minus* [Hedgc.]), which is variable in abundance but an important antagonist with the mutualistic fungi that benefit larval acquisition of nutrients from phloem tissues (Hofstetter and others 2006a). In their study the impact of *Monochamus* larvae was not found to be a significant mortality factor (Reeve and others 1998).

Black Turpentine Beetle, Dendroctonus terebrans

An additional member of the guild, *Dendroctonus terebrans* (Olivier) the black turpentine beetle, is found mostly in the basal 1 m of stem phloem. Because the adults respond to host resins and volatiles, black turpentine beetle is found frequently in stumps or pines injured during logging operations (Fatzinger and others 1987). It does show a preference for weakened trees or those damaged by fire, and although it frequently reproduces without causing significant damage to living trees, it is a species that is capable of killing healthy pines (Smith and Lee 1972). It is the largest beetle of the complex, about 10 mm in length (Figure 12.6). Adults can colonize and live in resinous phloem, and their attacks frequently produce large white and reddish pitch tubes with a distinct hole in the center (Fatzinger and DeBarr 1969). Eggs are laid in a single long cluster at the margin of a single gallery, and larvae feed gregariously, consuming phloem and creating a large cave-like gallery. Development may take 3-4 months, and pupation occurs in cells at the face of the inner bark. Development occurs throughout the year in the Deep South (Smith and Lee 1972). Black turpentine beetles primarily occur in the basal regions of the tree, and thus it is likely that competition with SPB is minimal (Berisford 1980).

The Ips Complex

Identification and descriptions

In the Southeastern United States three bark beetle species in the genus *Ips* are collectively termed southern pine engravers. These species all have the characteristically hollowed-out scoop in the top of their wing covers (elytra) with spine-like protuberances along the margins (Figure 12.2). The beetles differ significantly from each other in size and to some degree the portions of the tree that they inhabit. *Ips avulsus*, the small southern pine engraver, is the smallest of the three species, ranging in length from 2.1 to 2.8 mm, with four spines along the margins of their elytra. The elytra of *I. avulsus* are usually lighter brown in color than their thorax (Conner and Wilkinson 1983). *Ips grandicollis*, the eastern five-spined engraver, is 3.1-4.3 mm long and named for the number of spines along its wing covers. *Ips calligraphus*, the eastern six-spined engraver, is the largest of the group, ranging from 4 to 6 mm long. The relative differences in size and body shape are evident (Figure 12.2).

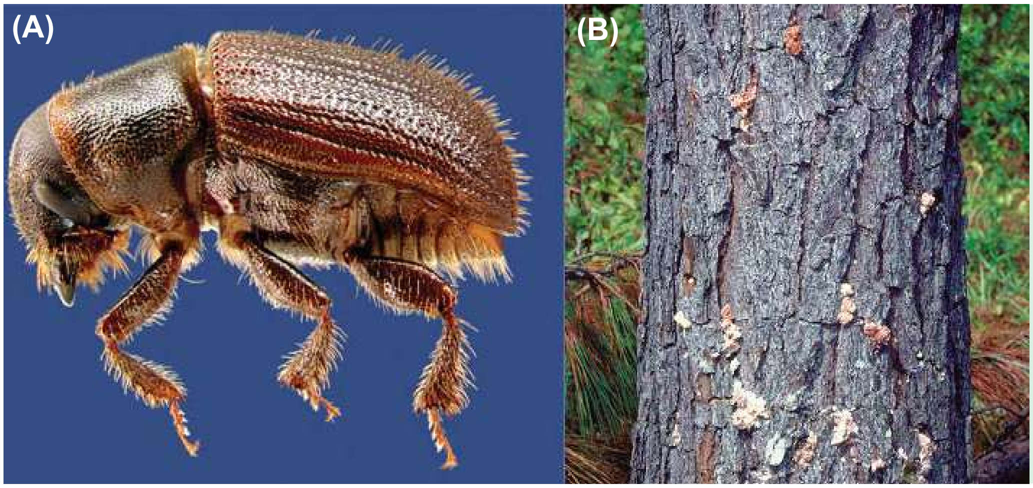

Figure 12.6—(A) Side view of black turpentine beetle, *D. terebrans* (Olivier), taken using an Auto-Montage digital microscopy system. (Photograph by David T. Almquist, University of Florida, www.forestryimages.org). (B) Basal region of a southern pine showing pitch tubes from black turpentine beetle attacks. (photograph by Lacy L. Hyche, Auburn University, www.forestryimages.org)

Within-tree distribution

A general representation of the spatial patterns of occurrence within trees, showing separation and overlap among these species, is illustrated in Figure 12.7. *Ips avulsus* has the widest niche, occurring from the thin phloem regions in the top of the crown, down through the mid-bole regions. It occurs at highest densities in the upper and mid-bole. *Ips grandicollis* is normally considered less aggressive than the other two species and not as much of a threat to healthy trees as either *I. avulsus* or *I. calligraphus* (Berisford and Franklin 1971). Although *I. grandicollis* may occur primarily in the upper bole, it can, like *I. calligraphus*, occur throughout most of the tree bole. Densities and spatial occurrence of both species vary greatly within trees (Wagner and others 1985). Paine and others (1981), investigating division of resources, niche breadth, and niche overlap, concluded that *I. avulsus* has the broadest niche breadth and *I. grandicollis* the narrowest. The upper bole is dominated by *I. avulsus* and the lower to mid-bole by SPB, which overlaps extensively with *I. calligraphus*. The greatest degree of overlap among the species is in the mid-bole regions (Paine and others 1981).

The spatial patterns of host colonization within trees by the southern pine bark beetle guild have been well described (Flamm and others 1987b, Paine and others 1981, Wagner and others 1985). What is more difficult to describe, and what is evident when sampling populations of these insects in field situations, is the high degree of variation in abundance and distribution that does occur in infested trees. Individual SPB infestations vary greatly in regard to species composition and abundance of the *Ips* guild. Seasonal phenology may be important, as is the background level of slash, logging debris, and other sources in which populations of *Ips* species reproduce and become abundant. The size of an SPB infestation and, by inference, the length of time in which SPB populations have been expanding in an area, can also influence the background population level of natural enemies, including *Monochamus* and the *Ips* guild. Source populations of SPB and *Ips* species must influence the initiation and outcome of competition. If background populations of SPB are sufficiently high, individual trees are colonized very rapidly (Flamm and others 1993); however, if SPB populations are sparse or distant from the tree being colonized, then the attack process will be slower and utilization of available phloem may be less complete, leaving more available resources for *Ips*. It is safe to say that despite the extensive research that has been completed, further studies should be directed toward understanding the simultaneous dynamics of these interacting factors.

Colonization and arrival patterns

Berisford and Franklin (1971) described the attack patterns of *I. avulsus* and *I. grandicollis* in four species of felled southern pines. Arrival of *I. avulsus* was more concentrated, occurring within a 5-7 day period, while *I. grandicollis* showed attacks extended over 30-50 days (Berisford and Franklin 1971, Flamm and others 1987b). This may be due to the more aggressive nature of *I. avulsus*, which frequently attacks and kills tops and limbs of live pines, while *I. grandicollis* often colonize slash and trees in a very weakened condition (Berisford and Franklin 1971). Each of these species, with the exception of *I. calligraphus*, colonizes less area than expected when in the

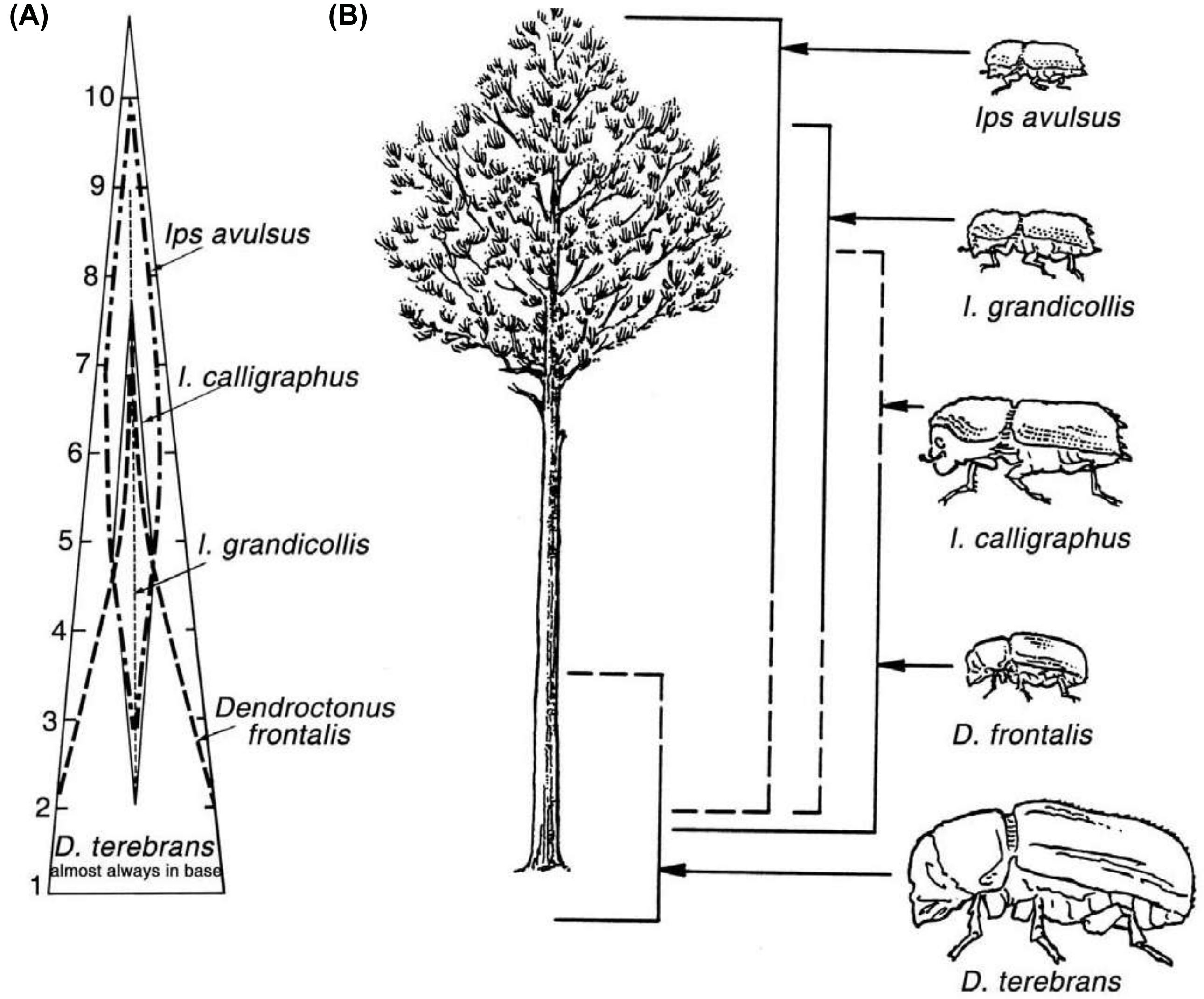

Figure 12.7—Two views of bark beetle guild spatial distribution within southern pines. (A) Diagram illustrating the approximate proportion of the tree bole occupied by the different species of the SPB guild. (adapted from Birch and Svihra 1979). (B) Different perspective of the same colonization patterns (redrawn from Wagner and others 1985), showing the different species and their relative spatial distribution. Probability of species occurrence is highest where indicated by solid lines.

presence of others, with *I. grandicollis* being most affected. Flamm and others (1987b) also report variation in the temporal patterns of attack by the *Ips* species following SPB mass attack. Although *I. calligraphus* is the first to follow SPB in most trees, *I. avulsus* shows the most concentrated attack pattern in others. A generalized illustration of the temporal arrival rates of SPB and the *Ips* complex adapted from multiple studies and Figures 7.5 and 7.6 in Stephen and others (1993) is shown here in Figure 12.3. Although not discussed in the published literature, it is likely that relative abundance of source populations in the vicinity of trees being colonized will also influence the rate of arrival of the different *Ips* species.

Feeding habits

Galleries of the *Ips* species are Y- or H-shaped, resulting from attacks initiated by males that are joined by one to four females, each of which constructs an egg gallery originating from the central nuptial chamber (Conner and Wilkinson 1983). Most egg galleries follow the wood grain. *Ips calligraphus* (Figure 12.8C) and *I. grandicollis* (Figure 12.8D) are more similar to each other than to *I. avulsus* or *D. frontalis*. The egg galleries emanate from a central nuptial chamber, with eggs oviposited in niches along the galleries, but the larval mines are elongate and often parallel in orientation. Both *I. calligraphus* and *I. grandicollis* are nonmycangial bark beetles that as larvae consume greater quantities of phloem than do mycangial species to compensate for the fact that they do not acquire nutrition from their fungal symbionts (Ayres and others 2000). It has been speculated that they would be at a disadvantage when phloem resources are limited and would be less able to compete with species such as SPB that acquire nitrogen from their fungal symbionts (Ayres and others 2000). Examination of the larval feeding gallery patterns of SPB in comparison with *I. calligraphus* and *I. grandicollis* (Figures 12.8 and 12.9) clearly show the extent of larval feeding differences. The egg galleries of Figure 12.8A are sinuate and may cross other galleries, and the larval mines, when in presence of mycangial fungi, are short and terminate in broad feeding cells. It is interesting to note that larval gallery foraging patterns of *I. avulsus* are much more similar to SPB than to either *I. calligraphus* or *I. grandicollis*. They are described as short galleries (4-8 mm) that terminate in broad feeding cells (Wagner and others 1988b). Within larval feeding cells is a white fungus, previously reported by W. C. Yearian and R. J. Gouger (see Klepzig and others 2001b), that may be a species of *Entomocorticium*, on which the larvae apparently feed (Klepzig and others 2001b). Although the larvae do not feed extensively on phloem and have a feeding cell similar to that of SPB, *I. avulsus* do not have a mycangium (Gouger and others 1975). The fact that *I. avulsus* have symbiotic fungi that aid in the acquisition of nutrition may enable it to be a more successful interspecific competitor than its two *Ips* cousins. This idea is supported by data from Gouger and others (1975), who report that *I. avulsus* feeds primarily on liquids, has almost no solids in its gut, and feeds extensively on ascospores of *Ophiostoma* (=Ceratocystis) *Ips* (Rumbold) Nannf. It was also determined that *I. avulsus* immatures are associated with nitrogen-fixing bacteria, but the significance of that was not established (Bridges 1979). It has been shown, however, that *I. avulsus* is able in the laboratory to complete multiple generations without *O. ips*, but adults are smaller and

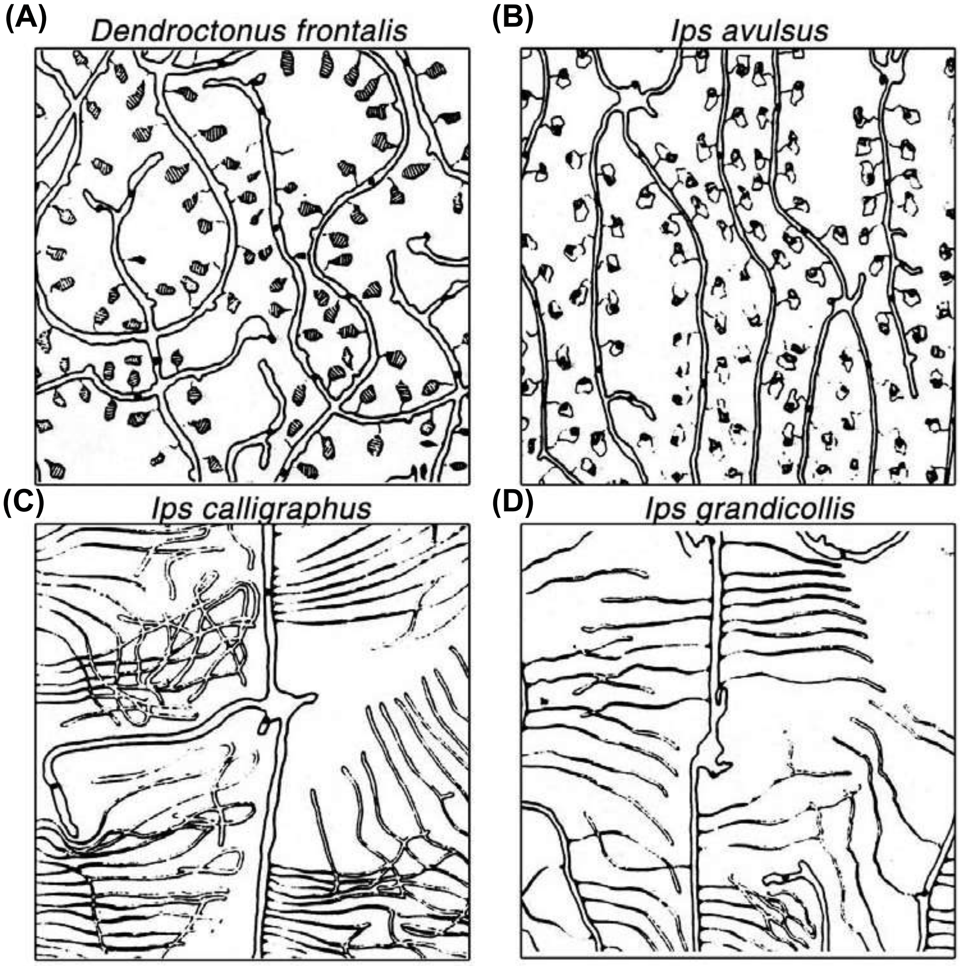

Figure 12.8—Typical southern pine bark beetle gallery patterns in subcortical pine phloem showing nuptial chambers, egg galleries, and larval mines arising from oviposition sites along the egg galleries. (adapted from Wagner and others 1985)

Figure 12.9 — Photographs showing differences between (A) *Ips calligraphus* and (B) *Ips avulsus* nuptial chambers, adult oviposition galleries, and larval mines in loblolly pine phloem. (photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

development is slower (Yearian and others 1972). Development time for *I. avulsus* at a constant temperature of 20 °C was about 2 months, but was only 2 weeks at 35 °C, the fastest of any of the southern pine bark beetle guild (Wagner and others 1988b).

Although the nutritional composition of thick and thin phloem is not well understood, *I. calligraphus* is influenced by the thickness of phloem within their host trees (Haack and others 1987a). In thick phloem of slash pine it lays more eggs per day, and its offspring develop faster than in thinner phloem. If beetle adults are in thin phloem they will oviposit rather than reemerge, but fewer eggs will be laid and more females are produced. The length of time to reemergence is not affected by phloem thickness (Haack and others 1987a). Cannibalism among larvae of *I. calligraphus* was shown to be a significant mortality factor (Wagner and others 1987), and as egg density increased, so did cannibalism. At optimal temperature for development, with higher brood densities, mortality from cannibalism averaged about 35 percent. The authors speculate that at higher brood densities, cannibalism in this species is also higher because of longer larval galleries and greater phloem area foraged.

Seasonal patterns

How important is seasonal phenology in regard to host utilization and relative growth of competitor populations? The pattern of SPB phloem colonization and utilization changes seasonally in that less of a bole is colonized during midsummer in epidemic situations (F. M. Stephen, unpublished). Maximum height of SPB infestation decreases in midsummer periods, and *Ips* populations may colonize this unclaimed resource, which may influence population buildup of *Ips*. Wagner and others (1988b) report that all of the southern *Ips* species develop faster than SPB at temperatures above 22 °C, and that their optimum development is between 34 °C and 37 °C, which is significantly higher than the optimum of SPB (30 °C). The *Ips* also appear more tolerant of high temperatures than do SPB, and the authors speculate that this is in keeping with observed decreases in SPB population growth during hot summer periods and simultaneous increases in *Ips* populations.

12.2.2. Cerambycidae

Multiple trapping studies have reported collection of a variety of Cerambycidae at SPB-infested southern pines, and limited information on their diversity and arrival at these pines has been published (Dixon and Payne 1979b, Dodds and Stephen 2002, Moser and others 1971, Overgaard 1968). The most common species are *Monochamus titillator* (F.), *M. carolinensis* (Olivier), *Acanthosinus obsoletus* (Olivier), *A. nodosus* (F.), *Xylotrechus* spp. and

Arhopalus rusticus obsoletus (Randall) (Dodds and Stephen 2002). Although a diverse number of species of cerambycids colonize pines killed by SPB, *Monochamus* species appear to be the most potentially important bark beetle competitor.

Monochamus titillator and M. carolinensis

Long-horned wood-boring beetles in the genus *Monochamus* Megerle, 1821 (Coleoptera: Cerambycidae) are important as secondary invaders of conifers worldwide (Cesari and others 2005), in that their larval galleries degrade timber, and some species vector pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer), a serious pest of pine in Europe and Japan (Evans and others 1996). In the Southeastern United States two species are commonly found in SPB-killed pines: *M. titillator* (F.) and *M. carolinensis* (Olivier) (Figure 12.10). These species are similar in life history and appearance—both are long-horned beetles, mottled gray-brown in color as adults, and range from about 17 mm to 30 mm in size. Although considered the same species by some, they have been taxonomically differentiated based on the shape of their elytra (Dillon and Dillon 1941).

Alya and Hain (1985) describe the life history of both species in the Piedmont of North Carolina. *Monochamus carolinensis* was more abundant in their study, but in most other reports from the Southeastern United States, *M. titillator* predominates. Flight period for both species was from late May through mid-October, with the predominate catches occurring from late May through July. Development times for each species varied greatly, with some individuals developing in less than 3 months and others (approximately 85 percent of the population studied) overwintering and emerging late in the following spring. Both Alya and Hain (1985) and Dodds and Stephen (2000) report most emergence as occurring in spring and early summer, and suggest there are frequently two generations per year.

Following successful SPB mass attack, *Monochamus* species arrive on infested trees, attracted by host volatiles (turpentine and ethanol) (Fatzinger and others 1987) and frequently by a kairomonal response to pheromones of the bark beetle guild (particularly ipsdienol, ipsenol, and *cis*-verbenol) produced by colonizing *Ips* species (Billings and Cameron 1984, Billings 1985). A significant response was found to a mix of SPB inhibitor (verbenone + *exo*-brevicomin + *endo*-

Figure 12.10—Long-horned wood-boring beetles (A) *Monochamus carolinensis* (Olivier) and (B) *M. titillator* (Fabricius). (photograph by Natasha Wright, www.forestryimages.org)

brevicomin) plus the *Ips* attractant noted above, and to a significant but lesser extent to a mix of SPB attractant (frontalin + *trans*-verbenol + pine turpentine) and SPB inhibitor (verbenone + *exo*-brevicomin + *endo*-brevicomin) (Billings and Cameron 1984).

It was noted that with felled pines, most were attacked by *Monochamus* within 7 days (Alya and Hain 1985). Dodds and Stephen (2000) observed that *M. titillator* arrived shortly after SPB mass attack, and on some trees *Monochamus* oviposition pits had fresh resin flowing from them. This suggests the possibility of much greater overlap in resource utilization than described in most other studies.

Hennier (1983) found some tendency toward a bimodal distribution of *M. titillator* oviposition pits, but could not reject the hypothesis of a uniform distribution along the bole of the trees sampled. Lower numbers of oviposition pits were noted toward the base of the tree, and larger trees had more oviposition pits. The length of the oviposition period was about 10 days (Thatcher 1960). Density of pits and numbers of eggs were found to be uniform at all tree heights, and may be a way of avoiding cannibalism. Adults chew oviposition pits in the bark and females oviposit a variable number of eggs in each pit (one to three for *M. carolinensis* and three to six for *M. titillator* (mean of 3.3 reported by [Hennier 1983]) (Figure 12.11). Incubation of eggs varies from 5 (Webb 1910) to 7 or 9 days (Alya and Hain 1985). Larvae feed in the phloem for about 18 to 32 days, then begin sapwood excavation, but will return to phloem for additional feeding (Webb 1910). Under laboratory conditions, at a constant temperature of 30 ^{o}C, development averaged 49 days (Linit 1985). Hennier's data suggest that initial oviposition occurs about 3.5 m up the tree bole; however, these trees were baited at that height with *Ips* pheromones. She also found maximum foraging, which averaged about 20 percent, in the mid-bole region (5-8 m) where bark beetle densities are also highest. The rate of foraging increased over time and was about 3.7 cm^2/day on day 26.

Coulson and others (1976a) demonstrated conclusively that *M. titillator* does significantly reduce survival of SPB when the two are coincident and concluded that interspecific competition does occur (Figure 12.11). While it is clear that the cerambycid can have an extremely negative effect on SPB, it is unlikely that SPB have a negative impact on *Monochamus*. This is a good example of asymmetric competition, commonly found in interspecific interactions (Denno and others 1995). In the most extensive study published on this competitive interaction, Coulson and others (1980a) report that on average about 20 percent of the infested phloem area of trees was foraged by *M. titillator*, and on the basis of an average tree, mortality to SPB was 14 percent. However, they also found that in the specific areas where *M. titillator* foraged, mortality averaged about 70 percent. Exclusion of *Monochamus* species from caged bolts containing *Ips calligraphus* resulted in significantly higher emergence of bark beetles compared with exposed controls (Miller 1986). Miller also estimated that subcortical foraging by *Monochamus* larvae accounted for about 50 percent of *I. calligraphus* mortality, while other natural enemies contributed an additional 38 percent mortality (Miller 1985). In that same study he reported that *Monochamus* foraging caused significant mortality to other insect predators of the *Ips* larvae.

The impact of *Monochamus* on bark beetle populations appears highly variable. In some studies cerambycid populations may be at sufficiently low levels as to cause minimal impact. While examining the impact of intraspecific competition on SPB brood survival, Reeve and others (1998) reported that mortality attributed to cerambycids was not statistically significant. Dodds and Stephen (2000) report *M. titillator* emergence densities up to 30/m^2 of bark surface. They also state that *M. titillator* midstage larvae were sampled at 20 days post attack, and at that time SPB was found in stages of development from midstage larvae to pupae. They also report that at 20 days post-attack by *M. titillator*, the cerambycid larvae were the most prolific phloem feeders, consuming large areas of phloem within infested trees, and they conclude that because of the timing of SPB and *M. titillator* arrival on host trees, it is probable that there was significant interspecific interactions occurring in phloem of host trees (Dodds and Stephen 2000). They found about 43 midstage *M. titillator* per sq m of bark (0.43/100 cm^2), and during midstage *M. titillator* development, SPB development in those trees varied from mid-larvae to pupae, with the majority being late-larvae. Research in North Carolina studying endemic, small SPB infestations reported that of 12 small infestations "with active SPB brood that were located, all but one were overtaken by cerambycid foraging, and

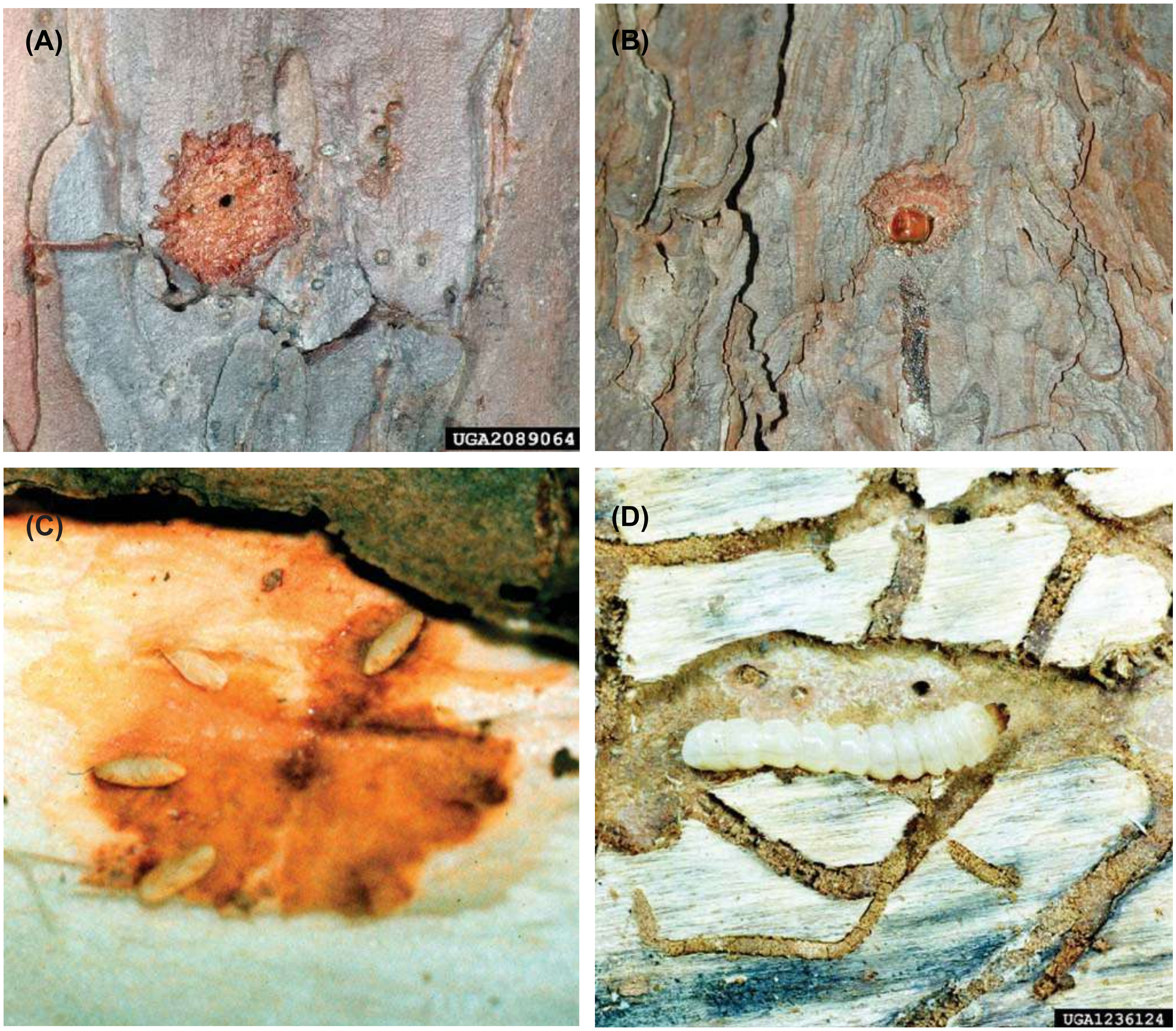

Figure 12.11—(A) *Monochamus titillator* (Fabricius) oviposition pit chewed in surface of pine bark (photograph by Lacy L. Hyche, www.forestryimages.org). (B) *M. titillator* oviposition pit on newly attacked pine showing fresh resin exuding from the oviposition hole (University of Arkansas, Forest Entomology Lab photograph). (C) Eggs of *M. titillator* in fresh phloem exposed beneath oviposition hole. (University of Arkansas, Forest Entomology Lab Photograph). (D) *M. titillator* larva foraging gallery consuming phloem and galleries of SPB (Clemson University, USDA Cooperative Extension photograph, www.forestryimages.org)

little SPB brood emergence occurred… under low-level conditions cerambycids can totally displace within-tree SPB populations" (Hain and Alya 1985).

Competition for phloem among cerambycids and bark beetles clearly results in a loss of resource for the beetle when they occur simultaneously with the much larger cerambycids. An additional reason that cerambycids can negatively affect bark beetle population is through intraguild predation, a combination of competition and predation (Dodds and others 2001, Polis 1981). When *M. carolinensis* and bark beetle larvae encounter each other in phloem tissue, the cerambycid larvae attacked the bark beetle larvae 74 percent of the time. Of those attacked, 85 percent were killed and 76 percent of those were ingested (Dodds and others 2001).

Other Cerambycidae

In Alabama, in a mixed loblolly and longleaf pine stand, Dodds and Stephen (2002) trapped 10 species, 3 of those *Acanthosinus obsoletus* (Olivier), *M. titillator,* and *Arhopalus rusticus* *obsoletus* (Randall) comprising about 70 percent of those caught. Other trapping and collection studies in Texas, Louisiana, and Mississippi report *A. obsoletus*, *A. nodosus,* and *M. titillator* as the most prevalent cerambycid species (Moser and others 1971, Overgaard 1968). The common but rarely studied cerambycid, *Acanthosinus nodosus* (F.), arrives on average from 8 to 14 days after initiation of SPB attack (Dodds and others 2002). It appears to colonize a different part of the phloem resource than the *Monochamus* species, being found in the thicker bark lower area of the bole, primarily from about 0.2 to 1.5 m from the base of the tree (Dodds and others 2002). It was arriving during the egg-oviposition stage of SPB, and some oviposition sites were noted to still have fresh resin exuding from the pits. It is interesting that on the trees examined by Dodds and others (2002), 99 percent of all *A. nodosus* oviposition sites were located on SPB entrance or ventilation holes, suggesting that although this species is confined to the lower region of the tree, it is a potential competitor with those *Dendroctonus* and *Ips* that also inhabit that part of the bole. Its impact on SPB is unknown; however, a related species in Europe, *Acanthosinus aedilis* (L.), was found to significantly reduce brood production of the bark beetle, *Tomicus piniperda* (L.) (Schroeder and Weslien 1994).

12.3. SAMPLING COMPETITORS AND EVALUATING THEIR IMPACTS

Much effort has been devoted to developing techniques for accurately estimating numbers of SPB within trees (Coulson and others 1975b, McClelland and others 1978, Stephen and Taha 1976). Unfortunately much less effort has been directed towards sampling methods for estimating numbers of their natural enemies or competitors. Stephen and Taha (1976) described the fact that different SPB life stages (e.g., attacking adults and emerging adults) exhibit different aggregation patterns, and as a result, to accurately assess density, either different numbers of samples or sample units of different sizes are required. They also showed that other associate species, including parasitoids and predators, are also aggregated, and that in order to get accurate estimates of their populations, more and larger samples are needed than would be the case for bark beetles. Further difficulties that arise when estimating densities of natural enemies or competitors have to do with timing of sampling. Because the subcortical environment is dynamic and constantly changing as multiple species of bark beetles and cerambycid beetles colonize phloem, samples taken too early or too late will always underestimate populations of those individuals.

Determining arrival times and numbers of bark beetles and cerambycid beetles that are attracted by host volatiles, pheromones, or kairomones is also challenging. Trapping of flying beetles either at the trees they intend to colonize or at or near the release site of the attractants is what is usually done. Traps on, or adjacent to, trees are frequently created from wire mesh screen or solid panels and then coated with sticky material such as Stick-em Special® or Tangle-foot® (Camors and Payne 1973, Dixon and Payne 1979b, Stephen and Dahlsten 1976). Although sticky traps function well to catch smaller flying insects, the large-bodied cerambycids may be able to escape by crawling from or sliding off traps, thus underestimating their abundance. Traps that mimic trees, such as Lindgren funnels® (Lindgren 1983), are alternatives to sticky traps, and a variety of other traps for bark beetles have been created (Browne 1978, Younan and Hain 1982).

Other research to assess the impact of competitors has relied on exclusion or cage studies (Linit and Stephen 1983, Miller 1984, Reeve and others 1998). Although these can be extremely valuable techniques to evaluate the role of competitors or natural enemies on bark beetle mortality, the same limitations regarding the difficulty of timing exclusion can frequently lead to errors in underestimating the impact of excluded species.

13

Southern Pine Bark Beetle Guild

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Keywords

development
gallery construction
hosts
host selection
identification
interactions
signs
symptoms

Abstract

Dendroctonus frontalis (southern pine beetle), *D. terebrans* (black turpentine beetle), *Ips avulsus* (small southern pine engraver or four-spined engraver), *I. grandicollis* (five-spined engraver), and *I. calligraphus* (six-spined engraver) comprise the southern pine bark beetle guild. Often they are found sharing the same hosts in the Southeastern United States. They exhibit a preference for trees that are stressed to various degrees. Members of this guild utilize chemical, visual, and acoustic cues to locate their hosts. Each has characteristic egg gallery patterns that assist in the determination of the attacking species. Development is temperature-dependent, resulting in two or three generations per year for *D. terebrans*, the largest in size of the guild members, to 10 or more for *I. avulsus,* the smallest in size. It appears that for members of this guild that cue into hosts colonized by other guild members, the result is increased resource availability to each.

13.1. INTRODUCTION

The southern pine bark beetle guild (Figure 13.1) is the most destructive guild of insects to pine forests in the Southern United States. A guild is defined as an intimately associated group of organisms that exploits the same resource in a similar way and may interact mutually (Flamm and others 1987a). As the name bark beetle implies, the life stages of this guild are found in the outer portion of pine trees, commonly referred to as the bark. This area is technically referred to as the phloem and has two distinct areas that include the outer corky dead bark and the inner bark (living layer of phloem) that transports nutrients throughout the tree. In addition, there is the cambium lying between the phloem and the xylem. The inner bark and cambium are rich in nutrients upon which beetles and their associated microorganisms develop. The xylem (sapwood) transports water to the crown and other parts of the tree.

Smith and others (1993) stated that five species make up the guild of insects known as the southern pine bark beetles. They are the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), black turpentine beetle (*D. terebrans* Olivier) (BTB), small southern pine engraver (four-spined engraver) (*Ips avulsus* Eichhoff), five-spined engraver (*I. grandicollis* Eichhoff), and the six-spined engraver (*I. calligraphus* Germar) (Figure 13.1). They inhabit the phloem tissue of all native southern pines, often with three or more species in the same tree.

This guild of bark beetles has been interacting for a long time. All are native to North America and have been evolving and adapting to the changing environmental conditions associated with the changing forested landscape and in particular the Southeastern United States. The SPB was responsible, in presettlement forests, for periodic perturbations that maintained uneven-aged forests and a diversity of plant species (Nebeker 2004). These outbreaks were beneficial events in normally functioning southern pine ecosystems. However, the SPB is now viewed as a pest because an economic value is placed on pine and because intensive management of pine forests has caused beetle populations to interfere with efforts to achieve management objectives. Other members of this guild have also been responsible for considerable mortality in this system, especially in times of extreme weather events such as drought- or hurricane-stressed trees. Singly or in all combinations this guild has caused tremendous mortality to the coniferous forests of the Southeastern United States, resulting in losses of millions of dollars. Greater discussions on losses are in the economics section. Their impacts are compounded when combined with events such as hurricanes Katrina and Rita that occurred in 2005. However, because of its history, aggressive behavior, and reproductive potential, SPB causes more concern than the other members of this guild and will be addressed in other sections of the encyclopedia. Within this section the remaining four species will be emphasized.

The engravers (common name derived from the fact that they tend to etch the xylem [wood] surface as the parent adults tunnel underneath the bark) are generally considered less aggressive than the SPB or BTB. They prefer host material that is stressed due to a moisture deficit, slash from harvesting operations, or wind-thrown material. It is essential to recognize that not just one species is responsible for killing pines in this region but could be any member of this guild or in combination. Tree killing appears to be a specialized or derived ecological strategy (Raffa and others 1993).

During periods of drought, as in 1999 and 2000 as well as the drought following hurricanes Katrina and Rita of 2005, *Ips* beetles attacked and killed vast acreages of pine. These events have increased public awareness of the impact that these insects can have on forest resources. During this period the SPB populations have remained relatively low to almost nonexistent. Increases and/or decreases in BTB populations have not been reported during this same time period.

13.2. IDENTIFICATION

The southern pine bark beetle guild is in the order Coleoptera (beetles), superfamily Curculionoidea, and family Scolytidae as classified by Wood (1982b). However, recent literature (Lawrence and Newton 1995) suggests changes in the taxonomy, with the family now being Curculionidae and subfamily Scolytinae to which members of this guild belong. For an extended review of this topic see Bright (1993) where he discusses the systematics of bark beetles. These systematic discussions continue, and the future systematic placement may change as molecular genetic profiles are elucidated.

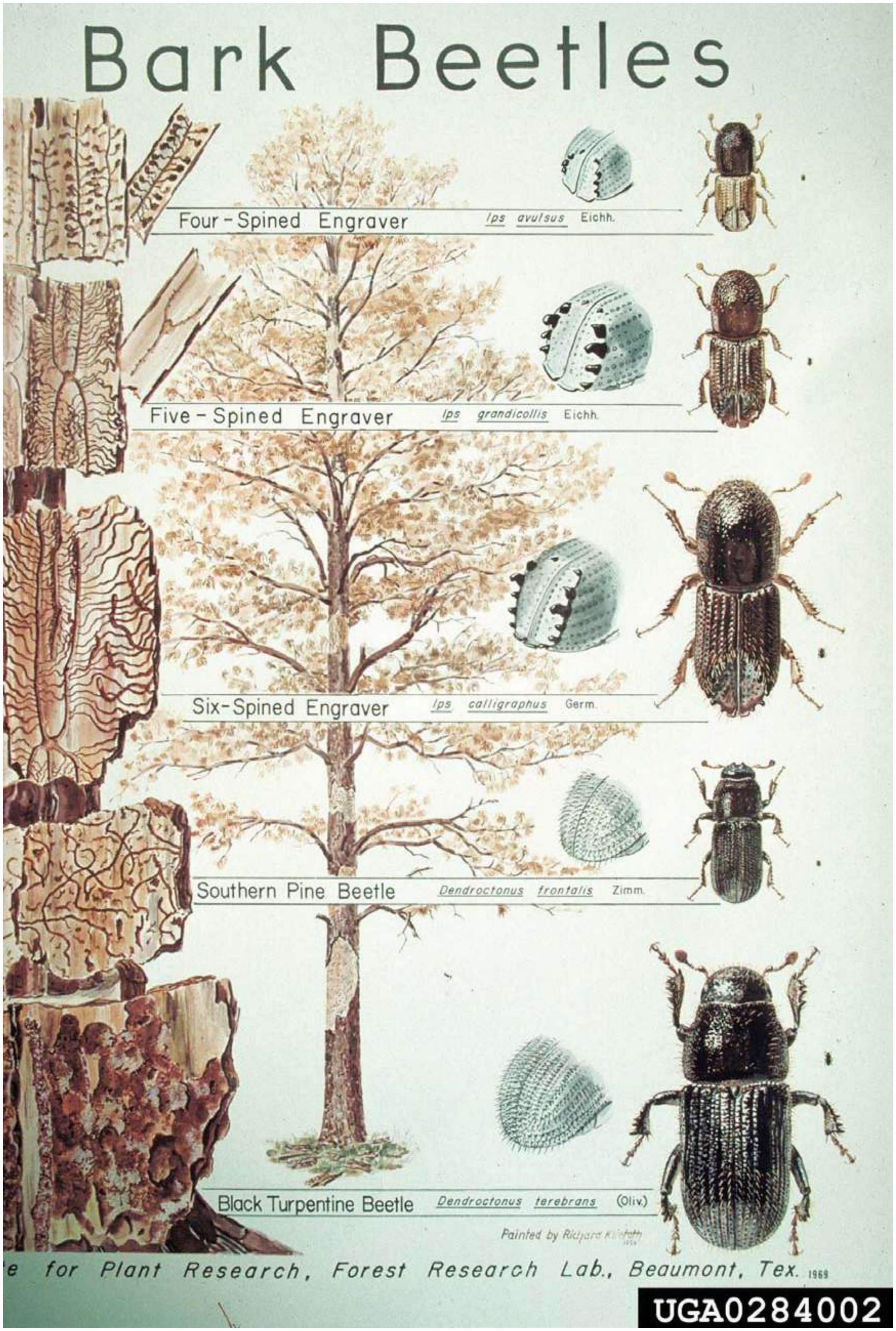


Figure 13.1—Southern pine beetle guild. (painting by Richard Kleifoth; Southern Forest Research Institute, photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

The SPB and the BTB appear rather similar except for size and are distinctly different from the engraver beetles that have a declivity at the distal end of their elytra (Figure 13.1). In addition there are spines on the outer margin of the declivity of the *Ips* spp. The distal end of SPB and BTB elytra are rounded with no spines. The SPB average 1/8-inch long and are 2.3 times as long as wide. They can vary at maturity from light brown to dark brown (Wood 1982b). The BTB is the largest of the guild members. The black, robust adult is 1/5-inch to 3/8-inch in length and 2.2 times as long as wide (Smith and Lee 1972, Wood 1982b).

Wilkinson and Foltz (1982) describe the *Ips* engraver beetles as small, brown to black, cylindrical beetles that live within the inner bark of southern pines. The name engraver refers to the fact that their tunnels are partially cut into the surface of the sapwood (xylem) underneath the bark. *Ips* beetles have a declivity at the distal end of the elytra (Figure 13.1). This declivity has spines on the margins from which members of this guild get their common names. Although the accepted common name for *I. avulsus* is the small southern pine engraver, it is frequently referred to as the four-spined engraver because it has four characteristic spines along each side of the declivity. As the common name implies, the five-spined engraver and the six-spined engraver have respectively five and six spines on each side of the declivity, making them relatively easy to identify with the aid of a hand lens. As one might expect, as the number of spines increases along the margin of the declivity, so does the relative size of the adult beetle. The four-spined engraver averages 1/8-inch long, the five-spined engraver about 1/6-inch long, and the six-spined engraver 1/5-inch long.

13.3. HOSTS

The southern pine bark beetle guild attacks a wide variety of coniferous hosts. Of particular concern are the commercial southern pines (Table 13.1) that come under attack, but attacks are not limited to those listed. During outbreak periods other tree species may come under attack as a result of high population densities and lack of other suitable hosts. However, this is considered a rare event, with mortality normally occurring to the commercial species that occupy the greatest percentage of the landscape, with loblolly, shortleaf, slash, pitch, and sand pine being principle hosts. As former agricultural land has been reforested the acreage of host material has increased.

Prolonged droughts, fire, lightning, wind events (straight line winds, tornadoes, and hurricanes), ice storms, logging/thinning activities, annosus root rot, little leaf disease, and offsite planting predispose host conifers to members of this guild. These factors individually or in combination contribute to an increase in susceptibility and suitability of available host conifers. For example, lightning-struck trees almost invariably serve as focal points of bark beetle infestations (Coulson and others 1983, 1985b; Wilkinson and Foltz 1982). Trees struck by lightning exhibit dramatic changes in levels of specific monoterpenes (Blanche and others 1985). Immediately following a lightning strike the primary defensive system (resin flow) is shut down. With the shutting down of the defensive resin system, the host is more susceptible and attractive to attack. Such trees serve as focal points (epicenters) for infestations to begin.

Table 13.1—Host of the southern pine beetle guild

Host Pine	SPB	BTB	4-Spined Engraver[c]	5-Spined Engraver[c]	6-Spined Engraver[c]
Loblolly	XXX[a]	XXX	XXX	XX	XX
Shortleaf	XXX[b]	XXX	XXX	XX	XX
Longleaf	X	X	X	X	X
Slash	X	XXX		XXX	XXX
Virginia	XX	X	XX	X	X
Pitch	XXX	XX	XXX		
Sand	X		XX	XXX	XXX
Table-Mountain	X	X	X		
Pond	X	X	XX	XX	XX

Key Interactions: [a]Annosum root rot, [b]Littleleaf disease, [c]Fire

Drought influences the hosts in a similar way, in that resin flow is greatly reduced. Pine trees growing in shallow or heavy clay soils are especially subject to high moisture stress during droughts. This decreases the ability of such trees to resist attacks by *Ips* and other bark beetles (Wilkinson and Foltz 1982).

For the nonaggressive *Ips* members of this guild, logging from wind or ice, wind throws, or slash from harvesting all provide suitable resources for colonization. Even trees that have had their canopies scorched, bark severely charred, and/or roots damaged during a prescribed burn or wildfire are more susceptible to attack because the trees' defensive systems have been weakened. *Ips* also infest otherwise healthy trees whose roots have been damaged by fire plows or other fire control equipment (Wilkinson and Foltz 1982). Anything that reduces tree health/vigor increases their attractiveness and susceptibility to attack by members of this guild.

13.4. HOST SELECTION

Host selection is different in the two genera represented in this guild. In *Dendroctonus* it is the female that selects the host and initiates the attack process, while in the *Ips* it is the male that selects the host and initiates the attack process. *Dendroctonus* are monogamous with a sex ratio of roughly 1:1, and *Ips* are considered polygamous with a sex ratio of greater than one female for every male. In some cases four or more females may be associated with a single *Ips* male attack. Cook and others (1983) indicated that the sex ratio of attacking beetles often favors the female in *Ips*. *I. calligraphus* was found to closely follow this pattern. The proportion of males to total beetles that emerged and reemerged was 0.465 and 0.284, respectively. These proportions correspond to a 1:1 sex ratio for brood adults and a 1:3 sex ratio for attacking adults. For *I. avulsus*, the smallest of the *Ips* species, the sex ratio has been observed by Cook and others (1983) to be 1:1 for beetles that emerged and reemerged. However, the average number of egg galleries per nuptial chamber was 2.91:1. Of interest was the observation that *I. avulsus* males and females frequently paired off, leaving the nuptial chamber open for use by other beetles.

Host selection is accomplished via primary and secondary attractions. Primary attraction is the response of the colonizing beetles to the cues given off by the host. These cues may be visual, chemical, or acoustic. Trap design for bark beetle surveys has long embraced the idea that bark beetles are attracted to vertical and/or horizontal silhouettes. They are also attracted by terpenes and other chemicals released by stressed or injured trees as well as freshly cut pine stumps. Trees weakened by fire, logging, drought, wind, lightning, and so forth are attractive hosts, especially for the engravers. Acoustic emissions that are given off during stress periods such as drought (Mattson and Haack 1987) are also utilized. For example, ultrasonic emissions produced during periods of moisture deficit are the result of water columns breaking (cavitation) in the xylem of stressed trees, and serve as short-range stimuli to trigger the biting response and initiate the attack process of bark beetles. They may also act synergistically with other cues to trigger attacks.

In addition to the primary attraction process that aids in host selection, a secondary attraction process is also in play. Smith and others (1993) state that in monogynous *Dendroctonus* species, females are responsible for host selection, initial attack, and gallery construction in new host trees. Male *Dendroctonus* enter the host only after females have selected and successfully attacked a host and pheromone production has begun. Once extensive feeding and defecation commences, the frass is not dislodged but is tightly packed in the galleries. Smith and others (1993) further state that in contrast, males of the polygynous *Ips* species select hosts, prepare nuptial chambers, and produce pheromones. Female beetles locate the entrance holes of established males via pheromones, and/or acoustic emissions, enter, mate, and then construct galleries along which they lay eggs. Continuous ejection of frass from the galleries provides for sustained release of the semiochemicals with the male frass. In both genera, as more beetles arrive at the tree and produce and release pheromones, the attraction of the host increases until the whole tree is colonized. Termination of beetle arrival is also apparently under pheromonal control. Smith and others (1993) have provided a historical review of the research on the semiochemical-based communication system of the five principal species of this guild. An expanded discussion on this topic concerning the SPB can be found under Behavior (see chapter 3).

13.5. EVIDENCE OF INFESTATION

In general, the identification of the insect causing mortality to a pine host is based on other characteristics than the insects themselves. Often by the time the attacked trees are detected or noticed, the insect attack, development, and emergence has already taken place. Hence other signs and symptoms have to be evaluated.

Attacks by this guild on standing trees are potentially partitioned as illustrated in Figure 13.1. The four-spined engraver, because of its size, may attack individual limbs in the cpy where the larger species are unable to because the phloem is not sufficiently thick to allow successful colonization and brood production. The colonization of these limbs results in the death of the limb and is termed flagging. Additional limbs may be attacked as the population builds up until most of the crown has been killed. The larger *Ips* spp., five- and six-spined *Ips* attack the larger limbs in the canopy where the phloem is sufficiently thick for their successful colonization. They may also occupy the area occupied by the SPB and BTB. It is not uncommon to find members of this guild intermixed with each other along the bole of an infested tree.

Figure 13.2—Pitch tubes of the black turpentine beetle. (photograph by Lacy L. Hyche, Auburn University, www.forestryimages.org)

The BTB confines its initial attacks to the base of the tree. They are generally located in the lowest 18 inches (Smith and Lee 1972). As the BTB continues to bore into the tree, a considerable amount of resin is released in an attempt by the host to resist attack, resulting in large pitch tubes being formed (Figure 13.2). These tubes are a mixture of resin, frass (insect excrement), and bark-boring dust, and are reddish to white in color, and quickly harden and darken in color. The pitch tubes are large, about the size of a quarter, with a distinct hole that allows the adults entry into the tree as they work and form the pitch tube. In addition, resin pellets are often found at the base of the tree. This is a result of the adults removing resin from the attack site and gallery. Ambrosia beetles almost always secondarily attack heavily infested trees. Ambrosia beetle attacks are readily recognized because of the fine light-colored (whitish) boring dust that forms a ring around the base of the tree and should not be confused with attacks by members of this guild.

After the BTB initially attacks at the base of the tree, including large roots that may have been exposed, BTB spreads upward. Some BTB attacks have extended up to 20 feet and as high as 55 feet, but the initial attacks almost always occur in the basal 18 inches of the tree and spread over the basal 10-12 feet of the tree (Clark 1970).

In contrast to the BTB, however, the first SPB attacks appear on the mid-bole, approximately halfway between the first live limbs of the canopy and the ground. As the SPB attack process continues, attacks spread from the mid-bole up and down the tree, generally occupying the bare bole of the tree from the ground to the first live limbs of the canopy. In standing stressed trees, the engraver beetles attack higher in the tree, although considerable overlap can occur, resulting in within-tree competition for available resources. Resource partitioning is generalized in Figure 13.1 in that all five species may occupy the same tree at the same time with varying degrees of overlap and intermixing. These interactions may, however, enhance each other's ability to secure oviposition sites by colonizing simultaneously, thereby overcoming tree resistance (Wagner and others 1985).

Pitch tubes made by the SPB are much smaller than the BTB, about the size of a piece of popcorn (Figures 13.3 and 13.4). As with the BTB there is a hole in the pitch tube allowing access of the parent adults. On recently attacked trees it is not uncommon to see the male and female beetles working the pitch tube. The size of the pitch tube is dependent on a number of factors. If the tree is under stress the pitch tube may be very small or nonexistent. Healthy trees not experiencing moisture deficits may produce coppice amounts of resin and pitch out the attacking beetles or entrap them in a process known as resinous.

Figure 13.3—Southern pine beetle pitch tubes. (photograph by USDA Forest Service – Region 8 Archive, USDA Forest Service, www.forestryimages.org)

An indication of a successful *Ips* attack is the presence of a hole in the pitch tube, if present. If there are pitch tubes, the size of the hole in the pitch tube is directly related to the size of the attacking adult. Pitch tubes made by the *Ips* spp. are generally much smaller than that of the SPB on trees because of their preference for severely stressed trees. On logs, logging debris, or scattered debris associated with wind events there are generally no pitch tubes. In the absence of pitch tubes, the presence of reddish-brown boring dust (Figure 13.5) in the bark crevices of standing trees, logs, or logging debris is the first, but often overlooked, sign of attack by *Ips* beetles (Wilkinson and Foltz 1982). It is also washed or blown away during rain and wind events. During the attack process it is continually produced and will also accumulate on the upper surfaces of leaves and in spider webs.

Figure 13.4—Southern pine beetle pitch tubes distributed along the bole. (photograph by Erich G. Vallery, USDA Forest Service, SRS-4552, www.forestryimages.org)

13.6. EGG GALLERY CONSTRUCTION

Upon successful entry into an acceptable pine host, the adults begin to construct galleries, tunneling in the inner bark and outer xylem. This construction behavior is similar for the three *Ips* species of this guild. Males attack first, followed by a number of females (usually two to four) that are attracted by the male (Wilkinson and Foltz 1982). The male begins by excavating an area commonly referred to as the nuptial chamber. The male may remain in this area for mating with the females as they begin egg gallery construction and oviposition. However, in recent observations by Richard Hofstetter, Northern Arizona University, Flagstaff, AZ (2007 personal communication), he observed males leaving the nuptial chamber area to mate with the females in their egg galleries.

Figure 13.5—Reddish-brown boring dust of engraver beetles. (photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

Figure 13.6—Egg gallery of the five-spined engraver. (photograph by Ron Billings, Texas Forest Service, Texas Forest Service Archive, www.forestryimages.org)

Egg galleries are constructed by each female, originating at the nuptial chamber following the grain of the wood up or down with common gallery shapes representing Y- or H-patterns, as depicted on the left-hand side of Figure 13.1. Eggs are laid individually along the gallery in small niches chewed out by the female and referred to as an egg niche (Figure 13.6). The egg galleries are for the most part devoid of frass, allowing the females and males to move freely in the gallery for mating purposes. Turning niches or ventilation chambers can be seen extending toward the outside of the tree (Figure 13.7). Upon completion of the egg gallery construction, the parent adults reemerge and go through the host selection process again and colonize additional trees. It is during these periods outside the tree that they are subjected to various forms of mortality that would limit their ability to successfully colonize additional trees.

Successful colonization of a tree opens the door for other organisms to also colonize the attacked tree. Connor and Wilkinson (1983) state that adult *Ips* beetles carry numerous spores of a blue stain fungus, *Ceratocystis ips* (Rumbold) C. Moreau, in their gut. See section on Symbionts (see chapter 9). When the adults attack trees or logging slash, the blue stain spores are excreted with beetle feces into egg galleries, where the spores germinate. Blue stain fungus colonies grow into the outer sapwood and phloem of infested pines, stopping the upward flow of water to the tree crown. Lack of water causes needles to wilt and die, gradually changing their color from dull green to yellow green to red brown. This is referred to as fading. These color changes may occur within 2-4 weeks during the summer, but take several months in the winter. This is also true for trees successfully colonized by the SPB and BTB.

Once the BTB adults successfully overcome the tree's defensive system and/or attack suitable host material, they begin to construct their egg galleries. These attacks, as described above, occur in the lower portion of standing trees, larges of weakened and dying trees, and stumps of recently cut trees. Attacks can continue to occur over an extended time period, with most attacks taking place in the first 5 weeks following the initial attack (Godbee and Franklin 1976). The egg gallery origin is at the site where the beetle intersects the inner bark and then tunnels downward, exhibiting a positive geotaxis between the phloem and sapwood. Hence, the boring activity and egg laying takes place in the area directly below the pitch tube. The eggs are laid as a group along one side of the gallery. After egg hatch the larvae feed gregariously together. When the bark is removed (Figure 13.8) there is no distinctive pattern. Pupation takes place in the outer bark or between the bark and the sapwood. If the bark has not loosened sufficiently by the time the new adults are ready to emerge, they will leave the tree through the pitch tube that the parent adults had created or bore holes through the bark and emerge. In most cases the parent adults have already reemerged prior to brood emergence. BTB attacks are not always fatal because there may be only a few attacks on one side of the tree, around the edge of basal wounds, or on some large exposed roots following a logging operation.

13.7. DEVELOPMENT

The southern pine bark beetles are holometabolis insects in that they pass through four distinct life stages—egg, larva, pupa, and adult. Temperature plays an important role in the development of *Ips* populations. In some early studies of the developmental rate of *Ips* populations, very little brood development was observed taking place below a base temperature of about 15 °C. With average daily air temperatures of 18 °C, the average length of a generation was 100 days, but with an average temperature of 29 °C the average length of a generation is 20 days (Wilkinson and Foltz 1982). A generation being defined as the average time it takes a female to replace herself, or more commonly thought of as the time from egg to new adult. It has been stated (Drooz 1985) that the four-spined engraver may have 10 or more generations per year, the five-spined engraver and the six-spined engraver may have six or more generations per year (Drooz 1985).

Wagner and others (1988a, 1988b) have provided more detailed information concerning the influence of constant temperature on the development for each life stage as well as temperature-dependent models of reemergence for the four-spined engraver. At constant temperatures of 15 °C and 35 °C the life cycle was completed in 55.5 days and 14.3 days respectively. In total, development of the four-spined engraver was studied at seven constant temperatures for 10°-35 °C. On average, eggs occupied 10.2 percent of the total time in the host, larvae 34.8 percent, pupae 11.8 percent, and teneral adults 43.1 percent. It was concluded that the insects are well adapted to high temperatures but sensitive to low temperatures. With the capacity to develop rapidly at higher temperatures, the engraver beetles are able to complete several generations per year. The exact number of generations is dependent on location. Hence, in the southern part of their range they are capable of passing through more generations per year. This is not particularly good news for hurricane-prone areas.

Figure 13.7—An example of the egg gallery of the six-spined engraver. (photograph by William M. Ciesla, Forest Health Management International, www.forestryimages.org)

Figure 13.8—Black turpentine beetle gallery. (photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

Significantly fewer days (34.9 vs. 38.1) were required for brood of the six-spined engraver to complete development and emerge in thick phloem vs. thin phloem hosts respectively (Haack and others 1987). BTB development is likewise dependent on temperature. The length of the lifecycle is 3-4 months, depending on temperature (Smith and Lee 1972). There are two to three BTB generations per year in the Deep South (Drooz 1985).

13.8. SEASONAL ACTIVITY

In general the southern pine bark beetle guild is active year round. However, flight and attack activity occurs primarily from March through October but varies regionally and can occur throughout the year (All and Anderson 1972, Godbee and Franklin 1976). Activity begins to pick up roughly when pine pollen is beginning to fly and the dogwoods are blooming. This begins earlier in the southern part of the range and progresses northward. The primary activity period also coincides with the growth and differentiation period (Lorio 1993) of the guilds hosts.

13.9. SPB GUILD INTERACTION

It is not uncommon to observe more than one member of the SPB guild attacking the same tree. The SPB and the four-spined engraver have concentrated attack periods, with peak arrival occurring 3-5 days and 12 days, respectively, following the initiation of attack. Afterwards, attack rates decline sharply. Both the SPB and the four-spined engraver have a more synchronous reemergence period of a shorter duration than the other three members of this guild. This synchronous emergence may aid each species in rapidly assembling large numbers for attack. This attack pattern, known as mass attack, is characteristic of more aggressive species that must rapidly overwhelm the natural defense mechanisms of their hosts. Interestingly enough, this attack pattern coincides with the higher numbers of expendable female SPB and the male four-spined engraver as reflected in their sex ratios (Smith and others 1993).

The six-spined engraver has a less concentrated attack period, with peak arrival occurring approximately 21 days following attack initiation, followed by a declining attack rate. Reemergence of the six-spined engraver is also less synchronous and more protracted, extending over a greater time period than that of the SPB and the four-spined engraver (Smith and others 1993). This is most likely due to their host preference of logging debris, slash, and trees with few remaining defenses. With the prolonged attack period and host preference, this species most likely interacts less with the other members of this guild that have more synchronized attack and emergence behaviors.

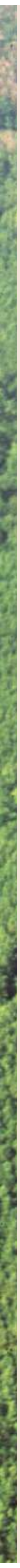
However, Flamm and others (1987a) conclude that the four-spined and the six-spined engravers have reemergence and emergence (allocation) patterns similar to the SPB. Similar patterns suggest a similar role for allocation in the population dynamics of the three species, that role being enhancement of resource acquisition. In addition, as members of this guild, interactions may benefit one or more guild members. At times when SPB densities are low, allocation by several species may provide enough beetles for successful colonization. In this way guild members may benefit by enhancing each other's ability to secure oviposition sites by acting mutually to overcome tree resistance (Wagner and others 1985).

The five-spined engraver lacks a concentrated attack pattern, with gradually increasing attack density for 18 days following initiation of attacks. It then maintains an intermediate attack rate, for an extended time period from 30 to 50 days. It was suggested by Berisford and Franklin (1971) that this extended attack period enables the six-spined engraver to succeed, since this species normally attacks logging slash or extremely stressed trees that have little or no primary or secondary defenses to resist attacks.

Raffa and others (1993) suggest that tree killing appears to be a specialized or derived ecological strategy. For example, regardless of the host's condition when adult beetles attack it, they require nonresistant, recently dead tissue for brood production. Healthy trees can be colonized following a population buildup in nearby weakened trees, but these outbreaks are usually less expansive and persistent than those of the more aggressive species. Concentrating on severely stressed trees, as do most members of this guild, allows them to avoid host defense mechanisms, and attacking in various combinations can successfully overcome any remaining defense the host may offer, thus providing a suitable resource for the beetles to successfully colonize and reproduce.

Flamm and others (1987a) suggest that maintenance of the southern pine bark beetle guild is based on the ability of each member to claim sufficient resources to perpetuate itself. Resource acquisition may be enhanced by mutually beneficial interactions among members but not inhibited by competition to the point of total exclusion of a guild member. Competition among guild members is reduced because they exploit niches sufficiently different to produce some separation of the species. Niche differences arise from guild members having variable arrival sequences and attack patterns, attacking different areas of the tree, well-defined pheromone systems, different habitat requirements, and size differences. Although not fully understood, acoustic communications (Ryker 1988) within trees may play a role in limiting direct competition between members of this guild.

In conclusion, it appears that for members of this guild that cue into hosts colonized by other guild members, the result is increased resources available to each species. Furthermore, the beneficial effects of their adaptation to the presence of each species appear to outweigh any of the negative effects resulting from competition. The interspecific, chemically mediated behavior by the guild species in colonization and resource partitioning results in reduced intensity of inter- and intraspecific competition at all population density levels allow the species to more fully exploit their southern pine hosts (Smith and others 1993)



Section II

II. Southern Pine Beetle Impact

Section II addresses impact of the southern pine beetle on the resources and conditions of the forest environment. This section contains two sub-sections: one dealing with impact assessment and the other dealing with monitoring the forest environment. *Impact* is defined broadly to mean any effect on the forest environment resulting from the activities of the southern pine beetle. Four perspectives on impact are examined: economic, ecological, social, and political. *Economic impact* is simply defined as the effect of the southern pine beetle on the monetary receipts from the production of goods and services on forest lands. *Ecological impact* refers to the functional roles that the southern pine beetle plays in forests. *Social (axiological) impact* refers to the effects of the southern pine beetle on aesthetic, moral, and metaphysical values associated with forests. *Political impact* refers to the effects of the southern pine beetle on the forest environment that result in actions, practices, and policies of local, State, or Federal governmental agencies. Three chapters are devoted to impact assessment. Much of the data needed for impact assessment results from monitoring the forest environment. Herein, *monitoring* means to observe critically in ways that do not affect resources and conditions of the forest environment. Monitoring involves collecting data about the forest environment. Two perspectives on monitoring are considered. The first perspective addresses how the State forestry agencies go about monitoring the forest environment. The second perspective deals with how the USDA Forest Service, Forest Health Protection, monitors forests.

Monitoring on State and Private Forests and National Forests

The Southern State forestry agencies and the USDA Forest Service (Forest Health Protection) use different approaches in monitoring the forest environment and each perspective is examined. The financial resources available to the State forestry agencies in the South for monitoring State and private forests are limited. There is also a great deal of variation in commitment to monitoring among the States, particularly in times when southern pine beetle activity is modest. Monitoring and reporting by States is done in cooperation with the USDA Forest Service, Forest Health Protection. A chapter is devoted to describing the general approach used by the States. Monitoring of public forest lands is conducted by USDA Forest Service, Forest Health Protection, in cooperation with individual national forests throughout the South. The approach taken involves sophisticated techniques, and four chapters are devoted to describing the procedure. The topics examined include aerial sketchmapping, survey (data collection), database management, and operational use of survey information.

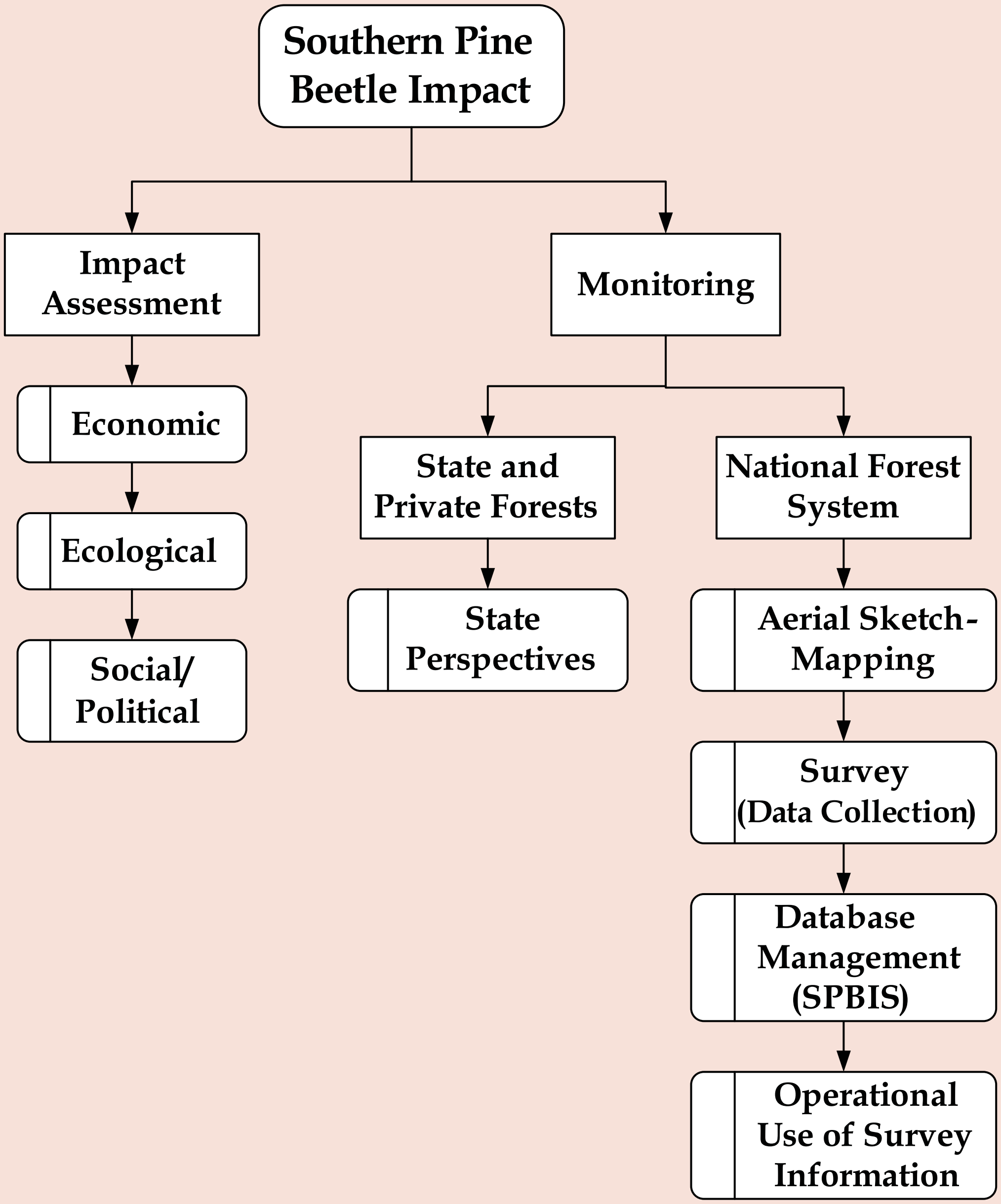


Figure II.1. Diagrammatic representation of the organization of Section II of *The Southern Pine Beetle II* dealing with impact. The unit is organized into two sub-sections and eight chapters. The first sub-section deals with impact assessment and contains chapters dealing with economic impact, ecological impact, and social/political impact. The second sub-section deals with monitoring southern pine beetle populations. The procedures used by the state forestry organizations are different than those used by the USDA Forest Service, Forest Health Protection. Both perspectives are examined.

14

Economic Impacts of the Southern Pine Beetle

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Abstract

This paper provides an overview of the timber economic impacts of the southern pine beetle (SPB). Although we anticipate that SPB outbreaks cause substantial economic losses to households that consume the nonmarket economic services provided by healthy forests, we have narrowly focused our attention here on changes in values to timber growers and wood-products consumers. Thus, the economic values reported here represent a lower-bound to the total economic impacts of SPB in pine-dominated forests. A theoretical framework for measuring economic impacts on individual forest landowners is described. This framework is then linked with a model of the timber market impacts of the SPB that allows us to estimate separate impacts for timber producers and wood-using firms. The salvage of timber killed by the SPB during large outbreaks creates a surge in the volume of pine timber entering the market that, in turn, decreases the timber market price faced by all timber sellers. This short-run impact decreases the economic welfare of timber producers while increasing the economic welfare of wood-using firms that can obtain timber at lower prices. Over longer periods of time, large SPB epidemics can reduce the volume of standing timber inventories, causing a smaller, but important, increase in the price of timber due to increased timber scarcity. Estimates of the short-run and long-run changes in economic welfare are computed using an empirical model. During the 28 years for which we have data, estimates of short-run impacts indicate that timber producers have lost about $1.2 billion to the SPB, or about $43 million per year, and wood-using firms have gained about $837 million or about $30 million per year due to SPB outbreaks. Because the broadscale effects of accelerated harvesting impact all timber owners in the affected areas, governments may play a role in reducing the negative impacts on timber producers. Strategies include: 1. holding SPB-killed timber on public forests off the market in order to limit the short-run price depression, 2. temporarily adjusting weight restrictions on public roads to help facilitate timber salvage on private forests, and 3. advising forest landowners with healthy forests to forego timber harvesting until the pulse of beetle-killed timber clears the market and prices return to more normal levels.

Keywords

disturbance valuation
impact assessment
SPB
timber market
welfare economics

14.1. INTRODUCTION

Southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), epidemics periodically cause widespread mortality in pine-dominated forests in the Southern United States and induce a variety of economic impacts. The SPB is native to the Southern United States and plays an ecological role, along with wildfire, in the recycling of nutrients in forest ecosystems. Despite its evolutionary role, the SPB disrupts the flow of economic goods and services demanded by modern society. The spectrum of contemporary economic impacts includes the loss of timber values to forest landowners and a loss of aesthetic and recreational values to a complement of resource consumers (Leuschner 1980). During catastrophic SPB outbreaks, aggregate markets for goods and services are affected, and economic impacts are transmitted across a broad complement of consumers and producers.

Estimating the economic impacts of a forest insect epidemic is not a simple matter. In contrast to agricultural systems, forests are long lived so that the economic impacts of current forest mortality are distributed over many years. Insect epidemics may suddenly terminate decades of productive forest growth and reduce stocks of commercially available timber for years to come. In addition, pine-dominated forests provide an array of ecosystem services, so that nonmarket economic damages need to be considered. Estimates of the total impacts of SPB damage, while difficult to approximate, are crucial data for evaluating the risk profile of forest investment decisions, optimal approaches to pest management, and government policies for responding to epidemics.

The exclusive focus of our analysis here is the effect of SPB epidemics on the returns to timber production in the South. Economic impacts to timber producers and wood-products firms are essential to consider because the SPB causes extensive mortality in forests that have high commercial value in a region with the most active timber market in the world (Prestemon and Abt 2002). We first consider the effects of localized tree mortality on individual landowners. We then examine how broadscale tree mortality affects markets and consumers and producers of timber in both the short and long runs.

14.1.1. Theory of Landowner Impacts

When the SPB kills a landowner's trees, changes in the plans for forest management result. Assuming that these plans represent the high-value course of action for the landowner, unanticipated mortality will lead to some loss of value. How are these losses defined? First the landowner faces an immediate decision regarding the treatment of the killed timber. Options may include: 1. A salvage harvest, 2. A sanitation cut to mitigate further damage, or 3. Nothing. All three options imply costs, both the costs of conducting the treatments and opportunities foregone associated with altering the schedule of forest management activities. For example, the landowner will suffer losses associated with harvesting timber earlier than planned—that is, losing the returns to additional years of tree growth. Prices for damaged timber will likely be lower than prices for undamaged timber, leading to even greater losses. In addition, higher costs are likely to be incurred for salvage harvests because they involve smaller stems and overall harvest volumes, and require extra measures to mitigate the hazards associated with cutting dead and damaged timber.

When a landowner decides to conduct a salvage harvest there are several factors that contribute to the total costs of the mortality. They can be derived by contrasting the net returns of management following the epidemic with the value that would have been derived from managing an undamaged stand (a precise mathematical derivation of these impacts can be found in Appendix A). There are five factors influencing this change in value:

1. Reduction in the price paid for the damaged vs. undamaged timber
2. The loss of volume that would have accrued in subsequent years (depends on the current age of the stand)
3. The higher costs of harvesting damaged vs. undamaged timber
4. Accelerated cost schedules; e.g., regeneration costs are incurred sooner, rather than later
5. Changes in value associated with harvesting the next crop of trees sooner

The first factor is very likely to be negative; the second, third, and fourth terms are unambiguously negative; and the fifth term is positive. Because of the effect of discounting in all cases we can envision, the negative terms far outweigh the small positive impact in the fifth term. Overall, the economic impacts of the epidemic for the owner with damaged timber are associated with: 1. harvesting timber sooner than planned, 2. the price penalty for the damaged timber, and 3. changes in the timing of management costs and subsequent timber harvests.

14.1.2. Theory of Market Impacts

When the SPB reaches epidemic conditions, so much salvage harvesting can be generated that it changes the overall market for timber. During the epidemic, for any given price, much more timber enters the market due to salvage harvests. Because the demand for timber is unaffected by the SPB, this surge in timber supply results in the reduction of timber prices and spreads the impacts of the epidemic beyond the landowners, with damaged timber to include all participants in timber markets:

1. *Owners of damaged timber:* Price reductions amplify the damages described above for these individuals. Because of rapid decomposition of dead logs, they have little opportunity to defer their harvests to await the return of higher prices.
2. *Owners of undamaged timber:* Price reductions harm all timber producers, either through the receipt of lower prices for their harvested timber or through the costly deferral of timber harvesting to later dates.
3. *Purchasers of timber:* Timber purchasers receive an economic gain from paying less for their timber. That is, they purchase more timber and at a lower price than would have ordinarily been the case.

So in the short run, SPB epidemics cause a surge in supply with a concomitant reduction in timber price, and result in losses to all timber producers and gains to timber consumers (Holmes 1991). In the language of welfare economics (Just and others 1982), the total return to timber producers is called Producer Surplus, referring to the difference between the revenue achieved in selling timber and the cost of delivering the timber. The surge in supply yields a smaller Producer Surplus. The total benefits accruing to the consumers of timber are called Consumer Surplus, and refers to the difference between the price paid and the value of the timber in the production of wood products. Surges in supply yield higher consumption and lower prices, and therefore a net gain in consumer benefits will result.

Economic impacts of an SPB epidemic may extend beyond its physical duration. Damage from the epidemic could be extensive enough to reduce the stock of standing timber available for harvest in future periods. If this happens, the long-run market will adjust to yield effects opposite to the short-run impact. Timber supply contracts, so that less is harvested at a given price and, *ceteris paribus*, timber prices increase. As a result, timber producers in these out-years will reap benefits (Producer Surplus increases), while timber consumers lose benefits (Consumer Surplus shrinks). In practice, these longer run impacts are much smaller than the short-run impacts. However, because impacts are spread across many years, they represent an important component of the total costs of a major SPB epidemic.

In the next section, we provide a summary of historical SPB activity in the South. We start with a rough estimate of the volume of timber killed by SPB on an annual basis and calculate the value of timber revenue foregone. Because we cannot estimate changes in the opportunity costs of individual landowners, this approach may underestimate the total damage suffered by individual landowners. We next evaluate the market impact of the epidemics as it provides a reliable index of direct damages. We estimate the effect of SPB mortality on timber prices, but our primary focus is on measuring changes in Producer and Consumer Surpluses for the timber markets in the South. We estimate the impacts of SPB using a model that accounts for both the short- and the long-run effects and provide insights into the impact of this insect through both endemic and epidemic periods over the past 30 years.

14.2. MORTALITY AND SALVAGE ESTIMATES

Southern pine beetle populations and associated timber damage exhibit dramatic swings even when aggregated across the South. The volume of timber killed by SPB from 1973 through 2004 has ranged from 3 to 417 million cubic feet (Figure 14.1). Eight outbreaks of varying intensity are apparent, each spanning only portions of the region.

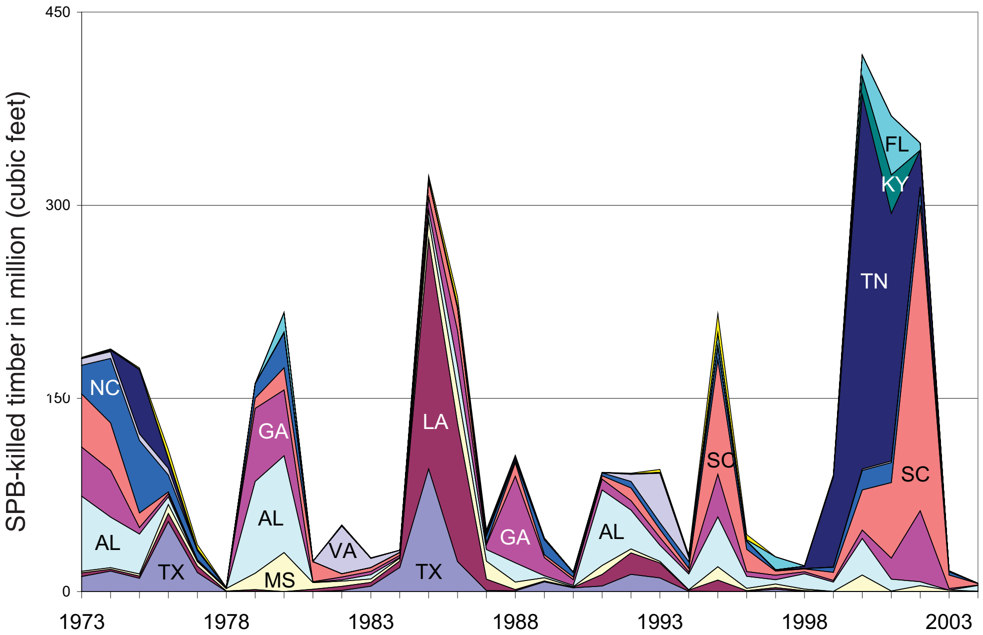

Figure 14.1—SPB-induced timber mortality by year and State.

The largest Southwide SPB outbreak was also the most recent, running from 2000 through 2002 and causing timber mortality exceeding a billion cubic feet. Damage in each year of this outbreak exceeded timber mortality in any other year of the historical record. Nearly half the total damage was reported in Tennessee.

The first 4 years of this record (1973–76) evidenced the second largest Southwide outbreak, which spanned most of the southeastern portion of the South. Damages were augmented during the final year of the outbreak by a geographically separate epidemic in Texas.

Nearly as large as the 1973–76 epidemic was the outbreak of 1984–86, which principally affected Texas and Louisiana. Other notable outbreaks include the 1979–80 outbreak in the Deep South, the 1995 outbreak in the Southeast, the 1988 outbreak in Georgia, the 1991–92 outbreak in Alabama, and the 1982 outbreak in Virginia.

In short, southern pine forests periodically experience a large SPB outbreak somewhere in the region on relatively short cycles. Although Southwide damages did not exceed 8 percent of typical sawtimber or pulpwood harvests in any given year, the concentration of mortality to subregions suggests that impacts to local timber markets would be more severe.

As described in the Theory of Market Impacts section above, the impacts of mortality include both short-term effects of timber salvage on timber harvest volumes, and longer term effects of mortality on timber inventory. Figure 14.2 plots both these factors for individual states and years. More specifically, the horizontal axis shows reported salvage amounts expressed as a share of typical softwood harvests during that year. The vertical axis shows the amount of timber killed by SPB expressed as a share of softwood inventories. All measures are for softwood sawtimber, and are annual and statewide.

In most years and in most States, damages and consequent salvage levels are low, hence the cluster of points near the origin. Extreme events are found away from the origin—only the most extreme are labeled. The wide scatter of points reflects the different character of outbreaks in particular states. Outbreaks such as experienced in Kentucky during 2001 and Louisiana in 1985 induced salvage levels amounting to more than a third of typical statewide harvest levels. These amounts would likely cause substantial short-term depression of stumpage prices.

Conversely, the outbreak in South Carolina in 2002 evidenced very low salvage amounts, relative to typical harvest levels. However, the mortality from southern pine beetle accounted for more than 2 percent of softwood inventories in that State. Such reductions in timber inventories are expected to result in longer term increases in local and statewide stumpage prices.

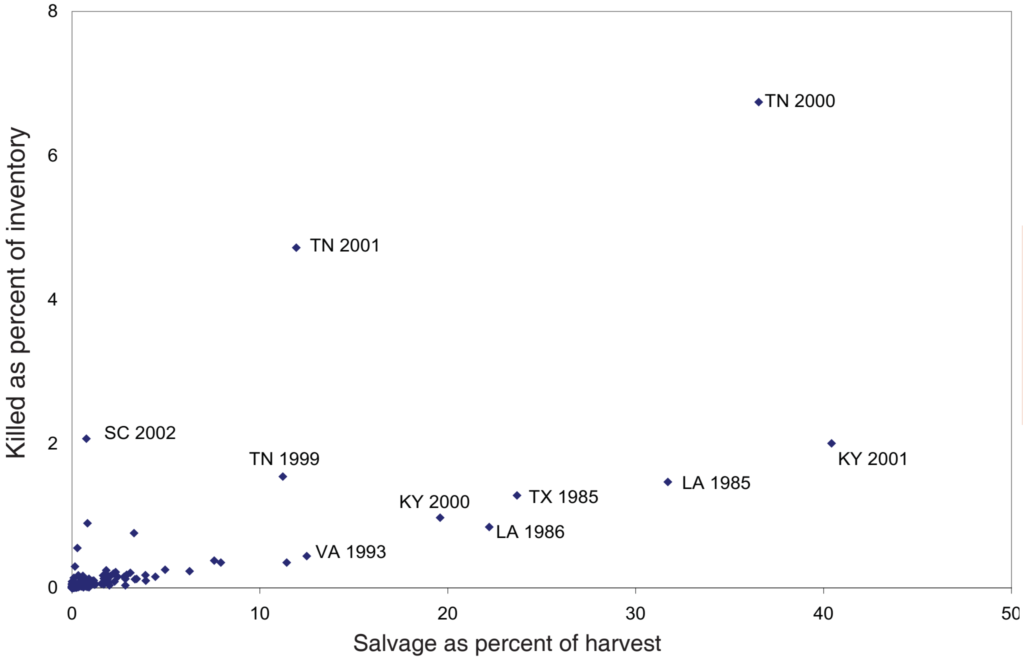

Figure 14.2—Annual salvage and mortality from SPB relative to harvest and inventory levels, key factors in short-term and long-term market impacts.

14.3. ECONOMIC DAMAGE ESTIMATES

As discussed in the preceding section, the salvage activity and broader timber mortality associated with SPB outbreaks have both near term and delayed effects on timber markets. These have differential effects on various participants in these markets. Assumptions used in this analysis are found in Appendix B.

14.3.1. Short-Run Aggregate Impacts

The short-run economic impacts of SPB outbreaks on timber markets in the South are large, and result primarily from the effect of salvaged timber on market prices. During the period for which economic data are available, 1977–2004, the SPB was estimated to cause a net, short-run economic loss to southern timber markets of about $375 million (in constant 2004 dollars). Dividing the total market impact by the total number of years included in the data record, the average net annual loss was roughly $13 million. However, annual damage estimates can be misleading in understanding the economic impacts of the SPB. Although SPB kills timber somewhere in its range every year (Figure 14.1), most economic impacts occur during a small number of large outbreaks. These catastrophic outbreaks have occurred every 5-10 years in southern forests during the past 3 decades (Figure 14.3).

Catastrophic timber market impacts caused by SPB epidemics are both episodic and geographically dispersed. For example, roughly a third of the timber market losses in 3 decades of outbreaks occurred during just 3 years (1984–86), accounting for $133 million in losses. Most of these losses were in Texas and Louisiana. The second-worst outbreak occurred during 2000–02 and caused timber market losses of about $110 million, largely in Tennessee and Kentucky. The third-worst outbreak occurred during 1979–80, caused losses of about $48 million, and was particularly severe in Alabama and Georgia. Finally, a relatively short epidemic occurred in 1995, causing timber market losses of about $25 million. This epidemic differed from the other catastrophic outbreaks in that it was geographically widespread and created major losses in Arkansas, Louisiana, Florida, Georgia, North Carolina, and South Carolina. Taken together, these four large outbreaks occurred in 10 states, with large outbreaks occurring twice in Louisiana and Georgia, and accounted for roughly 84 percent of the total losses.

14.3.2. Short-Run Winners and Losers

Our discussion of the net economic impacts of the SPB up to this point disguises the fact that SPB outbreaks have very different impacts on different timber market participants. As discussed above, during an SPB

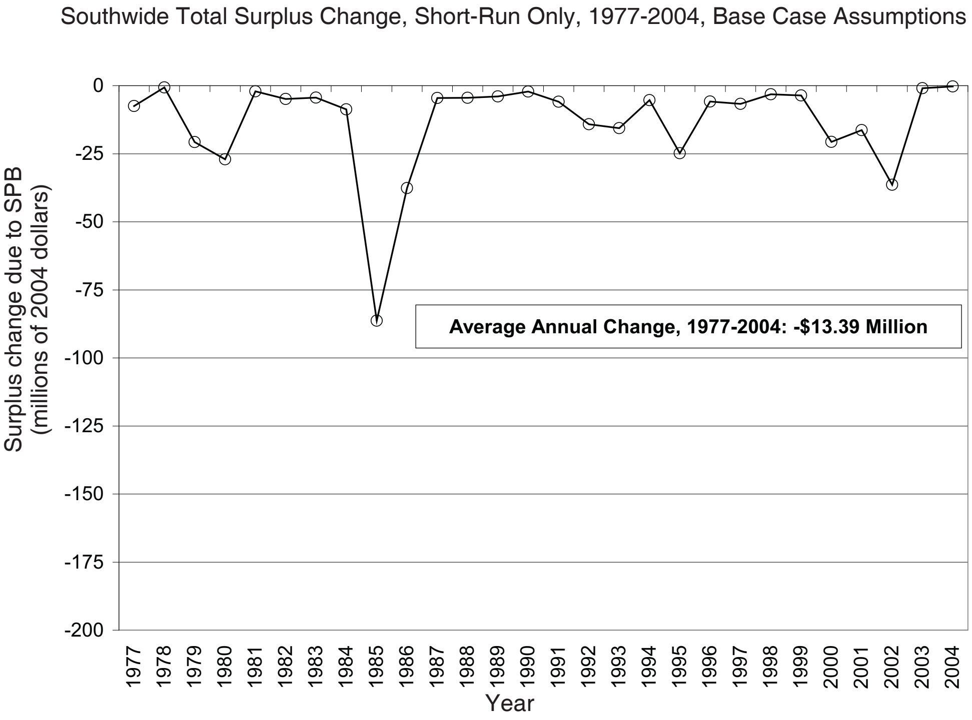

Figure 14.3—Southwide net short-run timber market impacts from SPB, 1977–2004.

outbreak, timber producers often try to limit their losses by harvesting and selling damaged trees to local mills. Live, undamaged buffer trees are also harvested and sold in an attempt to control the growth of SPB spots. The resulting pulse of salvaged and green timber depresses timber prices as local timber markets become saturated.

The pulse of salvaged timber, and lower-than-normal market prices, has a quite different effect on mills purchasing timber. Much of the value lost by timber owners who sell timber during the salvage period is transferred to wood-using mills, causing the aggregate short-run impacts described above to be potentially misleading. For example, although the aggregate short-run timber market losses occurring during the 1984–86 epidemic totaled about $133 million (Figure 14.3), the losses experienced by timber owners—due to the price depression—was approximately $429 million (Figure 14.4). A large share, but not all, of the short-run losses experienced by timber owners was transferred to wood-using firms in the form of low-priced timber. We estimated that, during this epidemic, wood-using firms gained roughly $296 million due to the availability of low-priced timber (Figure 14.5). During the 28 years for which we have data, timber producers have lost about $1.2 billion to the SPB, or about $43 million per year, and wood-using firms have gained about $837 million or about $30 million per year due to SPB outbreaks.

14.3.3. Long-Run Aggregate Impacts

As described above, the reduction in standing inventory due to SPB outbreaks causes a long-term shift in the amount of timber that is available for harvest during the subsequent rotation. A smaller volume of timber available for harvest creates a price increase in local timber markets, assuming the level of demand doesn't change from preoutbreak levels. As the timber inventory regrows during the subsequent rotation, prices gradually subside to precatastrophe equilibrium levels. Until then, the scarcity-induced, higher-than-normal price levels provide benefits to timber owners who hold stands of undamaged timber. Conversely, the higher prices reduce profits for wood-using mills that must pay a higher-than-normal price for timber.

The long-run impact of timber shortages caused by SPB epidemics, as a proportion of annual timber market benefits, is substantial and varies by state and year (Figure 14.6). For example, the epidemic of 1984–86 was severe enough to cause a long-run loss roughly equivalent to an entire year of timber market benefits in Louisiana and roughly 7 months (62 percent) of timber market benefits in Texas. While attributable to just a few years of

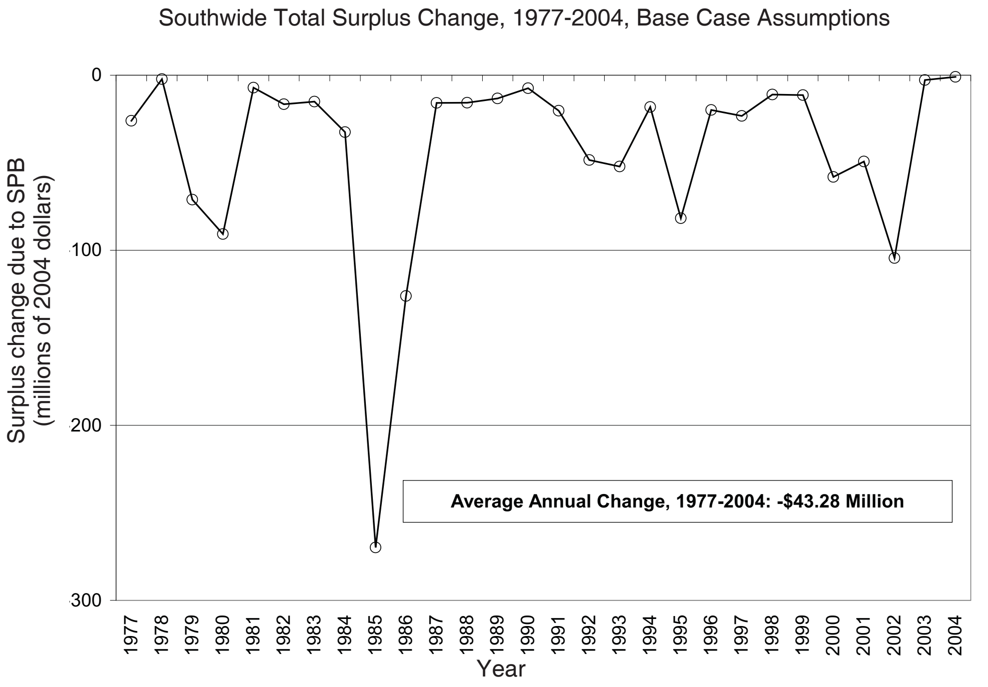

Figure 14.4—Southwide short-run losses to timber owners from SPB, 1977-2004.

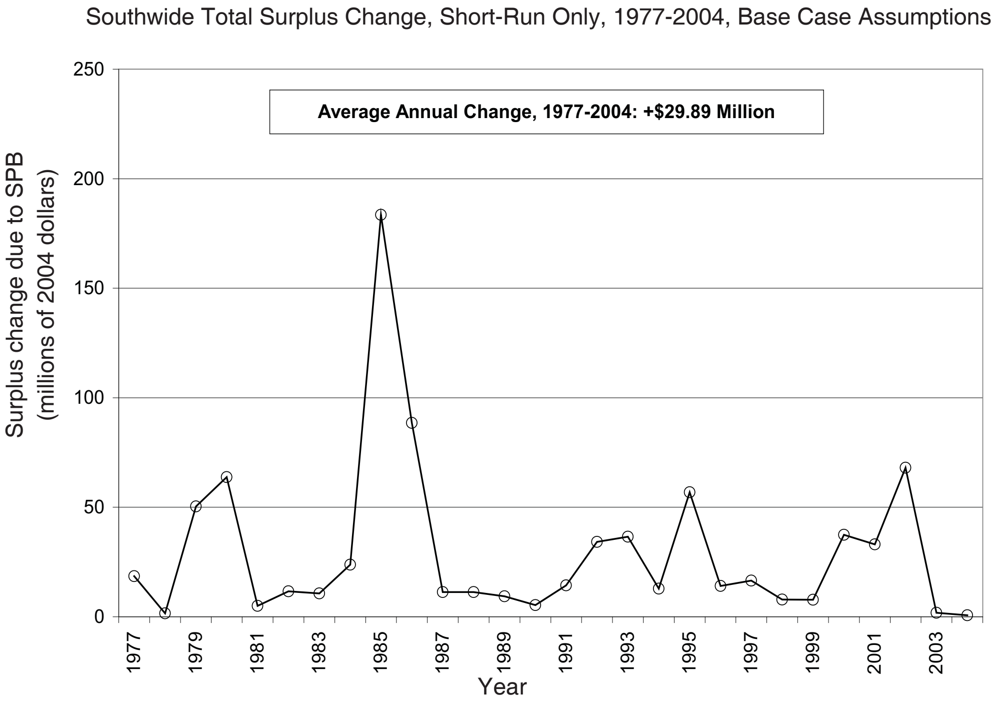

Figure 14.5—Southwide short-run gains to wood-using mills from SPB, 1977-2004.

outbreak, these long-run impacts are in practice spread across decades, and should diminish most quickly for pulpwood markets and only later for sawtimber markets.

14.4. DISCUSSION

Timber growing involves the risk of losses from a variety of disturbances including hurricanes, wildfires, and forest insects and diseases. Forestry is a capital-intensive activity because the factory (the growing forest) is also the output, such as wood products, recreational settings, wildlife habitat, or other ecosystem services. Mortality caused by disturbances such as the SPB disrupts the flow of goods and services provided by healthy forests. The loss of the productive capacity of capital invested in pine-dominated forests causes economic losses to the owners of that capital investment, such as the owners of productive timber land. The loss of the productive forest capacity also causes losses to the consumers of the outputs provided by healthy forests.

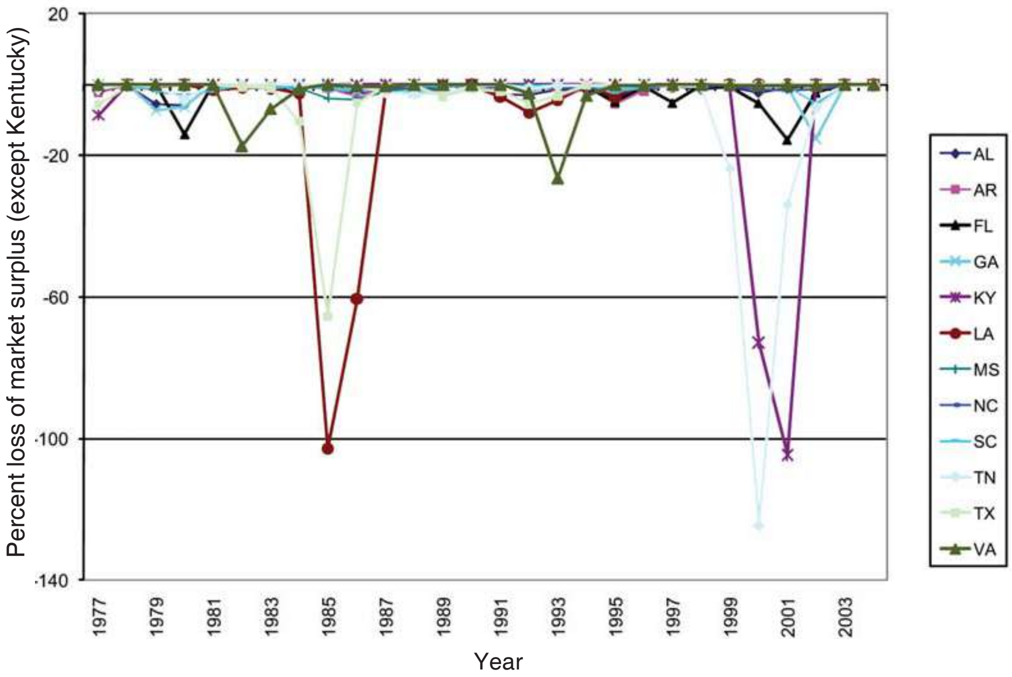

Figure 14.6—Southwide long-run losses to timber owners and wood-using mills from SPB, 1977–2004, as a percentage of annual market benefits.

Although we anticipate that SPB outbreaks cause substantial economic losses to households that consume the nonmarket economic services provided by healthy forests, we have narrowly focused our attention here on changes in values to timber growers and wood-products consumers. Thus, the economic values reported here represent a lower-bound to the total economic impacts of SPB in pine-dominated forests. A complete accounting of the total economic damages from SPB would require new research to estimate the economic impacts of the disruption caused by the SPB on recreational users of forests, on the production of aesthetic values on private and public landscapes, and on the changes in the risk of wildfires.

Because SPB outbreaks disrupt the timing of timber production activities, they have a negative impact on individual timber growers who must alter their production plans. By eliminating the possibility of future value growth on productive timber stands, SPB-induced timber mortality rapidly reduces the opportunity cost on the capital invested in timber production to zero. Thus, timber owners may try to salvage their beetle-killed timber to recover some economic value before it is lost.

In cases where SPB-induced mortality is widespread, such as during epidemics, many timber owners may attempt to salvage their timber or perhaps harvest healthy timber before it is attacked. In aggregate, this accelerated harvest of timber affects its overall supply. The pulse of timber entering the market during epidemic conditions reduces market prices for all timber owners. However, due to the loss in timber inventory, timber supply may shrink for many years following epidemic conditions.

Because the broadscale effects of accelerated harvesting impact all timber owners in the affected areas, governments may play a role in reducing the negative impacts on timber producers. If government-held forest lands are affected by an SPB epidemic, one action public forest managers can take is to withhold their beetle-killed timber from the market so that timber prices are not further depressed. To assist private landowners who wish to salvage beetle-killed timber, governments may aid the salvage process by temporarily adjusting weight restrictions on public roads. Governments may also advise forest landowners with healthy forests to forego timber harvesting until the pulse of beetle-killed timber clears the market and prices return to more normal levels.

14.5. APPENDIX A: ECONOMIC IMPACTS OF A SALVAGE HARVEST

In equation form, the landowner expects to reap a discounted or present value from managing the forest stand prior to the outbreak:

$$NPV^U = [p_U V_T - c_U]\, d^{-(T-a)} - Rd^{-(T-a)} + [p_U V_T - c_U]\, d^{-(2T-a)} - Rd^{-(2T-a)} + Zd^{-(2T-a)}$$

where NPV^u is the net present value anticipated for future management of the undamaged stand. The first term in brackets refers to the revenue (price [p] times volume harvested [V]) and costs (c) associated with harvesting at the planned rotation age (T=a+n) equal to the current age (a) plus n more years. The d variables are discounting terms that translate costs and revenues in the future to today's dollar value. Regeneration costs (R) are incurred following harvest. The next bracketed term in the equation refers to revenues and costs accruing to the second harvest rotation, and Z refers to the returns of subsequent rotations discounted from the time of the second harvest.

The net present value anticipated for the damaged stand (NPV^D), assuming that timber is salvaged, is defined as:

$$NPV^D = [p_D V_a - c_D] - R + [p_U V_T - c_U] d^{-T} - Rd^{-T} + Zd^{-T}$$

Here, the price received is the price for damaged timber ($p_D < p_U$) and the harvest volume is the volume for a stand of age a ($V_a = V_T - \Delta V$, where ΔV is the difference between standing volume and the volume expected at the planned harvest age).

To evaluate the change in value associated with the salvage harvest, we subtract the value of managing the undamaged stand from the value of managing the damaged stand. The result is the net present value of the economic damage associated with the mortality.

$$\Delta NPV = [(p_D - p_U d^n)V_a] - [p_U \Delta V d^n] - [c_D - c_U d^n] - [R(1+d^n)] - [(p_U V_T - c_U - R + Z)(d^{-T} - d^{-(2T-a)})]$$

The five terms in brackets describe the various costs associated with the SPB damage:

$$[(p_D - p_U d^n)V_a]$$

is the difference in value of harvesting the current standing volume today rather than at the optimal time in the future. Note that this term could be negative or positive depending on the difference between the price of damaged and undamaged timber and the value of the discount factor, but given the deep discount applied to damaged timber, it is likely to be negative.

$$[p_U \Delta V d^n]$$

is the difference in value associated with the loss of growth between today and the optimal harvest age. This leads to an unambiguous loss in value.

$$[c_D - c_U d^n]$$

is the difference between harvest costs for damaged and undamaged stands. This leads to a loss in value since costs are incurred sooner and the harvest costs for damaged stands are likely to be higher.

$$[R(1+d^n)]$$

is the difference in the cost of regeneration associated with moving up the regeneration date. This leads to a loss in value.

$$[(p_U V_T - c_U - R + Z)\ (d^{-T} - d^{-(2T-a)})]$$

represents the change in value associated with the change in timing for the second and subsequent harvests. This contributes a positive offset as subsequent harvests are now scheduled for nearer dates.

The first term above is very likely to be negative; the second, third, and fourth terms are unambiguously negative; and the fifth term is positive. Because of the effect of discounting in all cases we can envision, the negative terms far outweigh the small positive impact in the fifth term. Overall, the economic impacts of the epidemic are associated with: 1. harvesting timber sooner than planned, 2. the price penalty for the damaged timber, and 3. changes in the timing of management costs and subsequent timber harvests.

14.6. APPENDIX B: ASSUMPTIONS USED IN WELFARE ANALYSIS

Estimates of salvage and mortality are taken from www.srs.fs.usda.gov/econ/data/spb/. At that site are also found harvest and inventory estimates abstracted from Forest Inventory and Analysis reports.

Elasticities of supply and demand come from published sources. These are shown in Table 14.1.

In our simulations, we adapted the findings from Holmes (1991) to identify the elasticity of the price change of standing timber with respect to the volume of salvage entering the market. This figure was -0.73, where each percentage of salvage volume as a share of regular (pre-outbreak) harvest volume yielded a 0.73 percent decrease in price.

We also established a multiplier that would be used to compute the long-run consumer surplus impacts deriving from timber mortality. This multiplier was found through a simulation of actual inventory regrowth at varying growth rates, computed price effects due to the inventory losses at assumed elasticities (Table 14.1), and alternative discount rates. At our assumed discount rate (7 percent), growth rates, and elasticities (Table 14.1), the welfare multiplier was found to be 4.40. Applied to each economic measure (consumer surplus, undamaged producer surplus), the current year outbreak's effects on these are multiplied by 4.40 to arrive at the long-run impact, after salvage is exhausted. The simulation employed ordinary least squares and generated a model with an R^2 of 0.98, based on 280 simulated combinations of inventory regrowth and discount rates. In a separate analysis, not reported in our paper, we varied the discount rate, the regrowth rate, and elasticities to evaluate how our economic impact measures would be affected by uncertainties. The long-run multiplier was therefore adjusted to accommodate those variations in discount rate and regrowth using the estimated OLS parameters (Table 14.2).

14.6.1. Kentucky Special Assumptions

The Kentucky volume killed and salvaged for 1999–2001 were based on reported spot numbers for Kentucky. The volumes killed and salvaged were based on the average volumes killed per spot and the average salvaged rate per spot observed in Tennessee, 1995–2004.

Table 14.1—Key elasticities used in the southern pine beetle economic impact assessment

Elasticity	Value	Source
Pulpwood demand elasticity with respect to price	-0.425	(Abt and others 2000)
Pulpwood supply elasticity with respect to price	0.23	(Abt and others 2000)
Pulpwood supply elasticity with respect to inventory	1.00	(Adams and Haynes 1996)
Sawtimber demand elasticity with respect to price	-0.57	(Abt and others 2000)
Sawtimber supply elasticity with respect to price	0.55	(Abt and others 2000)
Sawtimber supply elasticity with respect to inventory	1.00	(Adams and Haynes 1996)
Pulpwood annual regrowth rate	0.05	(Smith and others 2004, p. 71, 110, 114)
Sawtimber annual regrowth rate	0.05	(Smith and others 2004) p. 71, 110, 114.

Table 14.2—Ordinary least squares estimates of the long-run surplus impacts of inventory losses as a proportion of the short-run effects found in the first year immediately following the exhaustion of timber salvage

	Coefficients	Standard Error	t Stat
Intercept	2.44	0.01	242.04
Discount Rate/100	-2.63	0.10	-26.42
Growth Rate	-20.46	0.34	-59.38
Growth Rate squared	98.08	3.05	32.12

15

Ecological Impacts of Southern Pine Beetle

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Abstract

The southern pine beetle (SPB) is the most important biotic disturbance in southern pine forests and causes extensive changes to the forest environment. In this chapter we provide an overview of the ecological impacts of the SPB on forest conditions (the state of the forest) and on forest resources (uses and values associated with the forest). We define ecological impact as the effects—positive or negative—of SPB activities on the forest ecosystem. The impact on forest conditions is the result of widespread tree mortality, which affects ecological processes such as: primary production, nutrient cycling, forest succession, and forest composition and configuration. We discuss how the SPB affects these ecological processes through modification of the physical environment and the temporal distribution of resources. For the ecological impact on forest resources, we emphasize the impacts of SPB on resources that are affected from an ecological point of view (e.g., hydrology and wildlife). Changes in forest structure resulting from SPB herbivory can modify key hydrologic processes that control the quantity and quality of water reaching a stream. The ecological impacts of the SPB on wildlife are the result of changes in the distribution and abundance of plant species and insect populations. Increases in SPB densities directly affect the food available for insectivore birds, mainly bark-foraging woodpeckers. The impacts on wildlife have been deduced from changes in wildlife habitat as a result of SPB infestations. An approach to estimate the impacts of SPB herbivory on wildlife habitat in a forest landscape is introduced.

Keywords

biotic disturbance
ecological impact
forest succession
hydrology
nutrient cycling
primary production
wildlife habitat

15.1. INTRODUCTION

The structure, function, and processes of forest ecosystems have evolved with natural disturbances such as fire, windthrow, and pest epidemics (Crow and Perera 2004). In the Southeastern United States, southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is the most important biotic disturbance and, along with fire, regulates the dynamics of nutrient cycling and succession of pine forests. Southern pine beetle outbreaks cause extensive change in forest conditions (the state of the forest environment) by modifying the processes of primary production, nutrient cycling, ecological succession, and the size, composition, and configuration of forest trees. The cumulative effects of SPB outbreaks can impact forest resources (uses and values associated with the forest environment) such as timber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, real estate values, biodiversity, endangered species, and cultural resources (Coulson and Stephen 2006). It is obvious that the impact on forest resources results in economic losses to forest landowners (economic impact) and affects how humans perceive and use the forest environment (social impact); these topics are discussed in chapters 14 and 16 respectively.

For the purposes of this chapter, ecological impact of the SPB is defined as the effects of SPB herbivory on the forest ecosystem. The effects can be perceived as qualitative or quantitative changes in conditions and resources associated with the forest ecosystem, and can be positive or negative (Coulson and Stephen 2006). The most evident impact of SPB herbivory on pine forests ecosystems is the reduction or mortality of host tree species. Tree mortality by insect herbivory results in increased light penetration through the forest canopy, reduced competition among plants, changes in plant species composition and biomass, increased rates of water runoff and nutrient leaching, higher rates of litter decomposition, and redistribution of nutrients (Coulson and Witter 1984). One ecological effect of SPB outbreaks is the shift of forest structure from mature and overmature host trees to regenerating seedlings and competing vegetation species (Land and Rieske 2006). This shift is known to influence other ecological processes such as nutrient redistribution, ecosystem succession, and alteration of wildlife habitat (Coulson and Witter 1984).

Evaluating the ecological effects of the SPB has been a more difficult task than characterizing its social and economic impacts. Understanding of the natural role of the insect is essential for a true understanding of the impact (Stark 1987). Insufficient and inadequate historical data and lack of ecological theory have limited the efforts to evaluate the probable role of the SPB in forest ecosystems. In spite of this, considerable research has been made on the role of the beetle as a regulator of southern forest ecosystems at multiple scales (Coulson and Stephen 2006, Raffa and others 2008, Schowalter and others 1981a).

The goal of this chapter is to present a current overview of the existing information on the impacts of SPB herbivory on forest ecosystems. The specific objectives are: 1. to consider the effects of the SPB on forest conditions (the state of the forest) and 2. to examine the effects of SPB herbivory on forest resources (uses and values associated with the forest). Figure 15.1 outlines the organization of the topics covered in this chapter. Although forest resources are considered in this review, we place emphasis on the impacts of the SPB on resources that are affected from an ecological point of view (e.g., water quality and quantity, wildlife, endangered species).

15.2. SPB IMPACT ON FOREST CONDITIONS

Widespread tree mortality by SPB herbivory modifies the structure, composition, and function of southern pine ecosystems. This section examines how the SPB brings about change in the forest environment. It considers how SPB outbreaks influence the abundance, composition, and configuration of forest vegetation through modifications of the physical environment and the spatial and temporal distribution of resources. The ecological processes of primary production, nutrient cycling, ecological succession, and forest composition and configuration are addressed in further detail.

15.2.1. Primary Production and Nutrient Cycling

Little is known about the effects of SPB outbreaks on ecosystem processes such as primary production and nutrient cycling. Insect herbivory may stimulate forest productivity by

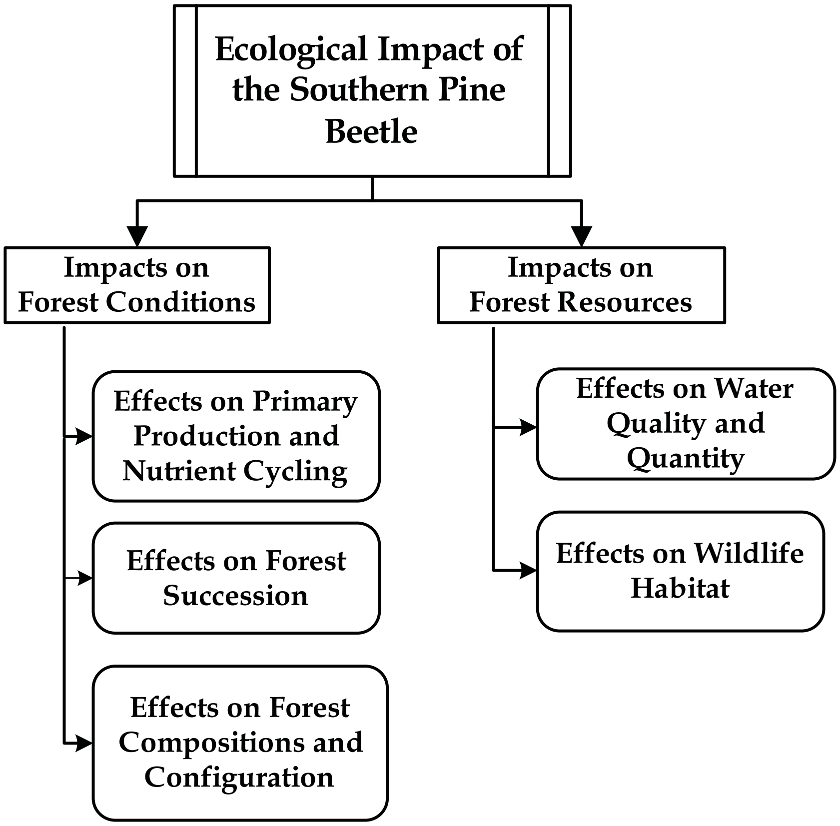

Figure 15.1—Diagram outlines the topics and organization of chapter 15. The probable impacts of the SPB on forest conditions and forest resources are examined.

selectively killing less productive plants or plant parts, therefore enhancing light, water, and nutrient availability for the survivor individuals (Mattson and Addy 1975). In general, nutrients become locked up in living biomass as mature ecosystems tend to have more closed nutrient cycles, with internal nutrient cycling exceeding nutrient input and output (Schowalter 1981). Insect herbivory accelerates the nutrient cycling by weakening/killing plants and increasing nutrient transfer from these nutrient-rich plants to the litter/soil complex. In addition, plant mortality releases resources such as space, nutrients, and light, increasing the establishment and vigor to other vegetation.

Successfully SPB-infested trees are usually dead within weeks of colonization. Resource distribution occurs as a result of leaf fall episodes lasting a few months and the falling of dead trees over a period of years (Romme and others 2006). The SPB selectively kills suitable mature host trees, and subsequent mortality increases nutrient release from pine biomass and increases growth of remaining trees (Schowalter 1981). A review of the literature revealed that no direct estimates on primary production and nutrient cycling following an SPB outbreak have been reported. In contrast, Romme and others (1986) reported that after a mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) outbreak, stand level primary productivity declines and leads to a more equitable distribution of biomass and resources. With time, individual surviving plants respond to the changes produced by the beetle outbreak and plant growth accelerates. The authors described growth increases of 20-70 percent in canopy lodgepole pines, and by 60-260 percent in understory vegetation for a period of 5-20 years after the outbreak.

15.2.2. Forest Succession

The SPB is the primary biotic agent affecting yellow pine forest ecosystems, and, in association with fire, determines the successional dynamics in these forests (Clarke and others 2000, Coleman and others 2008, Lafon and others 2007, Waldron and others 2007). Schowalter and others (1981a) suggested the interaction of SPB herbivory and fire disturbance as a mechanism to maintain early-successional southeastern coniferous forests, therefore preventing ecosystem development toward later-successional, shade-tolerant hardwood forest. These authors proposed that herbivory by the insect served to truncate ecosystem succession at a time when the forest had become stagnant or overconnected (Coulson and Stephen 2006).

Forest succession is a dynamic and cyclic process in which the normal conditional states of the forest change through time (Figure 15.2). In the Holling (1992) scheme of ecosystem succession (also known as adaptative cycle), the dynamics of the process include four stages: exploitation, conservation, release, and reorganization (Figure 15.3). These stages roughly correspond to birth (establishment), growth, death (disturbance), and renewal steps found in Figure 15.2. Each preceding stage of the cycle creates the conditions needed for the next stage. In the exploitation stage, establishment of early successional communities occurs. The transition from the exploitation to the conservation stage is slow; the system builds biomass (growth), connectedness, and potential for change. In the release stage (also known as "creative destruction") the accumulated and tightly bound biomass and nutrients are suddenly liberated by disturbances such as insect outbreaks, forest fires, or hurricanes. Rapid change and restructuring characterizes the transition from the release (disturbance) to the reorganization stage. The system collapses and begins to reorganize, and resources (e.g., light, nutrients, moisture) become available for the next phase of exploitation.

Within this scheme, the SPB serves as the agent of creative destruction, and its actions result in the release of biomass and nutrients (Coulson and Stephen 2006). The direction of ecological succession will be determined by the conditional state of the forest where the outbreak occurs and the severity of the attack. For example, Harrington and others (2000) observed that small patch mortality by the SPB increased structural complexity of late-successional pine-hardwood stands, and increased abundance of snags and dominance by late-successional hardwood species, indicating a hastening of succession towards the climax forest. In contrast, severely disturbed pine stands often resemble gaps containing early-successional vegetation; these conditions favor shade-intolerant species to get established and regenerate (Coleman and others 2008). Light, space, nutrients, soil, and moisture are released to early successional plants, which respond with greater gain in diameter, height, basal area, and volume (Coleman and others 2008).

Following an outbreak, overstory tree mortality by the SPB opens the canopy and changes the

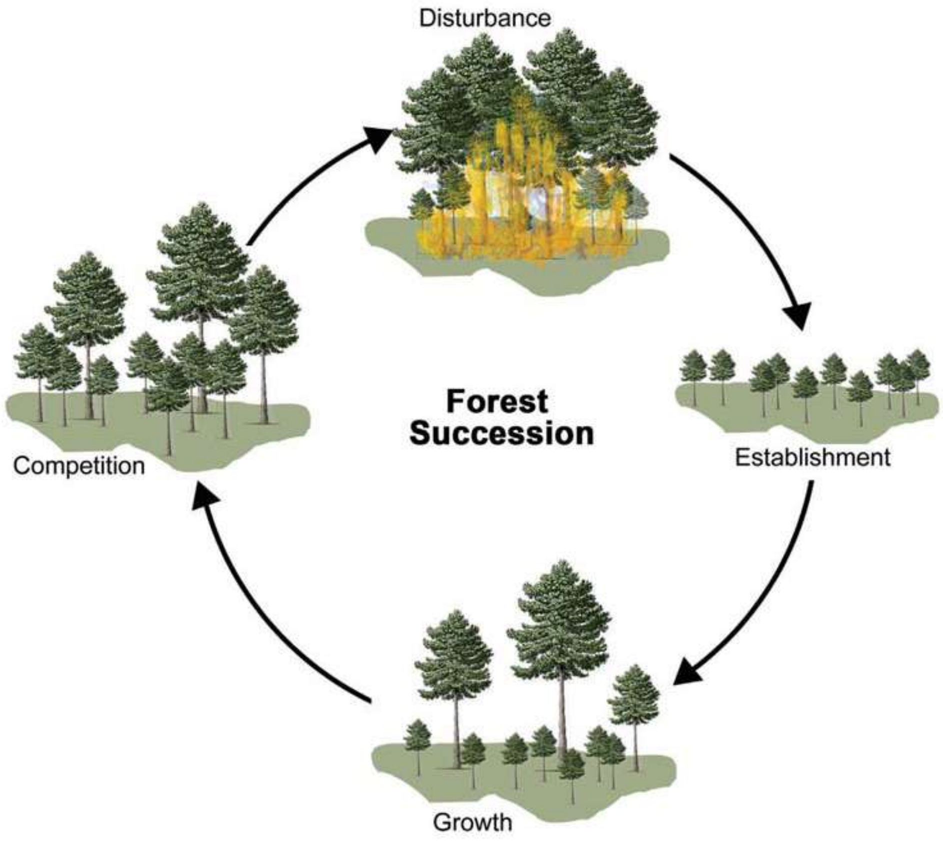

Figure 15.2—Forest succession dynamics. This figure depicts the conditional states of the forest changing through time. These states include: establishment, growth, competition, and disturbance. (modified from Bonnan 2008)

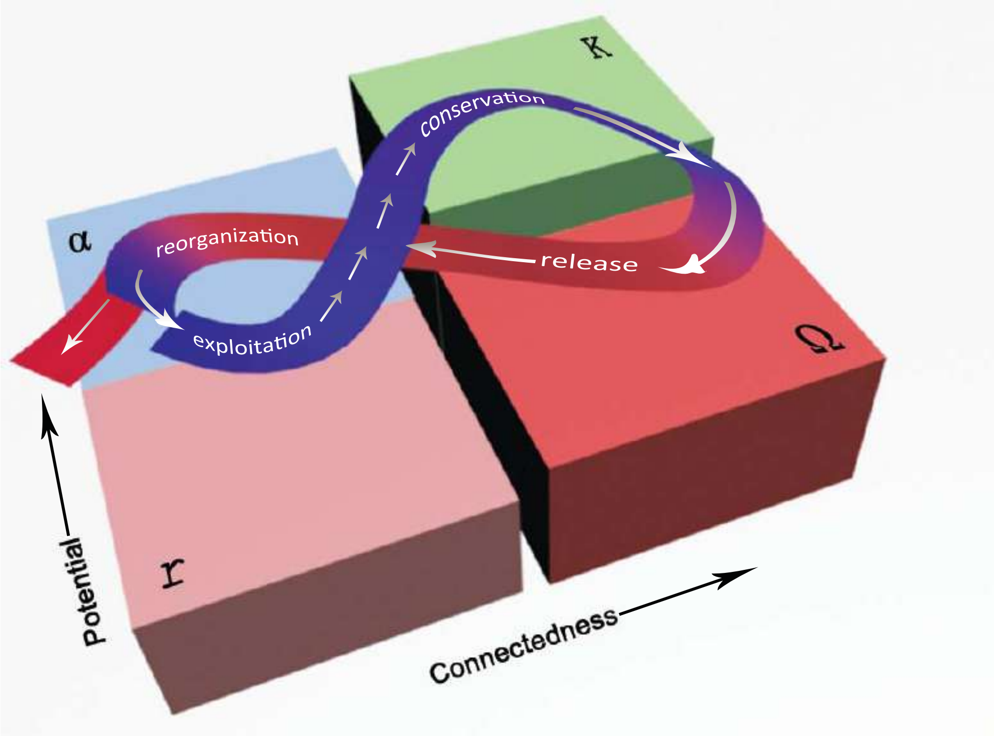

Figure 15.3—The general model of ecological succession. The stages of growth or exploitation [r], conservation [k], collapse or release [Ω], and reorganization [α] and the flow of events are illustrated in the figure. The speed of the flow in the cycle is shown by the arrows: short and closely spaced arrows indicate a slowly changing situation, and long arrows indicate a rapidly changing situation. (modified from Holling 1992)

pattern of light penetration to the understory. Abundance and composition of understory vegetation are significantly changed, favoring the establishment of shade-intolerant species and releasing competing vegetation. When the stands suffer extensive damage of canopy and subcanopy, ecological succession is reset to the herb, shrub, or sapling stage (Schowalter and others 1986). Leuschner and Maine (1980) estimated a 340-1700 kg/ha increase in herbage production beneath loblolly pine stands following mortality by the SPB. Similar results have been reported for the MPB. McCambridge and others (1982) documented increases of 555-962 kg/ha in understory vegetation beneath two ponderosa pine stands 3 years after a MPB infestation, and Kovacic and others (1985) described increases of 1,000-2,000 kg/ha of herbaceous biomass in ponderosa pines 5 years after MPB outbreaks. The increase in biomass following this type of disturbance is predictable based on a well-documented exponential inverse relationship between understory biomass and overstory canopy cover in many forest ecosystems (Stone and Wolfe 1996).

15.2.3. Forest Composition and Configuration

SPB herbivory plays an important role in the abundance, composition, and configuration of tree stands in southern pine forests. Outbreaks have been associated with stand conditions and climatic factors that stress the forest at the landscape level. Coulson and others (1999b) defined three types of habitat targets required by the insect in a forest landscape mosaic: acceptable host species (loblolly pine [*Pinus taeda*], shortleaf pine [*Pinus echinata*], slash pine [*Pinus ellioti*], and longleaf pine [*Pinus palustris*]), susceptible habitat patches, and lightning-struck trees. The SPB often selects older age classes of their preferred host species with high basal area and stagnant radial growth; such stands are considered to be high hazard for infestation (see chapter 22). Herbivory occurs initially in high-hazard stands; however, when insect populations become large, less preferred host species are also infested. The occurrence of high-hazard stands with high adjacency and connectivity increases the severity of the bark beetle outbreaks (Raffa and others 2008).

Large tree mortality by the SPB creates both structural and age class diversity within forest landscapes; i.e., more and different kinds of patches. How the outbreaks alter and fragment the pine forest is very much a function of the initial structure of the landscape. Cairns and others (2008b) suggested that highly aggregated forest landscapes will be characterized by more extensive insect infestations, greater outbreak severity, and larger disturbed patches than less aggregated forests. Their simulation results revealed "that insect disturbances can restructure a landscape in ways that influence the continued impact of that disturbance agent", and are consistent with outbreak observations in actual landscapes. Coulson and Wunneburger (2000) described an instance of how the SPB introduced a new age structure and resulted in fragmentation in the Little Lake Creek Wilderness Area on the Sam Houston National Forest in Southeast Texas. The 1,495 ha wilderness area was a homogeneous landscape vegetated with uniform old-growth pines (Figure 15.4A). SPB infestations occurred in the pine forest and created disturbed patches of killed trees (Figure15.4B). Pine regeneration within the disturbed patches followed, introducing a new age structure to the forest landscape. Years later, another SPB outbreak killed the remaining old-growth pines (Figure 15.4C). Once more, pine regeneration occurred in the disturbed patches. As time progressed, the pines in the initial infestations grew into the oldest age class in the landscape (Figure 15.4D), creating a template for future SPB outbreaks. Herbivory by the SPB modified the initial structure of the wilderness area by introducing age class diversity, resulting in a fragmented and heterogeneous forest landscape. Infestations of the SPB will occur as the forest matures; however, the impact will be less significant because of the fragmented suitable habitat (e.g., large continuous areas of old-growth pine no longer exists).

15.3. IMPACT OF SPB ON FOREST RESOURCES

The uses and values of the forest environment (forest resources) are intrinsically linked to the utilization of the forests by humans. Forest management planning considers the manipulation of human activities to achieve the desired conditions of forest resources. In this section we examine how the cumulative effects of the SPB impact forest resources. Although effort has been directed to the evaluation of impact on forest goods and services (e.g., timber production, real state, recreation), we focus on the forest resources that have an ecological impact as a result of SPB activity. The potential effects of SPB on hydrology and wildlife are examined below.

15.3.1. Hydrologic Impacts

Changes in forest structure resulting from bark beetle activity can modify key hydrologic processes that control the quantity and quality of water reaching a stream within a forested watershed (Figure 15.5). Interception, evaporation, transpiration, and groundwater storage processes may be affected by bark beetle herbivory. The hydrologic impacts can be measured in terms of annual water yield, peak flows, low flows, soil moisture, groundwater levels, and water quality (Uunila and others 2006). In general, changes in water quantity and quality occur in response to beetle-induced tree mortality. Removal of forest canopy results in a temporary increase in water yield as a result of a substantial reduction of water loss

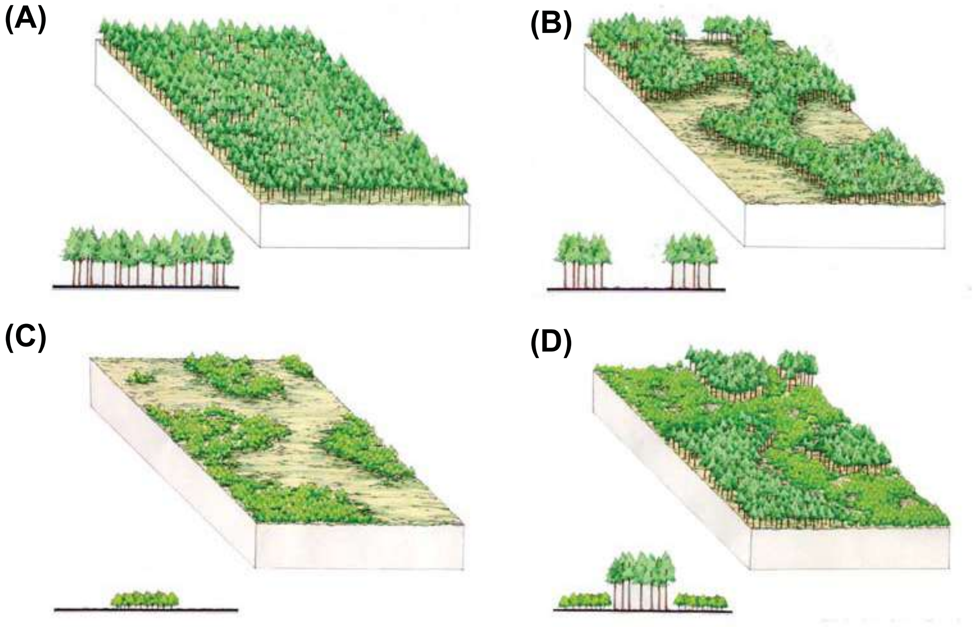

Figure 15.4—The effects of SPB herbivory on forest landscape structure and composition. (A) Homogeneous landscape with uniform old-growth pine optimal for SPB outbreaks. (B) Several infestation of SPB occurred and created disturbed patches of killed trees. (C) Another SPB outbreak killed the remaining old-growth pines. (D) Pine regeneration occurred. SPB herbivory introduced a new age structure and resulted in fragmentation of the forest. (KEL image)

via evaporation, transpiration, and the amount of precipitation intercepted by healthy trees. The magnitude of the responses is dependent on local climatology, forest age and species composition, understory response, and severity and location of the infestation (Elder and others 2008).

There are very few studies on the effects of bark beetle outbreaks on the hydrologic cycle of forested watersheds. A review of literature on large-scale beetle epidemics and their possible impact on hydrology was compiled by Hélie and others (2005) and Uunila and others (2006). The authors agreed that the published research on the topic is very limited and suggested that the effects of bark beetles on forest hydrology may be similar to those experienced after forest harvesting. In contrast to the bark beetle impact on the hydrologic cycle, the impacts of forest harvesting on hydrologic processes have been widely documented in the literature. These studies may contribute considerable knowledge on forest hydrology useful for understanding the potential impact of bark beetle infestations.

For the SPB, even less published research exists on the effects of herbivory on hydrologic processes. In one of such studies, Leuschner and others (1979) used a hydrologic simulation model to estimate changes in water yield after an SPB outbreak. They examined changes in water yields as stand basal area decreased at three different sites with high, average, and low precipitation. The authors reported a yield increase between 0.3-9.0 acre-inches per year for an acre of SPB spot, depending on the site, original basal area, and the amount of basal area reduction. Using these estimates on data from a real infestation in the Sam Houston National Forest, Leuschner (1980) concluded that the impact of the SPB on water yield is small and its impact on water quality is null. However, the author acknowledged that this conclusion was based on an infestation with small and dispersed spots and contended that the conclusions could change if the infestation configuration is large and contiguous. Uncertainty about the effects of SPB outbreaks on hydrologic processes leads to the following key research questions:

- How do small infestations compare in their hydrologic impact with larger infestations?
- How do density, type, and extent of forest understory affect hydrologic response?
- How do location, elevation, aspect, and weather control the hydrologic impacts of the SPB?
- What is the impact of standing dead timber on key hydrologic processes?

Despite the lack of reported research on the effect of SPB herbivory on water quantity and quality, insight could be gained from the extensive existing literature on harvesting and its effects on the hydrologic cycle in forested areas of the South (for a good review on this topic see Grace 2005).

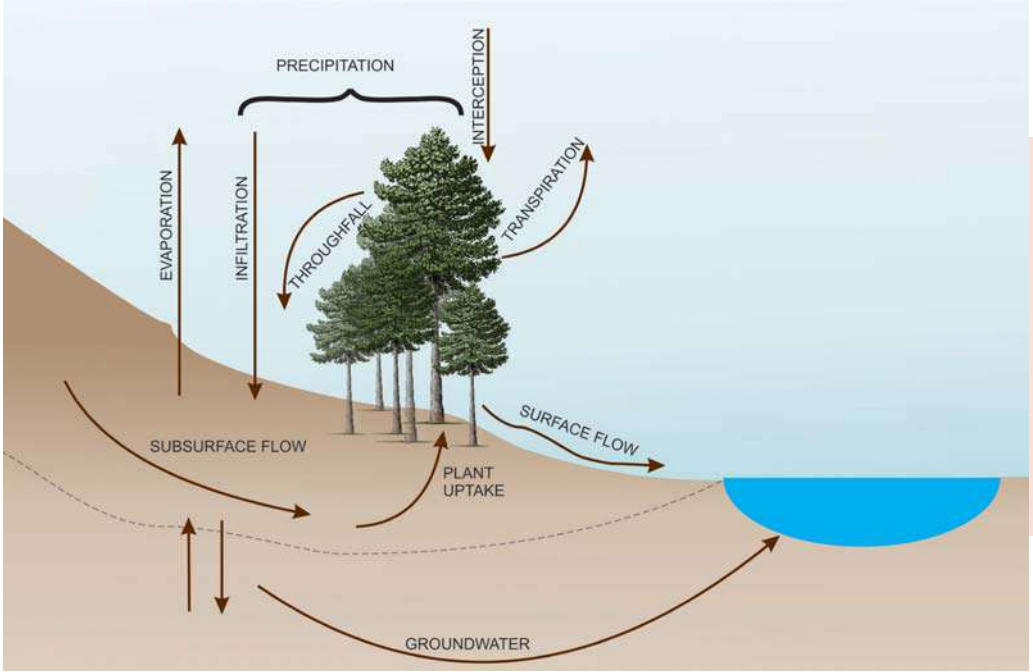

Figure 15.5—The forest hydrological cycle provides a model for understanding the movement of water in a forest landscape. Large tree mortality by SPB herbivory can alter key ecological processes that control the quantity and quality of water reaching the stream. (modified from Hélie and others 2005)

15.3.2. Wildlife Impacts

The impacts of the SPB on wildlife are the result of changes in the distribution and abundance of forest plant species and insect populations. During outbreaks, modifications in vegetation density, species composition, and age structure are likely to have cascading effects on wildlife food resources and habitat structure. Leuschner (1980) indicated that the primary or direct impact of the SPB occurs when it is a food for some species; i.e., outbreaks of the SPB may benefit populations of bark-foraging woodpeckers. The secondary or indirect impacts occur when SPB activities modify the structure and composition of the forest, causing changes in shelter, cover, and food available for the wildlife species inhabiting the forest.

Measuring the impacts of SPB herbivory on wildlife has a number of challenges. First, long-term studies of wildlife populations are needed to permit comparison of unimpacted and impacted populations during epidemic and post-epidemic conditions. Second, direct measurements of wildlife populations are difficult due to the labor-intensive censusing techniques and the associated costs. And third, more attention is given to the impact of the SPB on economic resources (e.g., timber production) during beetle epidemics. As a consequence, a limited number of studies have measured the impact of the SPB on wildlife. The few attempts have been focused on changes in habitat as a result of altered forest conditions caused by SPB herbivory.

In the following section we summarize information on how SPB outbreaks affect wildlife. We first consider the direct impacts of the SPB as a source of food to insectivores, primarily woodpeckers. We then examine the indirect effects of the SPB as it modifies habitat suitability for wildlife (e.g., birds and mammals).

Impact of the SPB on Woodpeckers

Pulses of food caused by SPB outbreaks increase the food available to insectivore birds, mainly bark-foraging woodpeckers. Southern pine beetle-infested trees represent a concentrated food source that is prized by the birds. Kroll and Fleet (1979) studied the impact of four woodpecker species (Downy [*Picoides pubescens*], Hairy [*P. villosus*], Pilaeted [*Dryocopus pileatus*], and Red-cockaded woodpeckers [*P. borealis*]) on populations of the SPB in East Texas. Their results showed that all four species preyed heavily on the beetles and had a significant impact on the densities of SPB pupae and adults. As a consequence of food availability, woodpeckers were found in higher numbers in infested SPB stands than when compared to uninfested SPB stands. According to Conner and others (2001a), woodpeckers show a "boom and bust" relationship with the SPB. Woodpecker densities initially increase with beetle abundance and then decline sharply as beetles run out of susceptible trees. Fayt and others (2005) identified the functional responses of woodpeckers associated with spruce bark beetles outbreaks. They suggest that the increase in woodpecker densities represents a combination of responses, in which the birds respond to higher prey densities by increasing the proportion of spruce bark beetle in the diet (i.e., predatory impact), and true numerical responses, in which the local woodpecker numbers increase as a result of aggregation or population growth to increases in beetle densities. These functional responses may apply in other woodpecker-bark beetle interactions; e.g., outbreaks of the SPB.

Red-cockaded woodpecker

Within the woodpecker guild, the relationship between the SPB and the red-cockaded woodpecker (RCW) is more complex and deserves special attention. The RCW (Figure 15.6) is an endemic species to the South that requires a constant supply of living, old pines with decayed heartwood (Conner and Rudolph 1991). Red-cockaded woodpecker populations declined dramatically as a result of logging, fragmentation, and suppression of fire in southern pine forests. Its preference for old-growth pines, particularly longleaf pine, and the loss of that habitat have resulted in the woodpecker becoming an endangered species (Jackson 1994). Southern pine forests, primarily longleaf, shortleaf, loblolly, and slash pine, are a critical resource to the RCW for cavity excavation and a key element for its recovery (Conner and others 1998).

Red-cockaded woodpeckers look actively for living old pines for cavity excavation, and these are the same trees susceptible to SPB attack. The cavity trees they create are essential for reproduction and roosting (Conner and others 1997). Red-cockaded woodpeckers peck shallow excavations, termed resin wells, around the entrance to the cavity. The resin exuded from the trees serves as a barrier against climbing rat snakes (*Elaphe* spp.) (Rudolph and others 1990).The volatile terpenes associated with the resin appear to increase the preference/vulnerability of such cavity trees to SPB attack. Conner and Rudolph (1991) reported that SPB infestations are the major cause of RCW cavity tree mortality in loblolly and shortleaf pines. The SPB can eliminate active single cavity trees, cavity tree clusters, and foraging habitat of the RCW, creating a potential problem to the conservation and recovery of the bird (Conner and others 1998).

Coulson and others (1999a) examined the nature of the interaction of the SPB and the RCW based on how the organisms perceive and respond to the elements of the forest landscape. They concluded that the interaction can be explained by the fact that there is spatial and temporal coincidence of the insect and the bird within the landscape; namely, the organisms respond to the same structural elements of the forest (i.e., similar habitat preferences). One important observation made by the authors is that the degree of the interaction is subject to the composition of tree species in the forest landscape. For instance, SPB outbreaks occur much less frequently in longleaf pine forests. Longleaf pine produces greater resin yield than any of the other southern pines. Resin yield production by the host trees is considered to be the primary defense mechanism against colonization by bark beetles. In contrast, nest site selection by male RCWs is directed to pines having high yield resin (Conner and others 1998). Given a preference, the RCW selects forests containing longleaf pine for nesting, roosting, and foraging. Therefore, longleaf pine-dominated forest landscapes minimize the interaction between the bird and the beetle (Coulson and others 1999a). The loss of longleaf pine forests and the replacement of this species with loblolly pine over large areas of the South have greatly increased the potential for a negative impact of the SPB on the RCW.

Impact of the SPB on Wildlife Habitat

Following an SPB outbreak, stand parameters such as vegetation density, species composition, and age structure are quite different from those that dominated before the infestation. These changes in vegetation have an effect on habitat structure and food resources to wildlife species living in the forest. The magnitude of the impact on wildlife species composition, distribution, and abundance depends on the degree to which resultant modifications in vegetation increase or decrease the resources necessary for reproduction and survival. The responses of individual species may differ significantly based on the ecological requirements of the species, the differences among the stands, and the ability of the species to exploit modified habitat (Matsuoka and others 2001).

Figure 15.6—The red-cockaded woodpecker (*Picoides borealis*). This endangered species looks actively for living old pines for cavity excavation, and these are the same trees susceptible to SPB attack. (USDI FWS photograph taken by Eric Spadgenske)

Published research on the probable impacts of the SPB on wildlife habitat is very limited. Most of the information available has been inferred by integrating published data on known biological associations (e.g., preferred habitat, food requirements, natural history) in terms of the altered forest conditions caused by the SPB. These studies have been qualitative because of the challenges associated with measuring wildlife populations. Maine and others (1980) conducted a qualitative study on the impact of SPB infestations on wildlife. They estimated the impact on amount and kind of food due to changing overstory and understory vegetation for several wildlife species (e.g., woodpeckers, turkey, quail, other birds, squirrels, deer, small mammals). The authors concluded that SPB outbreaks have a positive impact on wildlife, mainly due to increased food and habitat diversity. Other information has been the result of direct observations made after bark beetle outbreaks. For example, Stone and Wolf (1996) indicated that epidemics of bark beetle in pine forests increase the availability of forage and browse to livestock and wildlife, and offer nesting and foraging cover to small mammals and birds.

A major limitation of these studies is that they do not consider the spatial arrangement (configuration) of the SPB-infested stands within the forest landscape. The habitat requirements of wildlife are related not only to the structure of the habitat but also to the landscape surrounding the habitat (Store and Jokimaki 2003). Therefore, quantifying the impacts of the SPB on wildlife habitat requires consideration of infested stand adjacency and spatial configuration within the forest landscape. In the next section, we present an alternative approach for measuring the SPB impacts on wildlife habitat within a spatial context in a forest landscape.

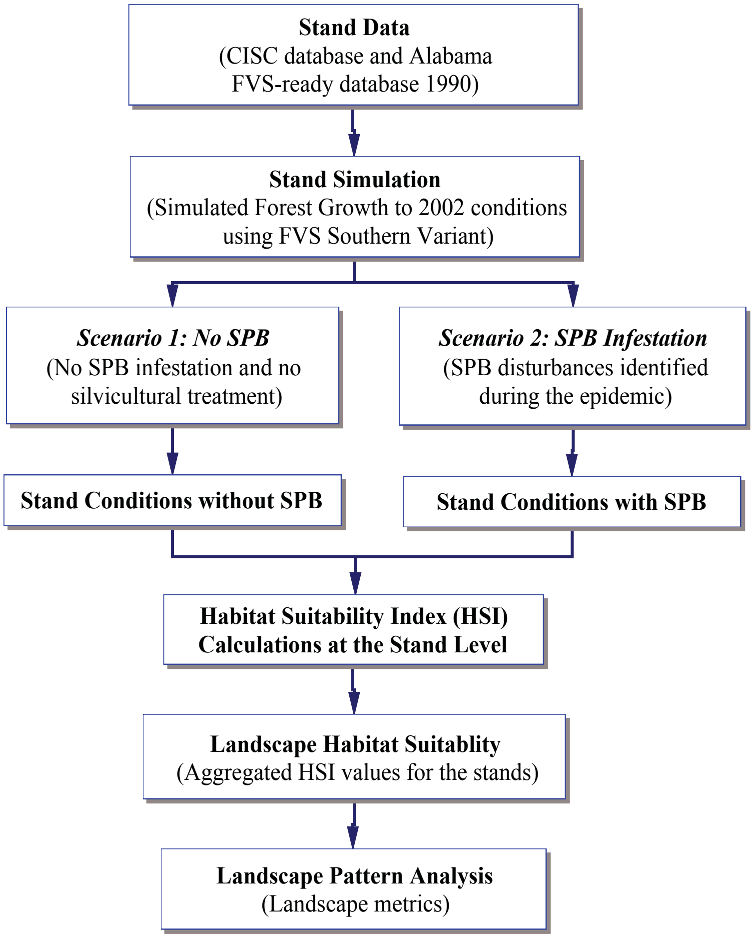

Figure 15.7—Diagram illustrating the methodology in assessing the impact of SPB herbivory on wildlife habitat suitability at the Bankhead National Forest, Alabama. (KEL image)

Estimating SPB impacts on wildlife habitat suitability in forest landscapes, a case study

Approach description. We evaluated how changes in forest landscape composition and configuration resulting from SPB herbivory impact the wildlife habitat suitability in the William B. Bankhead National Forest, AL. From 1998 to 2001, this national forest experienced SPB infestations at epidemic levels, primarily in loblolly pine forests. We used a spatially explicit approach that integrates forest inventory information (FIADB–Forest Inventory and Analysis Database), vegetation growth models (FVS – Forest Vegetation Simulator Southern Variant), SPB infestation data, geographic information systems (GIS) data, and published wildlife habitat suitability indices (HSI) developed by the USDI Fish and Wildlife Service.

To assess the SPB impact on wildlife habitat at the stand and landscape level, we implemented the Habitat Evaluation Procedure (HEP) developed by the USDI Fish and Wildlife Service. Integral to HEP is the use of habitat suitability indices (HSI). These single-species models are based on the premise that habitat suitability can be linked to habitat attributes (i.e., measurements of specific habitat features and environmental variables) by some quantitative functional relationship (Morrison and others 2006). The relationship is represented as HSI value ranging from 0.0, no habitat value, to 1.0, optimal value (USDI Fish and Wildlife Service 1981).

The steps used in the methodology are illustrated in Figure 15.7. Landscape level data included forest stand inventory information (i.e., tree-based measurements) and spatial location and size of SPB spots. The Southern Variant of the FVS was used to simulate forest growth and to project stand conditions under two different scenarios. One of the scenarios allowed the forest stands to grow without SPB herbivory and with no silvicultural treatment. The other scenario included the SPB disturbance identified in the SPB damage stand using the GIS coverage. The projected stand conditions (i.e., habitat variables) were evaluated using published habitat suitability models for four wildlife species: pine warbler (*Dendorica pinus*) (Schroeder 1982), gray squirrel (*Sciurus carolinensis*) (Allen 1982), eastern wild turkey (*Meleagris gallopavo sylvestris*) (Schroeder 1985a), and northern bobwhite (*Colinus virginianus*) (Schroeder 1985b). These species were selected because they are considered management indicator species.

Landscape habitat suitability was defined by preparing maps of aggregated HSI values of the stands within the national forest. Landscape habitat suitability maps were created for each species under the two different scenarios. The resultant HSI values were classified in five categories (Table 15.1), where classes 3 and 4 represent the areas suitable for optimal habitat. The spatial pattern of suitable/optimal habitat areas was analyzed for each map based on landscape metrics calculated with FRAGSTATS version 3.3 (McGarigal and others 2002)

Results and Discussion. The results of the analysis are summarized in Table 15.2; the calculated landscape metrics include: total habitat area (AREA), number of habitat patches (NP), patch density (PD), mean patch size (MPS), and mean core area (MCA). The results from each scenario fluctuate for pine warbler, eastern wild turkey summer food/brood habitat (SFB) and fall/winter/spring food habitat (FWSF), and northern bobwhite, but show no significant change for gray squirrel and eastern wild turkey cover habitat.

Pine warbler habitat area showed a decline of 37 percent for class 3 and 15 percent for class 4 under the SPB infestation scenario. The number of patches and patch density increased, whereas the mean patch size and mean core area decreased, resulting in a more fragmented habitat. The decline in habitat area resulted from reduction in standing volume of late successional pine trees killed by SPB.

The SFB habitat for eastern wild turkey had a considerable increase in all of the landscape metrics in the SPB infestation scenario (Table 15.2). Habitat area for class 3 increased by 1,280 percent as a result of the openings caused by SPB-killed stands. SPB creates openings that promote increased cover, understory growth, and edge that are favorable for SFB eastern wild turkey habitat.

The eastern wild turkey FWSF component showed a decreased in habitat area of 27 percent for class 3 and 8 percent for class 4. Patch number and density increased and mean patch size and mean core area decreased, resulting in a fragmented habitat. The FWSF habitat loss was a consequence of the reduction of pine canopy cover under the SPB outbreak scenario.

The habitat area for northern bobwhite quail increased by 56 percent for class 3. Larger numbers of patches and mean patch size resulted in a more connected habitat under the SPB outbreak scenario. The habitat gain was a result of the reduction of canopy cover, increased edge, and increased understory vegetation created by SPB spots.

Table 15.1—Habitat suitability classes

Classes	HSI Values
0	HSI = 0
1	0.01 ≤ HSI<0.25
2	0.25 ≤ HSI<0.5
3	0.50 ≤ HSI<0.75
4	0.75 ≤ HSI ≤ 1

Table 15.2—Landscape metrics calculated from the aggregated HSI value maps

		Scenario 1(No SPB)					Scenario 2 (With SPB spots)				
Species	Class	AREA	PN	PD	MPS	MCA	AREA	PN	PD	MPS	MCA
Pine Warbler	3	22,822	606	1.47	37.66	6.92	14,464	794	2.57	18.22	2.51
(General Habitat)	4	7,732	372	0.91	20.78	2.76	6,548	404	1.31	16.21	1.96
Gray Squirrel	3	18,624	419	1.37	44.45	9.00	18,293	424	1.95	43.14	8.70
(General Habitat)	4	3,511	99	0.32	35.46	1.63	3,394	101	0.47	33.60	1.44
Eastern Wild Turkey -SFB	2	37,063	356	0.94	104.11	36.23	37,063	356	0.73	104.11	36.23
(Summer Food and Brood Habitat)	3	824	65	0.17	12.68	0.94	11,378	658	1.36	17.29	2.28
Eastern Wild Turkey -FWSF	3	29,875	618	0.87	48.34	12.64	21,572	813	1.37	26.53	5.29
(Fall, Winter, and Spring Food Habitat)	4	41,092	371	0.52	110.76	44.37	37,672	443	0.75	85.04	29.83
Eastern Wild Turkey	3	7,407	259	0.37	28.60	4.30	6,959	272	0.85	25.59	3.52
(*Cover Habitat)*	4	25,519	397	0.56	64.28	14.05	24,937	408	1.28	61.12	13.04
Northern Bob White	3	18,550	419	0.59	44.27	9.29	28,924	626	1.88	46.20	15.15
(Winter Food Habitat)	4	4,402	228	0.32	19.31	2.43	4,401	228	0.68	19.31	2.43

Note: AREA, total area (*ha*); PN, number of patches; PD, patch density (*Patch#/100ha*); MPS, mean patch size (*ha*); MCA, mean core area (*ha*).

Gray squirrel habitat was not affected under the SPB outbreak scenario, mainly because this is a species that inhabits hardwood forests. The winter food HSI model used to evaluate the habitat did not consider pure pine stands which are the most affected by SPB.

The cover habitat for eastern wild turkey did not show a significant change among the SPB scenarios. Although turkeys utilize both hardwood and pine forests, hardwood forest types are preferred for cover. Pure pine stands are not considered suitable/optimal cover habitat for eastern wild turkey

Conclusions. The methodology used in this study facilitates the description of SPB impacts at the stand level of resolution and at the forest landscape level. The integration of stand data, vegetation growth models, and habitat evaluation procedures allowed us to define the suitable/optimal habitat in a forest landscape. Using data from actual SPB infestations, we simulated the effects of SPB outbreaks on the habitat suitability of four wildlife species. The analysis of two different SPB scenarios permits comparison of unimpacted (no SPB) and impacted habitat (with SPB infestations). From this comparison we can draw the following conclusions: The impact of the SPB varied in predictable ways depending on the ecological requirement of the species. Pine warbler habitat was destroyed, grey squirrel habitat was not affected, eastern wild turkey habitat was affected both negatively and positively, and northern bobwhite quail habitat was enhanced. The effect of the insect outbreak was to perforate the landscape, which generally decreased the habitat patch size, increased habitat patch density, increased habitat patch number, and reduced the core of habitat patches for species using pine stands as preferred habitat. One positive aspect of the infestations is that the infested stands provide wildlife habitat components that include early successional vegetation, open canopies, hardwood introduction, and the presence of standing pine snags. These habitat components create conditions for a more diverse wildlife.

15.4. SUMMARY

Large tree mortality by SPB outbreaks causes extensive changes in the forest environment. In this chapter, we examined the ecological impacts of the SPB on forest conditions (state of the forest environment) and forest resources (uses and values of the forest environment). We defined SPB ecological impact as the effects, positive or negative, of SPB herbivory on forest ecosystems. Some of the ecological impacts we investigated are summarized as follows:

- The activities of the SPB may stimulate the ecological processes of primary production and nutrient cycling, having a positive effect on survival vegetation.
- Southern pine beetle herbivory regulates the dynamics of southern pine forests and affects the direction of forest succession, depending on the severity of the epidemic.
- Forest structure is greatly affected by SPB activities. The heterogeneous landscape resulting from repeated SPB infestations is likely critical to maintaining forest diversity.
- The studies of the impacts of the beetle on water quantity and quality have been limited, and more research is needed in this area.
- The SPB affects wildlife directly as a food source and indirectly through changes and modifications of wildlife habitat. Bark-foraging vertebrates are positively affected by the SPB.
- The ecological impact of the SPB on wildlife habitat varies depending on the ecological requirements of individual species.

16

Social and Political Impact of the Southern Pine Beetle

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Keywords

human habitat
impact
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recreation
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ESA
HFRA
NEPA
REIT
TIMO

Abstract

Impact is defined broadly to mean any effect on the forest environment resulting from the activities of the southern pine beetle (SPB). In this chapter we focus on social and political impact. Social impact deals with effects of the SPB on aesthetic, moral, and metaphysical values associated with forests. Two aspects of social impact are investigated: how the SPB affects recreational use of the forest environment, and how the insect affects the human habitat; i.e., the urban/suburban environment. Political impact deals with the effects of the SPB on the forest environment that result in actions, practices, and policies of local, State, or Federal governmental agencies. The mechanism of political impact is the corpus of laws and regulations that have evolved to provide for protection, conservation, and use of public and private forests. Four important acts relating directly or indirectly to SPB political impact are examined: the National Environmental Policy Act (NEPA), the Endangered Species Act (ESA), the Wilderness Act, and the Healthy Forest Restoration Act (HFRA). We conclude with an examination of how corporate taxation laws have affected forest land ownership in the South and the likely consequence on SPB outbreaks in the future.

16.1. INTRODUCTION

In the introduction to Section II of this volume, the term "impact" was defined broadly to mean any effect on the forest environment resulting from the activities of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB). Assessment of SPB impact is a multidimensional task that involves consideration of economic (chapter 14), ecological (chapter 15), social, and political perspectives. Although partitioning the subject of impact assessment into four compartments is convenient for discussion purposes, distinction among the categories is often fuzzy. Clearly, an SPB infestation creates economic loss to a commercial forest landowner. However, in a forest landscape, the infestation also initiates the process of ecological succession and the recycling of nutrients, creates new habitat for wildlife species, and increases plant species diversity. In an urban setting the infestation could change the aesthetic appearance and utility of a public park. In a suburban setting, infested trees in neighborhoods are unsightly, can result in injury to residents, and are a liability on private property.

Impact assessment is a fundamental component of integrated pest management (IPM) (chapter 29). In the activity dependency diagram for IPM (Figure 29.4), impact evaluation involves a reciprocal interaction with SPB population dynamics and host tree and forest dynamics components. The results of impact evaluation feed directly to the environmental assessment component and ultimately to management decision and execution. This flow illustrates how IPM activities link directly to the upper echelons of the management hierarchy; i.e., forest protection ➔ forest management ➔ environmental management.

In this chapter our goal is to summarize contemporary information on social and political impact of the SPB. Our specific objectives are: 1. to examine impact from a human social perspective and 2. to consider political impacts from a statutory viewpoint. Figure 16.1 illustrates the general organization of topics examined in this chapter. Although economic and ecological impacts have been examined in a research context, the knowledge base on social and political impact is largely qualitative and thereby subjective; i.e., neither topic has been considered as the focus of organized or rigorous social scientific research since the 1970s. Accordingly, the approach in this chapter is similar to that taken by L.O. Howard in his 1930 treatise, *A History of Applied Entomology (somewhat anecdotal)*, in that our examination of social and political impact is "somewhat observational and interpretative." The impacts of insects in forest landscapes and the relations to forest health management were examined in detail by Coulson and Stephen (2006).

16.2. SOCIAL IMPACT

Social (axiological) impact refers to the effects of the SPB on aesthetic, moral, and metaphysical values associated with forests. Coulson and Saarenmaa (chapter 29) distinguish among six types of forest, each varying in the degree of ecological integrity and human intervention (Figure 29.1). Although social impacts are often difficult to express in quantitative terms, they are important to a large number of forest users. Interest in social impacts of the SPB surfaces when the insect affects recreational use of the forest environment or when it disrupts the human habitat. Each circumstance is discussed below.

16.2.1. Social Impact Associated with Recreational Use of the Forest Environment

Forests are used for many types of recreation. The most popular include walking, doing nonconsumptive wildlife activities, biking, sightseeing, nonpool swimming, fishing, family gathering, and picnicking. To define the potential or actual impacts of the SPB on outdoor recreation, it is necessary to consider the basic elements associated with the activity. Clawson and Knetsch (1966) identified five distinctly different phases of outdoor recreation: anticipation, travel, on-site experience, travel back, and recollection. The net effect generated to the recreationist of a single recreation experience is a composite of these phases. The SPB can have an impact on recreation by intervening into one or more of the phases. Negative or positive impacts influence not only the individual(s) involved directly in the recreation activity, but also the service industries that provide the facilities and means for recreation (Leuschner 1980).

Economists working with social scientists have attempted to define social impacts in a precise manner by examining patterns of use of forests. In general, aesthetic values stem from

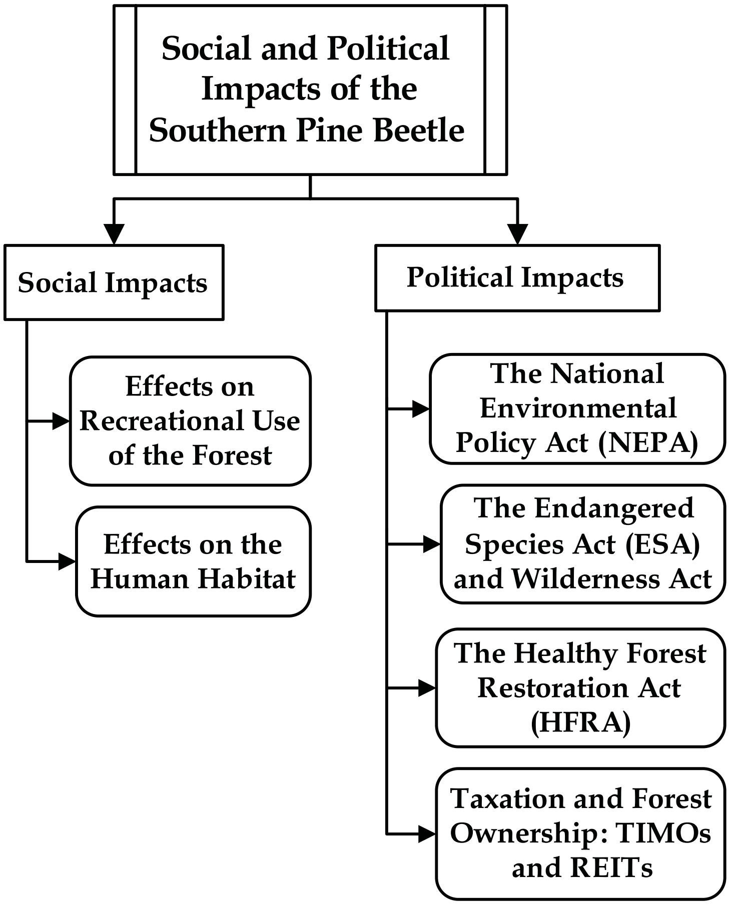

Figure 16.1—Diagram illustrating the organization for this chapter. The discussion considers social impact as it relates to recreational use of forests and effects on the human habitat. Political impact is considered from a statutory perspective.

recreational uses of forest; that is, aesthetic values usually occur in conjunction with other primary activities such as hiking, fishing, and camping. To some degree, which may be very difficult to define, SPB outbreaks can influence the primary activities in both positive and negative ways. For example, infestations may be unpleasant to a hiker, beneficial to a hunter, and inconsequential to a fisherman.

One technique employed by economists in defining social impacts is to measure patterns of recreational use of forests. During or after an SPB outbreak, a recreationist might continue to use a particular site, substitute another site, or no longer recreate (Buhyoff and Leuschner 1978). Of course the type of recreation and degree of distraction created by the SPB outbreak enter into the use pattern (Leuschner and Young 1978). An approach to evaluating social impact is to define human response to the presence of SPB infestations. For example, if a recreationist decided to change campsites because of the presence of an infestation, the added expense to the recreation experience is termed "psychological disutility" (Leuschner and Young 1978, Buhyoff and others 1978). Various motivational factors could influence the decision to change locations; i.e., unsightly appearance of the campsite, presence of dangerous snags, lack of shade, and so forth.

To this point we have emphasized social impacts of the SPB as they relate to individuals physically in the forest and involved in some type of primary activity. Social impacts are also perceived by those individuals who view the forest from a distance. Scenic vistas are often protected and maintained as a part of forest management practice (Buhyoff and others 1979). The importance of scenic vistas is a function of physiography. Areas with substantial terrain relief often provide opportunity for viewing natural landscapes. Generally, SPB outbreaks in coastal plain forests are not an issue, as scenic vistas are sparse. However, outbreaks in mountainous terrain or in the plateau (e.g., the Cumberland and Piedmont) regions of the South are consequential.

In summary, social or aesthetic impacts resulting from SPB outbreaks, although difficult to define in quantitative terms, are important components of the concept of impact. In some cases it is possible to define social impacts in terms of economic values. This definition is usually based on primary recreational uses of forests. When outbreaks of the SPB occurred in the past, research emphasis was generally directed to topics other than social impact evaluation. The research agenda for social impact of the SPB has not been addressed in a systematic manner, and this subject is in need of rigorous investigation.

16.2.2. Southern Pine Beetle Social Impact on the Human Habitat

We are using the term "habitat" to mean the physical place where humans live. For most people in the Southern United States, this place is the urban and suburban environment of cities. The rapid population growth in the South has resulted in the expansion of the suburban environment of cities into natural forest lands or those established for commercial forest production. Southern yellow pine forests (*Pinus* spp.) are a common backdrop to housing developments in the suburban South. In the urban environment, parks, greenbelts, and recreation areas are often associated with remnant pine forests.

In both the urban and suburban environments, mature pines are particularly valued. Hosts in this state are particularly vulnerable to colonization by the SPB. Furthermore, various types of natural and cultural disturbances associated with the built environment (e.g., road construction, land clearing, site preparation, alteration of drainage patterns, placement of utility conduits, and so forth) contribute to the incidence of the SPB, as they often do in production forests. Research results from investigations of the relation of SPB population dynamics and soil, site, and stand characteristics have been used to develop guidelines for pine arboriculture in urban and suburban settings. Although undefined by objective measure, the guidelines are useful in reducing the effects of disturbances to residual pines in urban and suburban settings and presumably reduce infestation by the SPB. Instructions for identification of the SPB (and associated guild members –see chapter 13) and for application of various control procedures have been prepared by the USDA Forest Service, State Forestry Organizations, and the Cooperative Extension Service.

Nevertheless, infestations of the SPB in urban and suburban forest settings are commonplace during outbreaks of the insect. The social impact of infestations occurring in the suburban environment is of particular interest. This impact can include change in the aesthetic appearance of a neighborhood, reduction in property value resulting from loss of yard trees, reduction of buffering effects on weather conditions, and so on. Individual private landowner responsibilities to the presence of infestations on their property are generally not defined and are largely unregulated. In some instances homeowner associations have intervened to set guidelines. Furthermore, there is ambiguity regarding what constitutes a proper or effective response to the presence of infestations. Although studies of population dynamics have demonstrated how infestations enlarge by colonization of adjacent hosts and that there is contagion among infestations, allegations of cause and effect relations of infestations on adjacent parcels of private property are speculative from a legal perspective.

In general, there is an implied expectation among neighbors that when an infestation occurs, the homeowner is responsible (perhaps obligated) to take some type of action. The range of possibilities runs from application of insecticides to suppress populations of the SPB to the removal of infested trees. These services are provided on a fee basis by arborists or pest control companies. However, there is a range of interpretation of social responsibility among homeowners. Responses by homeowners to infestations on their properties are driven by a variety of issues. In some instances an individual homeowner simply may not have the financial resources to respond to the presence of an infestation. In other cases the homeowner may be apathetic to concerns of neighbors. In still other cases the homeowner may be purposefully spiteful. Again, the social obligations and legal responsibilities for the occurrence of SPB infestations on private as well as public property need further investigation.

In the preceding discussion, we have emphasized social impacts on private property as they relate to neighbors in urban and suburban settings. However, SPB infestations associated with the interface of public to public and private to public ownerships in production forests are also of paramount concern. Many of the same issues identified for private ownerships play out in this public-private arena as well.

16.3. POLITICAL IMPACT

Political impact refers to the effects of insects on the forest environment that result in actions, practices, and policies of local, State, or Federal governmental agencies. The mechanism of political impact is the corpus of laws and regulations that have evolved to provide for protection, conservation, and use of public and private forests (Smardon and Karp 1993). From a forest protection perspective, we are particularly concerned with: 1. Laws that charter and enable governmental agencies (e.g., the USDA Forest Service); 2. Laws that govern forest management practice and policy (e.g., the Wilderness Act); and 3. Laws that regulate inter- and intrastate (and country) movement of plant and animal materials (e.g., the Plant Pest Act). Within the U.S. government a number of departments deal with issues associated with political impact of insects on the forest environment: for example, departments of Agriculture, Commerce, Army, Interior, Labor, and Treasury, and the Environmental Protection Agency. Within the Department of Agriculture, the USDA Forest Service, the National Institute of Food and Agriculture, Natural Resources and Conservation Service, and Animal Plant Health Inspection Service (APHIS) are particularly important (NRC 1998). Within the individual States, there are similar agencies that deal with political impact, such as, the State forestry organizations and departments of agriculture.

In our examination of political impact associated with the SPB, we focus on two aspects of this issue. The first deals with the Federal statutes relevant to impact assessment and response. The second deals with taxation laws relating to industrial management of forest lands. Each of the topics is treated in turn below.

16.3.1. Federal Statutes Relating to Southern Pine Beetle Impact

Numerous U.S. laws govern forest management practice and policy that directly or indirectly involve the SPB. The impact that the SPB has had on forest lands in the South is linked in part to the various models historically used to guide forest management. The history of formal forest management in the United States traces from the 1870s and includes five different models; i.e., dominant-use management; multiple use management; environmentally sensitive, multiple use management; ecosystem management; and landscape management (Yaffe 1999). These models greatly influenced the conditional state of public forest land and how resources were utilized. Coulson and Stephen (2006) examined each of the models and reviewed the basic tenets of the legislation that enabled each approach.

In the following sections we examine four statutes that are particularly relevant to SPB political impact: the National Environmental Policy Act (NEPA), the Endangered Species Act (ESA), the Wilderness Act, and the Healthy Forest Restoration Act (HFRA). The first three of the acts figured prominently in the Federal response to the most recent outbreaks of the SPB. The fourth act, which is the most recent, represents a proactive approach to addressing the cause of catastrophic effects created by wildfires and bark beetle outbreaks.

The National Environmental Policy Act (NEPA)

Impact of the SPB is addressed as a component of environmental assessment. For our purposes environmental assessment deals with evaluating change to the environment resulting from human actions. The substance of environmental assessment is defined by the National Environmental Policy Act of 1969 (as amended) – NEPA. The basic tenets of this act are reviewed by Coulson and Saarenmaa in chapter 29. This act requires that Federal agencies assess the environmental impact of implementing their major programs and actions. For projects or actions that are expected to have a significant effect on the quality of the environment, the responsible agency is required to file a formal environmental impact statement (EIS). Actions associated with suppression and prevention of the SPB clearly fall within "major programs and actions" designation. The EIS is a substantial undertaking and involves the preparation of a document that addresses key issues for a proposed action. The EIS for the SPB (Management Bulletin R8-MB 2) is a massive multivolume document.

Outbreaks of the SPB, which have not in the past been predictable and often cover areas of large spatial extent, are a significant challenge to the environmental assessment processes. When outbreaks occur it is difficult, if not impossible, for the responsible Federal agency to develop an EIS and provide for protection of valued forest conditions or resources in a timely manner; i.e., the need to implement suppression and prevention actions is usually immediate. This dilemma is one of the challenges of forest protection. In addition, the EIS mandate and procedure applies only on federally managed public land, which represents a minor portion of the pine forest land in the South. On private commercial forest lands, environmental assessment is bundled as part of the certification programs; e.g., SFI®.

The Endangered Species Act and the Wilderness Act

The Endangered Species Act (ESA) of 1973 (as amended) and the Wilderness Act of 1964 (as amended) have factored into SPB impact on Federal forest lands of the South through an unanticipated scenario. Following, we identify important features of each act and illustrate how the SPB became an issue in the decisionmaking regarding compliance to the mandate of these laws.

The ESA was created to provide protection of plants and animals and their habitats identified (listed) by the U.S. government as endangered or threatened. An endangered species is one that is in danger of extinction throughout all or a significant portion of its range. A threatened species is one that is likely to become endangered within the foreseeable future. Two features of the ESA are particularly important to our discussion of SPB impact. The first feature deals with taking of endangered species; i.e., it is unlawful for anyone to take a listed animal or plant. Significantly modifying the habitat of the endangered species is explicitly included in the meaning of "take." The second feature deals with the responsibility of Federal agencies in protecting endangered species and habitats. This responsibility includes issuing permits for private activities that could affect endangered and threatened species or habitat.

The Wilderness Act provided a new Federal land classification system intended to preserve wild lands in their natural state. The specific definition of wilderness taken from the act is as follows: "A wilderness, in contrast with those areas where man and his own works dominate the landscape, is hereby recognized as an area where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain." The Wilderness Act initially applied to federally managed lands, such as national forests, national parks, and national wildlife refuges. It also greatly restricted most management practices and means of access; e.g., motorized vehicles and later bicycles were excluded.

The ESA and Wilderness Act came together in a political impact context as a result of the interaction of the SPB and the Red-cockaded woodpecker (RCW) *(Picoides borealis)* on forest lands designated as wilderness. The essence of the management problem centered on the fact that the RCW is a listed endangered species and therefore protected under the ESA. In cases where SPB infestations impinge on colony sites, suppression procedures are implemented on public forest land to protect the bird. However, in some instances RCW colony sites and SPB infestations occur in close proximity within wilderness areas. Normally, when an SPB infestation occurs within a wilderness area, the Wilderness Act prohibits management intervention. The management dilemma centers on whether to protect the RCW from an impinging SPB infestation by implementing suppression tactics or to allow the SPB infestation to follow its natural course and by so doing destroy the RCW colony site. The ESA requires protection of the RCW, and the Wilderness Act prohibits management intervention. The Wilderness Act provides considerable flexibility regarding controlling wildfires on wilderness areas, and this latitude was used to intervene on behalf of the RCW. However, it did not prevent litigation initiated by citizen groups.

The Healthy Forest Restoration Act

The state of the forest environment frequently leads to predictable responses from the agents of change. The Healthy Forest Restoration Act (HFRA) of 2003 is a set of guidelines for directed actions that are intended to adjust (and perhaps regulate) the conditions of the forest environment and thereby alter the frequency and amplitude of natural disturbances (fire and insect and disease outbreaks in particular). Outbreaks of the SPB are often associated with overstocked old-growth pine forests (See chapter 22). Consequently, one means of addressing the depredations caused by the SPB involves a restoration strategy that returns the forest environment to a state where large infestations cannot occur (See chapter 24). The HFRA is intended to guide the restoration processes.

The HFRA has six sections, referred to as Titles. Title IV, which deals with insect infestations and related diseases, is particularly relevant to impact of the SPB. The purposes of this title are: 1. To develop an accelerated basis and applied assessment program to combat infestations by forest-damaging insects and associated diseases; 2. To engage the stakeholders (including universities, State agencies, and private landowners) to carry out the program, and 3. To implement applied silvicultural assessments. Silviculture deals with the theory and practice of controlling forest establishment, composition, and growth (See chapter 23). The SPB and several other species of forest-damaging insects were specifically identified to be of immediate concern (Coulson and Stephen 2006).

The HFRA is significant in that the intent is to address altering the state of the forest environment in ways that reduce the opportunity for large-scale (broad spatial extent) outbreaks. An ancillary consequence is that the HFRA has stimulated thought into alternative utilization pathways for plant biomass associated with restoration projects as well as natural disturbances; e.g., hurricanes, ice storms, SPB outbreaks, and so forth. Traditional utilization pathways using saw logs and pulpwood are not sufficient, and alternative pathways, particularly bioenergy applications, may offer other profitable uses of forest plant biomass (Curry and others 2008).

16.3.2. Taxation and Political Impact

Taxation laws relating to corporate forest management have substantially changed forest land ownership in the South. The shift of ownership from large industrial companies to nonindustrial private ownership has important implications relating to SPB impact, and this issue is examined below from an interpretative viewpoint. Specifically, we consider: 1. How forest land ownership in the South has changed, and 2. The consequences of changed ownership on SPB outbreaks.

Change in Forest Land Ownership in the South

In the past, the strategy of the large industrial timber companies (often referred to as vertically integrated forest product companies –VIFPCs) in the South was to acquire ownership of forest lands. The rationale for this strategy was that by owning forest land, the company had control over the supply and conditional state of raw materials needed by their manufacturing facilities. Variables such as time of harvest, delivered costs to the mills, tree species, volume, and log size could be controlled if the company owned the source of the raw product; i.e., the forest land. The largest VIFPCs in the South and nationwide have divested their forest land holdings (Figure 16.2). Clutter and others (2005) evaluate strategic factors driving timberland ownership changes in the South. Important questions that follow from this reality are why was the forest land sold, who purchased it, and how is it being managed? Each of these questions is addressed below.

Why was Industrial Forest Land in the South Sold?

There are numerous reasons cited for forest land divestment by the VIFPCs. The most prominent are poor stock performance, the need to increase shareholder returns, debt

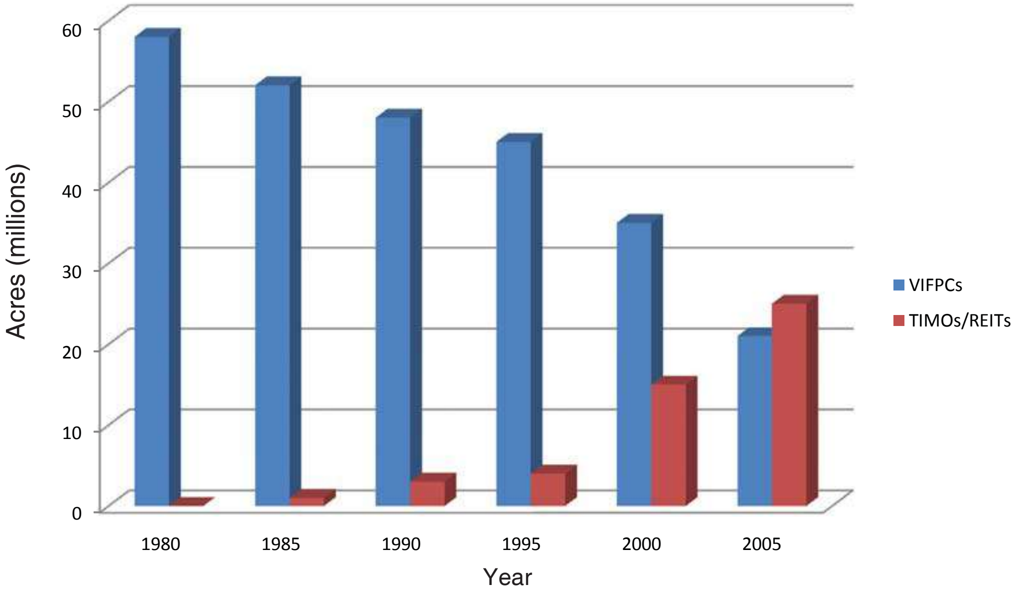

Figure 16.2—Bar graph illustrating the trend in U.S. forest land ownership by TIMOs (Timber Investment Management Organizations) and REITs (Real Estate Investment Trusts) in relation to large industrial timber companies (often referred to as vertically integrated forest product companies –VIFPCs). The Y axis is in millions of acres and the X axis is in years, beginning in 1980 and ending in 2005. The trend is for VIPEC ownership to decline progressively and for TIMOs and REITs to increase in ownership. (illustration from Hickman 2007)

reduction, increased tax efficiencies, and the development of tax strategies that minimize capital gains (Clutter and others 2005). By far the most important driver is taxation. Although a significant concession to simplification, the basic explanation is as follows. If the timber company is classified as a Sub-chapter C Corporation, profits are taxed twice: once at the corporate level by way of a corporate income tax (35 percent) and again at the individual shareholder level if a dividend is declared (15 percent). The practical effect of this taxation policy is that investors who own both the manufacturing plants and forest land often recoup as little as 50 cents out of every dollar of profit made from cutting trees. Investors who own just forest land can normally capture at least 85 cents out of every dollar (Hickman 2007). Consequently, VIFPCs have chosen to restructure in order to separate ownership and control of timber holdings from ownership and control of their mills. Almost all VIFPCs have restructured in this manner (Hickman 2007).

Who Purchased Industrial Forest Land?

The commercially valuable forest land, the property that supplied raw material for use in manufacturing forest products, was in large part acquired by two basic entities:Timber Investment Management Organizations (TIMOs) and Real Estate Investment Trusts (REITs). These entities are classified as Sub-Chapter S and Limited Liability corporations for income tax purposes and are taxed only once. The incentive to restructure and separate timberland and mill ownership is straightforward. Comparatively, each of these entities has unique characteristics. A TIMO buys, manages, and sells forest land and timber on behalf of various institutional investors, such as insurance companies, pension funds, foundations, and endowments. Funds from these sources are invested for the clients for a specified time period, usually 10-15 years. TIMOs have implicit fiduciary responsibility to manage the investment so as to yield the best possible returns; i.e., to maximize profits. TIMOs do not actually own forest land. The forest land is owned by the investors the TIMOs represent. An REIT is an entity that buys, manages, and sells real estate or real estate related assets (such as mortgages) on behalf of private investors. In contrast to TIMOs, REITs own the forest land. Investors are participating in a mutual fund type of instrument (Hickman 2007).

How is Forest Land in the South Being Managed?

The shift in forest land ownership from VIFPCs to TIMOs and REITs was well advanced by 2005 (Figure 16.2). However, empirical evidence for evaluating the impact of this change is currently lacking. Clearly, there is ample incentive for the TIMOs and REITs to manage their forest lands using the best practices available. Both entities employ a small staff of professional foresters, but it is important to recognize that actual "on the ground" management activities are performed by contractors, and all expenses influence the investment return. Unlike VIFPCs of the past, TIMOs and REITs do not possess the large equipment and other resources used in forest management. Among the unanswered questions to be addressed in the future, the following are of paramount significance: what type of forestry will be practiced, given the overarching emphasis for profitable investment; what goods and services, including environmental amenities, will be produced; what will be the relation of ownership tenure and forest land fragmentation; will forest land be converted to other uses; will the new owners be an effective voice for the forestry enterprise in general (i.e., the activities and services performed by the State forestry organizations and the USDA Forest Service)?

The Consequences of Changed Ownership on SPB Outbreaks

The change in forest land ownership from VIFPCs to TIMOs and REITs will likely factor into future regional outbreaks of the SPB. The general investment strategy for TIMOs and REITs centers on convincing clients that land and timber values will increase incrementally over time, and that the trees associated with the forest property can be marketed profitably. The real estate investment component is compelling, but the forest marketing aspect is highly speculative, given that the standing crop of biomass of forest trees in the South exceeds projected demands for traditional wood products (Wear and others 2007). One of the marketing strategies advocated by the TIMOs and REITs is to time timber sales when demand, and hence price, is high. This option was often not possible for the VIFPCs when mill and forest land ownership were bundled; i.e., supply demands of the mills dictated when raw materials were purchased. If waiting for favorable market prices translates into storing mature and overmature trees in the forest ("banking on the stump," in colloquial terms), then the opportunity for herbivory by the SPB is dramatically increased. Recall that most tree mortality attributed to the SPB is associated with mature stands, at least initially. The impact of widespread losses attributed to fire, insects, and disease will have a major effect on market prices for timber. Pye and others (chapter 14) address the economic impact of SPB outbreaks on market value of timber. During SPB outbreaks, markets are swamped with infested wood and prices are greatly depressed. A similar situation occurs following events such as hurricanes and other atmospheric disturbances. Traditionally, forest protection activities on industrial forest land were taken on by the VIFPCs, often in collaboration with the State forestry agencies. There has not been a large regional outbreak of the SPB since land divestment by the VIFPCs, and it is not clear what type of response by the current owners will follow. The State forestry agencies and USDA Forest Service, Forest Health Protection, can provide assistance, but actual suppression and salvage activities on forest land held by TIMOs and RIETs will fall to private contractors. Risk, traditionally associated with forest protection (insects, disease, fire, and other natural disturbances) is not factored into forest real estate investment strategies.

16.4. SUMMARY

We defined impact to mean any effect on the forest environment resulting from the activities of the SPB. Our focus was directed to social and political impact. Neither of these topics has been examined in a rigorous social science context since the 1970s, and our approach has been observational and interpretative. Social impact was examined from two perspectives: The first dealt with SPB impact on recreational use of the forest environment, and the second dealt with the SPB as an element of the human habitat. Political impact was investigated by an examination of selected Federal acts and statutes that influence the actions, practices, and policies of the Federal government. We concluded the section on political impact by evaluating the probable effect of change in ownership of forest lands in the South as a consequence of divestment by the timber industry. The likely effects of TIMOs and RIETs on the potential for future outbreaks of the SPB were considered.

17

Aerial Detection, Ground Evaluation, and Monitoring of the Southern Pine Beetle: State Perspectives

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Abstract

The southern pine beetle (SPB), is recognized as the most serious insect pest of southern pine forests. Outbreaks occur almost every year somewhere within its wide range, requiring intensive suppression efforts to minimize resource losses to Federal, State, and private forests. Effective management involves annual monitoring of SPB populations and aerial detection and ground evaluation of multiple-tree infestations during outbreaks. The 16 southern and northeastern States that face periodic SPB outbreaks have developed operational methods for detection and evaluation of new infestations and pending outbreaks of this destructive forest pest. Methods used by State forestry agencies for State and private forest lands often differ from those used on Federal forest lands and also vary significantly among States. This chapter describes the methodologies used by various States for conducting aerial detection flights and subsequent ground check evaluations for SPB. New technological developments, including geographical information systems, global positioning systems, digital sketchmapping systems, and coordinated Internet-based reporting systems, are being incorporated into traditional suppression operations to better manage this bark beetle pest. Also, a unique region-wide system for monitoring SPB populations and predicting infestation trends has been developed and implemented throughout the South. The first of its kind for any bark beetle species in the world, this system utilizes a network of pheromone traps deployed in early spring. Predictions of SPB activity to expect at the county, ranger district, and State level are made by comparing relative catches of SPB and those of a major SPB predator, the clerid *Thanasimus dubius*. Standardized monitoring, aerial detection, and ground evaluation protocols have become widely used by State forestry agencies and are considered essential components for the effective management of SPB.

Keywords

bark beetles
Dendroctonus frontalis
loblolly pine
pheromones
prediction

17.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), is considered the most destructive pest of southern pine forests (Branham and Thatcher 1985, Thatcher and others 1980). Outbreaks occur periodically throughout the range of its principal hosts, loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*). The SPB also infests other native pine species in Mexico (Cibrian Tovar and others 1995) and Central America (Vité and others 1975). During these outbreaks, which may last 3-4 years or longer (Price and others 1998), SPB typically creates an abundance of multiple-tree mortality centers, termed “spots” (Figure 17.1). Under favorable conditions, numerous small spots may converge if not controlled to impact thousands of acres (Figure 17.2) (Clarke and Billings 2003).

Since SPB has 3-10 generations per year (Payne 1980), outbreaks may develop rapidly, causing severe economic losses to Federal, State, and private forests. For example, in 2001 and 2002, the worst outbreak on record was recorded in the Southeastern United States More than 150,000 infestations were reported on Federal, State, and private ownerships in Alabama, Florida, Georgia, Kentucky, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia. For reasons that remain unclear, however, no SPB infestations have been reported in States west of the Mississippi River since 1998 (USDA Forest Service 2004). Due to periodic outbreaks and the impact they may have on commercial pine forests, the SPB has been the target of more extensive suppression efforts than any other bark beetle species in the world (Billings 1980b).

Figure 17.1—Example of an expanding SPB infestation characterized by infested trees in various stages of foliage fade. (photograph by Ron Billings, Texas Forest Service)

Detection and evaluation of infestations and monitoring of population trends are key components of an SPB pest management program (Billings 1980b, Clarke and Billings 2003, Thatcher and others 1982). State forestry agencies, responsible for detecting and monitoring bark beetle infestations on State and private forest lands, have developed methods that differ somewhat from those the USDA Forest Service uses on Federal lands. Methodologies for detection and monitoring also will vary among the 16 States (Oklahoma, Arkansas, Texas, Louisiana, Mississippi, Tennessee, Kentucky, Alabama, Georgia, Virginia, Florida, South Carolina, North Carolina, Maryland, Delaware, and New Jersey) that routinely conduct these operations. Thus, aerial detection, ground evaluation, and monitoring procedures for SPB on State and private forest lands will be described separately in this chapter.

Figure 17.2—Example of a large area devastated by SPB: Indian Mounds Wilderness, Sabine National Forest, Sabine County, Texas, August 1993. (photograph by Ron Billings, Texas Forest Service)

17.2. UNIQUE CHARACTERISTICS OF SPB INFESTATIONS

Unlike other species of *Dendroctonus* in the Western United States and Canada (Fettig and others 2007), SPB may be capable of killing trees throughout the year in a large portion of its range. Adult beetles may emerge, fly, and infest host trees whenever minimum temperatures exceed 59 °F, the threshold for flight (Moser and Dell 1979a). However, SPB dispersal, reproductive capacity, and attack behavior, among other factors, are known to vary seasonally (Payne 1980, Texas Forest Service 1978, Thatcher and Pickard 1964). Detection and control programs are predicated on these seasonal differences. For example, detection records indicate that most multiple-tree SPB infestations or spots are initiated in the late spring or early summer and detected from May through August (Coulson and others 1972, Thatcher and Pickard 1964).

Adult SPB disperse from overwintering sites usually in March or April in Gulf Coastal States (later in northeastern portions of the insect's range) and seek out weakened trees to initiate attacks. Long-range dispersal in the spring coincides with the flowering of dogwood (*Cornus florida*) or production of loblolly pine pollen (Billings 1988). Many spots at this time of year are initiated when the beetles attack lightning-struck pines (Coulson and others 1983, Hodges and Pickard 1971) or trees weakened by drought stress, competition with other trees, or other factors that produce slow radial growth (Coster and Searcy 1981, Coulson and others 1974).

Healthy pines usually are capable of resisting initial SPB invasion by "pitching out" attacking beetles with a strong flow of oleoresin (Hodges and others 1979). To overcome a pine's defense mechanisms, initially attacking female SPB produce a potent aggregation pheromone, frontalin (Kinzer and others 1969), which combines with host odors from the tree to attract other SPB flying in the area (Coster and Johnson 1979a, Coster and others 1977a, Gara and Coster 1968). A weakened tree typically is unable to withstand the mass attack of SPB that results, and is rapidly killed. Once the pine's defense system is overcome, adult beetles colonize the initial tree while other SPB adults are induced to land on and attack adjacent pines. This switching behavior is triggered by different beetle-produced semiochemicals, in this case, verbenone and endo-brevicomin produced by male SPB (Gara 1967, Renwick and Vité 1969).

Attacking SPB introduce a blue stain fungus into the tree's sapwood, which helps to kill the tree. Once SPB colonization is complete, eggs are laid in the inner bark along characteristic S-shaped galleries (Figure 17.3) to establish a new generation of beetles (Payne 1980). Under favorable temperatures (70-85 °F), the eggs

Figure 17.3—Winding, S-shaped galleries beneath the bark of infested pines are characteristic of infestation by the SPB. (photograph by Ron Billings, Texas Forest Service)

develop into larvae, pupae, and then callow adults, emerging within 4-6 weeks after initial attack (Thatcher and Pickard 1967). Brood development and emergence may be prolonged by high or low temperature extremes (Beal 1933, Tran and others 2007). The foliage of the infested tree will eventually change color from green to yellow (fading) and then to red before eventually dropping from the tree (Doggett 1971). The signature produced in expanding SPB infestations by dead and dying pines in various stages of deterioration (Figure 17.1) is easily visible to aerial observers during summer months (Billings and Ward 1984, Ciesla and others 2008). By the time an infested pine's foliage has turned red or brown, the SPB will have completed development within the bark, emerged, and flown off in search of another pine to attack. The exception is the winter season, when red-crowned or bare trees may still harbor SPB brood (Billings and Kibbe 1978, Doggett 1971).

Presumably, a persistent, expanding SPB spot develops during the late spring if beetles continue to immigrate into the new infestation for at least 30 days or one SPB generation. By this time, the SPB brood will have completed development and begun to emerge from trees at the spot origin (the first trees infested). Newly emergent brood adults and reemergent parent beetles during summer months will tend to respond to pheromones produced on the periphery of the same infestation from which they emerged, attacking additional pines and creating the phenomenon known as "spot growth" (Gara 1967, Hedden and Billings 1979).

Once a large, expanding infestation becomes established, exposure of adult SPB to environmental hazards outside the tree is minimized and survival is maximized. The pine's defense systems (oleoresin exudation) may be rapidly and successfully overcome by the high concentrations of attacking beetles. Accordingly, even healthy pines capable of resisting the attacks of a few SPB are colonized in rapid succession as the spot expands (Cameron and Billings 1988, Hedden and Billings 1979). Operational records from East Texas have shown that only 25-30 percent of all detected SPB infestations enlarge for prolonged periods (Billings 1974, Leuschner and others 1976). Such spots are the target of direct control programs because they account for some 70 percent of timber losses (Billings 1980b, Thatcher and others 1982).

Spots in which the synchrony between pheromone production on the spot periphery and brood emergence from within the same spot is not maintained are destined to soon go inactive with no further enlargement (Cameron and Billings 1988, Hedden and Billings 1979). In this case, emerging beetles do not encounter aggregation pheromones and disperse (Gara

1967), often failing to establish new multiple-tree infestations once the preferred long-distance dispersal period (March through June) is over (Texas Forest Service 1978). Inactive spots can be recognized from the air during summer months by their small size and absence of trees with fading yellow foliage (Figure 17.4) (Billings 1979). Large infestations that exhibit no fading trees as a result of prolonged high temperatures, however, may contain sufficient SPB populations to resume spot growth processes when favorable temperatures return (Figure 17.5).

When ambient temperatures become more favorable for dispersal in the fall, a portion of the SPB population may leave established infestations upon emergence to initiate new

Figure 17.4—Example of an SPB infestation that is no longer active (e.g., lack of trees with fading crowns indicate that the beetles have abandoned this spot). (photograph by Ron Billings, Texas Forest Service)

Figure 17.5—Large or concentrated areas of infestation that show no recent SPB activity (e.g., no trees with fading crowns) due to hot, summer weather may experience renewed beetle activity when favorable weather conditions return. (photograph by Ron Billings, Texas Forest Service)

infestations nearby. Thus, during outbreaks, the SPB population typically passes the winter in scattered trees, in small, recently initiated spots, and/or in large infestations that remain uncontrolled (Texas Forest Service 1978, Thatcher and Pickard 1964). In contrast, when SPB populations are latent, it is common to observe few or no SPB-infested trees, a condition that may prevail for a decade or more (e.g., as in States west of the Mississippi River since 1998). Presumably, during these latent periods, a few SPB survive by inhabiting scattered trees colonized primarily by other members of the southern bark beetle guild, *Ips* spp. and/or the black turpentine beetle, *D. terebrans* (Payne 1980).

Given this unique attack behavior, the goal of both aerial observers and ground evaluation personnel during periodic SPB outbreaks has become to identify those SPB spots capable of causing extensive resource losses if not promptly controlled and distinguish them early in their development from infestations likely to soon go inactive. Accordingly, aerial detection and ground evaluation protocols unique to SPB have been developed over the years to achieve this goal.

17.3. AERIAL DETECTION OF SPB ON STATE AND PRIVATE FOREST LANDS

The detection of multiple-tree infestations likely to be caused by the SPB is the first step in suppression programs (Billings 1980b). Aerial detection (Billings and Ward 1984) is followed by on-the-ground (ground check) evaluations to identify or confirm the causal agent and determine the need for control (Billings and Pase 1979a). SPB infestations, particularly those that have the potential to expand over time, are then targeted for direct control (suppression) as a means to reduce further timber losses (Billings 1980b, Swain and Remion 1981).

The purpose of aerial detection is to identify and map the location of dead and dying groups of pine trees that show characteristic signs of being infested by SPB (Ciesla and others 2008, Thatcher and others 1982). An expanding SPB spot typically consists of five or more infested trees in various stages of foliage fade (see Figure 17.1). During summer and fall months, red-crowned pines (those from which SPB brood has emerged) will be visible from the air adjacent to trees with fading or yellow crowns (Billings and Doggett 1980, Ciesla and others 2008). The latter are likely to contain SPB broods in development (larvae, pupae, and/or new adults). Expanding infestations also will contain recently attacked pines usually situated near fading pines, but these trees will still have green crowns and be indistinguishable from uninfested trees to aerial observers. The presence of one or more pines with fading yellow crowns indicates SPB spots that are most likely to be in the process of expansion (Billings 1979).

17.3.1. Aircraft Used in Aerial Detection of SPB

A recent survey of southern pest management specialists conducted by the author reveals that State agencies use different types of aircraft to conduct SPB aerial detection operations. Certain State forestry agencies (Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, New Jersey, North Carolina, and Virginia) own airplanes used for detection, while the other States contract private planes for this purpose. The State of Alabama contracts private planes to supplement its own aircraft when needed.

Typically, aircraft used for aerial detection are single-engine, high-winged aircraft that seat four persons, such as Cessna models 172, 182, 185, 206 or 207 (Figure 17.6). One observer, usually an agency forester or technician, is responsible for detecting spots visible out the right side of the plane, while a second observer records spots out the left side. When SPB populations are low, a single aerial observer and/or the pilot may record infestations. In many cases, pilots who fly aerial detection flights in search of wildfires also will report any suspected SPB infestations during fire season.

17.3.2. Preferred Seasons for Aerial Detection

SPB detection flights are generally flown during warm months, May through September, when multiple-tree SPB spots are most abundant and easy to identify from the air. The frequency of summer detection flights may vary from one every 1 or 2 weeks to one per year, depending on the State and the level of SPB activity. Fading pines are more difficult to detect during the spring and fall months, when hardwood tree crowns are coming into leaf or turning color, respectively. Thus, SPB detection flights are typically discontinued during these months. During the winter months, SPB populations tend to be more scattered, and the crowns of

Figure 17.6—Small, high-winged aircraft, such as this Cessna 182, are typically used for conducting aerial detection flights for SPB infestations. (photograph by Ron Billings, Texas Forest Service)

infested pines often turn from green to red without exhibiting fading foliage (Billings and Doggett 1980). A few States (Tennessee, Alabama, and North Carolina) routinely conduct winter detection flights to pinpoint large, overwintering SPB infestations during outbreak periods.

17.3.3. Flight Lines and Altitudes

To survey for SPB infestations, detection flights follow predetermined north-south or east-west flight lines over pine-forested areas, usually at an altitude of 1,000-2,000 feet aboveground. During SPB outbreaks, flight lines are generally spaced 1-5 miles apart and observers cover 100 percent of the area flown by recording SPB spots out to 0.5-2.5 miles from the plane (Aldrich and others 1958). In years when SPB populations are not expected to reach outbreak levels, State forestry agencies may fly 25-50 percent of the area by flying every second or fourth flight line. The total number of spots is then extrapolated from the data collected. In Arkansas, when SPB populations are at less than outbreak levels, detection flights follow even-numbered flight lines on the first flight and odd-numbered flight lines on the next flight scheduled 2-3 weeks later, so that 100 percent of the infested area is covered.

17.3.4. Flight Maps and Digital Sketchmapping Systems

Traditionally, suspected SPB spots have been plotted onto recent aerial photographs or topographical maps. With the advent of global positioning system (GPS) units, aerial detection procedures are becoming more sophisticated (Wainhouse 2005). Certain States (e.g., Georgia) locate the geographical position of SPB spots by flying directly over them in order to capture the coordinates with a GPS unit in the plane.

In recent years, Red Castle Resources, Inc., a private company, in cooperation with the USDA Forest Service, Forest Health Protection, has developed a digital sketchmapping system that has greatly aided aerial detection operations (see the Web site at http://redcastleresources.com/tech_eval_development/digital_aerial.html). The system integrates computer hardware, software, and assorted electronic components to provide a digital moving map display integrated with a GPS. Electronic maps or digital aerial photos are loaded into a laptop computer, and aerial observers plot suspected spots onto electronic map images using a touch-sensitive screen (see chapter 10).

A GPS unit installed in the plane provides the exact location of the plane throughout the flight, while an icon on the touchscreen shows the aerial observer where the plane is located on the electronic map. This technology greatly improves the accuracy of plotted spot locations. In most cases, two separate laptops and touch screens are installed in one plane to allow two aerial observers to plot SPB spots or other mortality centers independently. By the time the detection flight is completed, records of the newly detected spots are downloaded into a shapefile to be transferred to ground check crews. At present, only Arkansas, Delaware, and New Jersey use digital sketchmap systems for SPB detection, but all Southern States have plans to purchase and utilize this new technology in the near future, according to the recent survey of State pest management specialists.

17.3.5. Information Collected During Detection Flights

Information recorded during SPB detection flights varies among States. Certain States (Arkansas, Louisiana, Mississippi, and Delaware) only record the location of the spot while others (Tennessee, Alabama, Georgia, Florida, and South Carolina) also record an estimate of spot size based on number of red- and yellow-crowned trees. In Texas, Virginia, North Carolina, Maryland, and New Jersey, aerial observers assign each spot a ground check priority, in addition to recording location and estimated spot size (Billings and Ward 1984).

Spot Size Threshold and Spot Number

State agencies have set a threshold for spot detection, based on the number of pines with red and yellow crowns. This threshold usually varies from 5 (Arkansas, Delaware, Louisiana, Maryland, Mississippi, Oklahoma, and South Carolina) to 10 trees (Alabama, Georgia, Texas, and Virginia). Florida uses a threshold of 6 trees while North Carolina uses 2-3 trees, Tennessee 1-2 trees, and New Jersey 1-5 trees. Spots with less than 10 trees are difficult to detect if flight lines are spaced more than 1 mile apart (Aldrich and others 1958).

The 10-tree threshold was adopted in Texas in 1974, based on operational records that revealed that most SPB spots with less than 10 trees at detection were inactive upon subsequent ground check evaluation (Billings 1974). Small spots that are below this flight threshold are recorded on subsequent detection flights if they remain active and expand beyond 10 trees. Such detection thresholds are effective in reducing ground check work loads and serve to focus control operations on spots most likely to expand and cause unacceptable timber losses. With the exception of Mississippi, South Carolina, and Maryland, each State assigns a unique number to each SPB spot upon detection. This number identifies the spot throughout the season and is used to track specific ground check and control information in data management systems.

Assigning an Initial Spot Size

It is useful for aerial observers to assign an initial spot size to spots at the time of initial detection, since newly detected spots may vary greatly in number of infested trees and need for direct control. At this stage, the spot size estimate does not have to be precise. It is sufficient to place the spot in a broad category, based on estimated number of trees observed with fading and red crowns (e.g., 10-20, 21-50, 51-100, and > 100). Admittedly, currently infested trees are most likely to be ones with fading and green crowns. But infested trees with green crowns are indistinguishable from unattacked trees to aerial observers. Thus, the number of red-crowned and fading trees combined provides aerial observers the best estimate of the number of beetle-infested trees actually present in the spot (Billings and Ward 1984).

Assigning a Ground Check Priority

During severe outbreaks when several hundred new SPB spots may be detected in a single aerial detection flight, it is useful to assign each spot a ground check priority during the aerial detection phase. In Texas, for example, high priority is given to SPB spots having more yellow-crowned fading trees than red or bare trees, particularly those in dense, sawtimber stands (pines with diameters > 9 inches). In turn, low priority is given to spots with few yellow-crowned trees, those in sparsely stocked stands, particularly pulpwood stands (pines < 9 inches in diameter), or those located in mixed pine hardwood stands. Other spots are assigned a moderate priority for ground checking (Billings and Ward 1984).

Ground check crews should evaluate high-priority spots first, as these are most likely to expand and require control. Low-priority spots may not need to be evaluated on the ground, particularly when manpower and time are limited, as they often are during outbreaks. The status of these low-priority spots (e.g., if they are inactive or will eventually grow large) may be most efficiently updated during subsequent aerial detection flights. Small spots may be declared inactive from the air with no further need for control action if they are observed to no longer contain trees with fading yellow foliage (see Figure 17.4) (Billings 1979).

17.3.6. Scheduling Detection and Reevaluation Flights

The scheduling of SPB flights will depend on the season, level of SPB activity, current weather, availability of contract aircraft, and other factors (Billings and Doggett 1980). Flights should not be scheduled on cloudy or excessively windy days. Also, aerial observers should limit detection flights to no more than 4 hours/day, usually between 10am and 4pm, the time of day when aerial signatures are most visible (Ciesla and others 2008).

During mid- to late summer, it is recommended that all SPB spots that remain to be ground checked or controlled be given a unique symbol on flight maps and checked for recent activity during detection flights (Billings and Doggett 1980). Spots revisited by aerial observers that no longer contain trees with fading crowns may be listed as inactive, with no need for direct control (Billings 1979). Previously detected spots that initially were small (low priority for ground check) at first detection may be given a high priority for ground check if they have grown large in the interim.

17.3.7. Improving Aerial Detection Operations

Timely detection of SPB infestations while they are still small, combined with accurate plotting of their location on available aerial photos or maps, are key first steps in SPB suppression programs. Experienced aerial observers who are not colorblind or overly susceptible to airsickness are essential. Plotting an SPB spot in the wrong location or repeatedly reporting trees killed by casual agents other than SPB are actions of inexperienced aerial observers. Such actions will increase the workloads of ground crews and cause undue delays in suppression projects. Clearly, aerial observers should be trained to recognize the characteristic signature of SPB infestations and be able to distinguish them from those of other mortality agents (Billings and Ward 1984). Ciesla and others (2008) have developed an illustrated guide of aerial signatures characteristic of common mortality agents in forests of the Eastern United States. This guide should prove useful for training foresters and pest management technicians as aerial observers.

Digital sketchmapping technology promises to greatly increase the efficacy of SPB detection, once southern States have purchased the required equipment and trained their aerial observers to use it. With digital sketchmapping systems, the geographical locations of detected spots can be immediately downloaded as shapefiles into ground-based computers or field data loggers, accelerating the next step in SPB control operations, that of ground evaluation.

7.4. GROUND CHECK OPERATIONS

Once a suspected SPB infestation is detected, usually from the air, the next step in SPB control operations consists of ground evaluation or ground checking. The geographical location of an SPB spot, the actual level of SPB activity within the spot, the ability of SPB infestations to expand continuously, and the need for direct control may be different from that reported by aerial observers. Thus, to the extent possible, newly detected spots should be visited on the ground by trained foresters or technicians soon after detection.

17.4.1. Purpose of Ground Checking

The purpose of ground checking is multifold (Billings and Pase 1979a):

- To verify that SPB was indeed the causal agent
- To confirm or correct the geographical location of the spot given by the aerial observer
- To determine the potential for additional timber losses and identify the direction(s) of spot expansion (active heads)
- To establish a priority for control
- To identify the landowner
- To mark a buffer strip in the case of cut-and-remove or cut-and-leave control options

17.4.2. Ground Check Methods

Usually two trained State-agency foresters or technicians make up the ground check crew for safety reasons. Ground crews locate spots based on the geographical coordinates provided by aerial detection crews or position of the spot shown on aerial detection maps. Upon arriving at the spot, a ground check crew member will verify that SPB was the primary causal agent by observing the characteristic S-shaped parent galleries of SPB beneath the bark of infested trees (Figure 17.3). A pine with a fading yellow crown is the preferred candidate to inspect for SPB galleries because the bark is easy to remove with a hatchet or machete, and the parent galleries are plainly visible beneath the bark. In red-crowned trees, SPB galleries may be difficult to discern due to more extensive fungal growth and/or feeding by larvae of the pine sawyer, *Monochamus* spp. (Coleoptera: Cerambycidae).

Once SPB is confirmed as the causal agent, a hand-held GPS unit is used to verify or correct the geographical coordinates. Next, ground check crews should walk around the periphery of the spot to ascertain its relative size and to

Table 17.1—Symptoms associated with various stages of SPB-infested trees (from Billings and Pase 1979a)

Symptom	Stage 1 (fresh attacks)	Stage 2 (with SPB brood)	Stage 3 (vacated by SPB)
Foliage	Green	Green, fading to yellow before brood emerges	Red, needles falling, or bare
Pitch tubes	Soft, white, or light pink	White, hardened	Hard, yellow, crumble easily
Checkered beetles	Adults crawling on bark	Pink or red larvae about 1/2 inch long in SPB galleries	Larvae and pupae are purple; occur in pockets in outer bark
Bark	Tight, hard to remove	Loose, peels easily	Very loose, easy to remove
Color of wood surface	White, except near adult galleries	Light brown with blue or black areas	Dark brown to black
Exit holes on bark surface	None	Few, produced by re-emerging parent beetles	Numerous
Ambrosia beetle dust	None	White, localized areas at base of tree	Abundant at tree base, turns yellowish with age

determine if the spot contains more than one active head or direction of expansion.

Identifying Three Stages of SPB Attack

Ground crews should be able to identify three stages of SPB-infested trees in an expanding SPB infestation (Table 17.1). Stage 1 trees are those just coming under attack. These are pines with green crowns (Figure 17.7A) and fresh pitch tubes or boring dust in bark crevices (Figures 17.7B and C). The bark is attached tightly to the bole of the tree. Adults of the bark beetle predator *Thanasimus dubius*, family Cleridae, may be seen crawling on the outer bark of the tree (Figure 17.7D). When bark is removed, the inner bark and sapwood surface are white, as on a healthy tree (Figure 17.7E). Bark beetle galleries are not present or are less than 1 inch long.

Stage 2 trees are those with developing SPB brood (eggs, larvae, pupae, or new adults). These trees are characterized by having green or yellow fading crowns (Figure 17.8A) and well-developed S-shaped galleries beneath the bark (Figure 17.8B). Unlike with Stage 1 trees, no adult clerids will be present on the outer bark. The inner bark and surface of the sapwood will have turned light brown (Figure 17.8C), in contrast to the white color of the sapwood-phloem interface of Stage 1 trees (Figure 17.7E). There may be evidence of white sawdust accumulating at the base of Stage 2 trees, produced by attacking ambrosia beetles (Coleoptera : Platypodidae) that bore into the sapwood of beetle-killed pines. In most cases, the pitch tubes along the bole of Stage 2 trees will have hardened and turned yellowish. As SPB larvae mature, they move toward the bark surface, and observers must shave away thin layers of bark with an axe or machete to expose them or the pupae they become. The white pupae will soon transform to light brown callow adults, which will darken as they age (Figure 17.8D). Callow adults also can be found embedded in the bark of Stage 2 trees, until they emerge by boring a small circular hole in the outer bark and fly in search of another host tree.

In turn, Stage 3 trees are those infested pines from which SPB brood has completed development and emerged. Typically, these trees have red or brown-colored needles or bare crowns (Figure 17.9A). Numerous emergence holes or "shot holes" about the diameter of a pencil lead may be visible in the bark surface, signs that the SPB brood has abandoned the tree (Figure 17.9B). Ambrosia beetle dust is abundant at the base of Stage 3 trees (Figure 17.9C). The bark along the tree's bole is loose and easy to peel off, but the S-shaped SPB galleries may be largely obliterated by feeding larvae of sawyer beetles and other insects. The

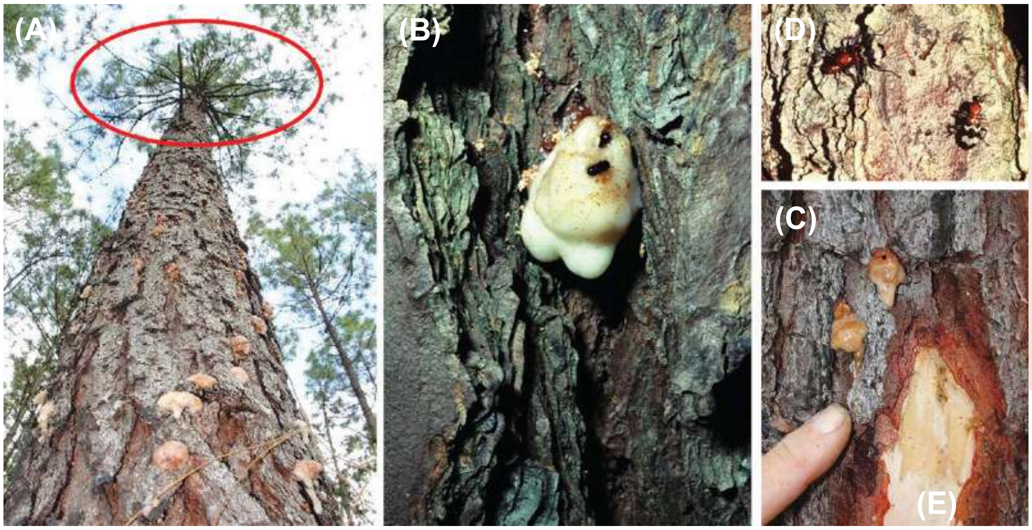

Figure 17.7—Symptoms of pines freshly attacked by SPBs (Stage 1) include (A) green crowns, (B, C) fresh pitch tubes in bark crevices, (D) adult clerid predators on bark, and (E) a white inner bark and sapwood surface.

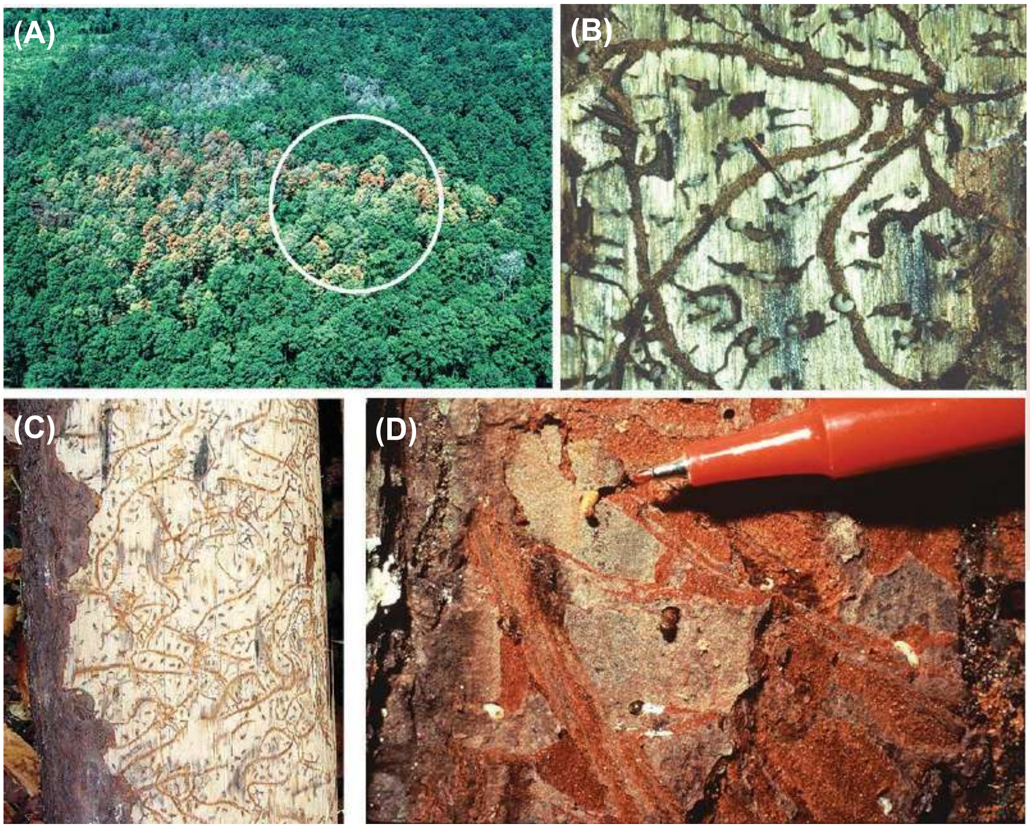

Figure 17.8—Symptoms of infested pines with SPB brood (Stage 2) include (A) green or fading crowns, (B) well-developed S-shaped parent galleries beneath the bark, (C) a brown-colored inner bark-wood interface, and (D) larvae, pupae or callow adults in or under the bark.

sapwood surface may be stained blue or black by blue stain fungi carried into the tree by the attacking bark beetles (Figure 17.9D). No SPB brood can be found within the bark of Stage 3 trees.

Spots that contain multiple trees in Stage 1 and Stage 2 are most likely to expand. Those that contain only trees in Stage 2 and Stage 3 still contain SPB brood but are unlikely to expand due to lack of a pheromone source produced only in Stage 1 trees. Spots with only Stage 3 trees are inactive, with no need for control. Particularly in late spring, ground crews may encounter spots containing primarily Stage 1 trees. This is indicative of a recently established spot. Whether such spots will eventually expand depends on several factors, principally the level of airborne SPB in the area and the initial spot size.

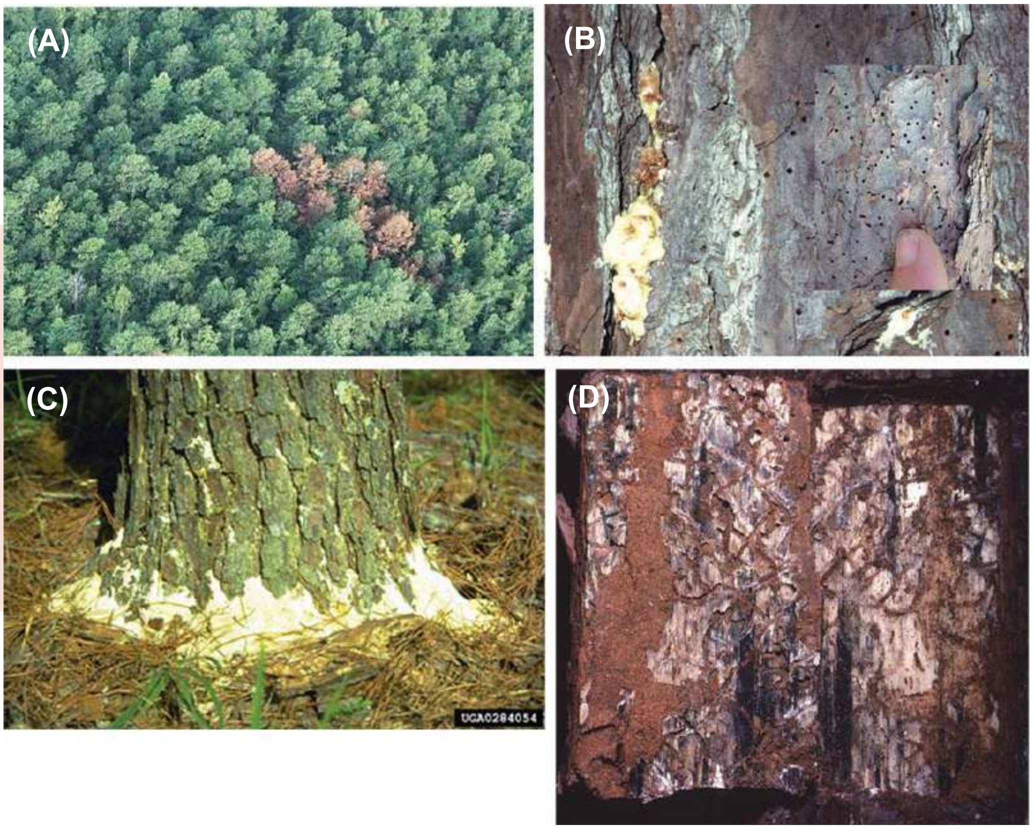

Figure 17.9—Symptoms of pines abandoned by SPB brood (Stage 3) include (A) trees with red or no foliage, (B) hardened pitch tubes with numerous exit holes on bark surface, (C) abundant white sawdust from ambrosia beetle dust at tree base, and (D) inner bark with sawyer galleries and blue stain masking SPB galleries.

Setting a Control Priority

Ground crews should determine the need for control and set a control priority at the time of ground check. As described in detail by Billings and Pase 1979a, the control priority is based on several factors (Table 17.2):

- The presence of Stage 1 trees, indicating a high probability for spot expansion
- The estimated number of infested trees
- Basal area of the stand at the active head
- Whether the stand contains pulpwood (average tree diameter at breast height < 9 inches) or sawtimber (average tree diameter > 9 inches)

Several predictive models have been developed to estimate tree losses to be expected in expanding SPB spots within 30-90 days if no direct control is applied (Billings and Hynum 1980, Reed and others 1981, Stephen and Lih 1985). These models may help pest managers make informed control decisions based on factors that can be easily measured in the field. They also may be useful to inform landowners about the extent and value of resources that are in jeopardy if direct control is delayed.

Marking a Buffer

The most recommended control measures for SPB infestations—cut-and-remove and cut-and-leave—require felling uninfested trees adjacent to Stage 1 trees to ensure that spot growth is halted. If direct control is likely to be applied to a spot shortly after the date of ground check, crews may mark the buffer strip during the ground check operation. Typically, the buffer is marked in a horseshoe-shaped pattern to encompass all Stage 1 trees and a few Stage 2 trees (Figure 17.10). Maximum width of the buffer will vary with the number of active trees in the spot and average tree height. In general, for most small to medium-sized spots (< 100 active trees), the buffer width is equal to the average height of the trees in the spot. Buffer widths will need to be expanded to control larger infestations (Billings 1980b).

The purpose of the buffer is to ensure that all SPB-infested trees are felled and pheromone production is disrupted in control operations. Because the SPB typically initiates attacks at mid-bole, early signs of beetle attack may be difficult to detect. The buffer provides a margin for error when identifying the trees under attack. Also, the buffer is essential to account for the fact that SPB spots may expand between the date of ground check and the date of control.

Table 17.2—Guide for setting SPB control priorities (May through October) (from Billings and Pase 1979a)

Key to spot growth	Your spot's classification	Risk-rating points
A. Stage 1 trees	Absent	0
(Fresh attacks)	Present	30
B. Stage 1 and 2 trees	1-10 trees	0
(Containing SPB brood)	11-20 trees	10
	21-50 trees	20
	More than 50 trees	40
C. Pine basal area (square feet/acre)	Less than 80 (low density)	0
(or stand density) at active	80-120 (medium density)	10
head or heads	More than 120 (high density)	20
D. Stand class by average	Pulpwood (9 inches or less)	0
d.b.h. (in inches)	Sawtimber (more than 9 inches)	10
	Total*	

* If total is 70-100, control priority = high

If total is 40-60, control priority = moderate

If total is 0-30, control priority = low

Indeed, if a delay of more than 1 week is anticipated between ground check and control operations, it is best to postpone marking the buffer until just before the control operation is begun. The final responsibility of the ground check crew is to flag a path back to the nearest road for subsequent visits by a control crew or to monitor the spot.

Landowner Notification

Identifying the landowner is an important step required only for spots on privately owned forest lands. Most State forestry agencies conduct ground checks of all spots on non-Federal lands following detection, then notify the appropriate landowner of the spot's occurrence and need for control. At least one State, Alabama, notifies landowners following the detection flight, leaving the ground check responsibilities and control decisions up to the landowner. All State agencies provide technical information to private landowners on identifying, evaluating, and controlling SPB infestations, as well as prevention guidelines.

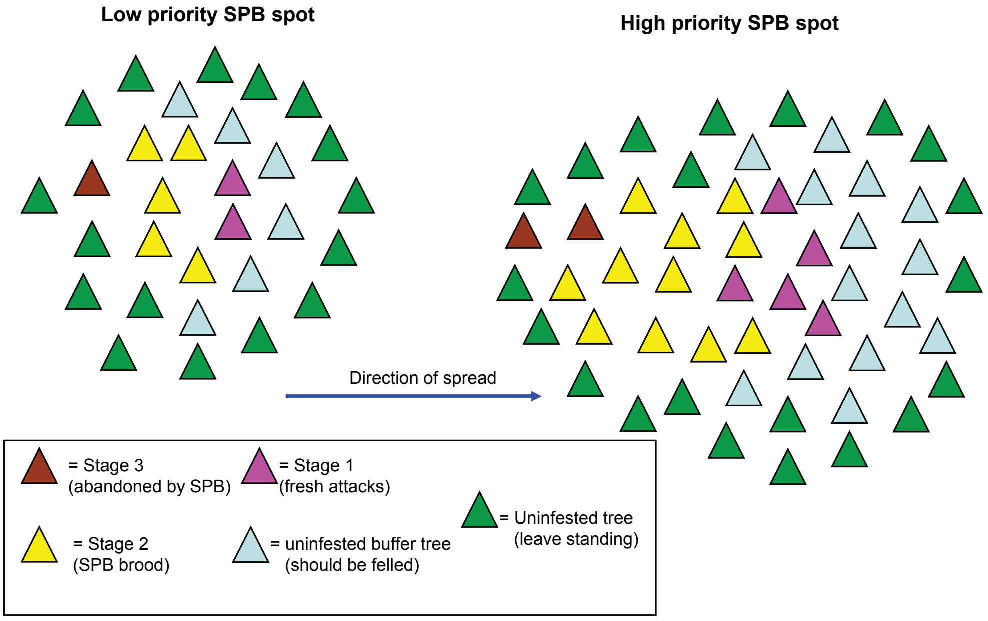

Figure 17.10—Diagram showing how to mark buffer strips for low- and high- priority SPB infestations (spots). All Stage 1 and Stage 2 trees, plus buffer trees, should be felled for cut-and-remove and cut-and-leave applications.

Recording SPB Operations Information

Each southern State has its unique methods for recording detection, and ground check and control information on SPB infestations during outbreaks. Some States maintain these records on Microsoft® Excel spreadsheets (Oklahoma, Arkansas, and Florida) while others (Alabama, Delaware, Georgia, New Jersey, South Carolina, and Texas) have developed electronic data management systems. The Texas Forest Service developed the first computer-based data management system for SPB, known as the SPB Operations Informational System (SPBOIS), in the early 1970s (Pase and Fagala 1979). This system served as a model for the Southern Pine Beetle Information System (SPBIS) later developed by the USDA Forest Service for National Forests (see http://www.fs.fed.us/r8/foresthealth/programs/spbis/spbis.shtml). Analysis of operational data from the Texas Forest Service SPBOIS has proven useful for identifying spot detection thresholds and other means to improve SPB control operations (Billings 1974).

To better coordinate and share information among State and Federal agencies on SPB infestations detected and controlled during outbreaks, the USDA Forest Service, Forest Health Technology Enterprise Team, in cooperation with State forestry agencies, is developing an Internet-based SPB information system (Anthony Courter, Softec Solutions, Fort Collins, CO, personal communication). Once developed, each southern State with SPB infestations will report detection and impact information into a single database via individual Web-based portals. This system will require that each State report a minimum of six standard variables, but will accommodate a wide variety of additional data variables to be chosen by each State. The six variables that are required from each State will be:

- Unique spot number
- Date of spot detection (month, day, year)
- Geographical location of the spot (county, latitude: longitude in decimal degrees)
- Final area affected (acres)
- Total volume of timber killed (cubic feet)
- Total value of trees affected (dollars)

Other variables are optional but may include additional aerial detection, and ground check and control information (e.g., spot size at detection, ground check priority, date of ground check, number of infested trees at ground check, mean tree diameter and stand basal area, landowner name and contact information, date of control, type of control, volume of pulpwood and sawtimber, and so on). Specific data, in addition to the six required variables, to be collected and recorded in the Southwide information system within a given State, will be determined by the State pest management specialist(s) in that State.

For the first time, standardized SPB operational information will be available across the South as it is collected by pest managers in up to 16 States, the national forests, and other public forest lands once this system is implemented. The new system will allow the USDA Forest Service and other stakeholders to monitor SPB activity and control programs across the South as the season progresses.

17.5. SPB MONITORING AND PREDICTION WITH PHEROMONE TRAPS

An operational system to forecast SPB infestation trends (increasing, static, declining) and relative population levels (high, moderate, low) has been developed and implemented throughout the range of this forest pest in the Southern and Eastern United States (Billings 1988, Billings and Upton, in press). The Texas Forest Service (TFS) developed the Southwide SPB Prediction System with inputs from Federal and State cooperators across the South. The system involves monitoring numbers of SPB and those of a major predator, the clerid beetle, *Thanasimus dubius,* using pheromone traps (Figure 17.11).

17.5.1. How to Predict SPB Infestation Trends

In general, from one to three multiple-funnel traps (Lindgren 1983) baited with the SPB aggregation pheromone, frontalin (Kinzer and others 1969), and host volatiles are placed in each county or National Forest Ranger District to be surveyed (Figure 17.11 A, B, C). Federal and State forest pest specialists in 16 States (Oklahoma, Arkansas, Texas, Louisiana, Mississippi, Alabama, Kentucky, Tennessee, Georgia, Virginia, Florida, South Carolina, North Carolina, Delaware, New Jersey, and Maryland) have participated annually in the region-wide prediction system, most for more

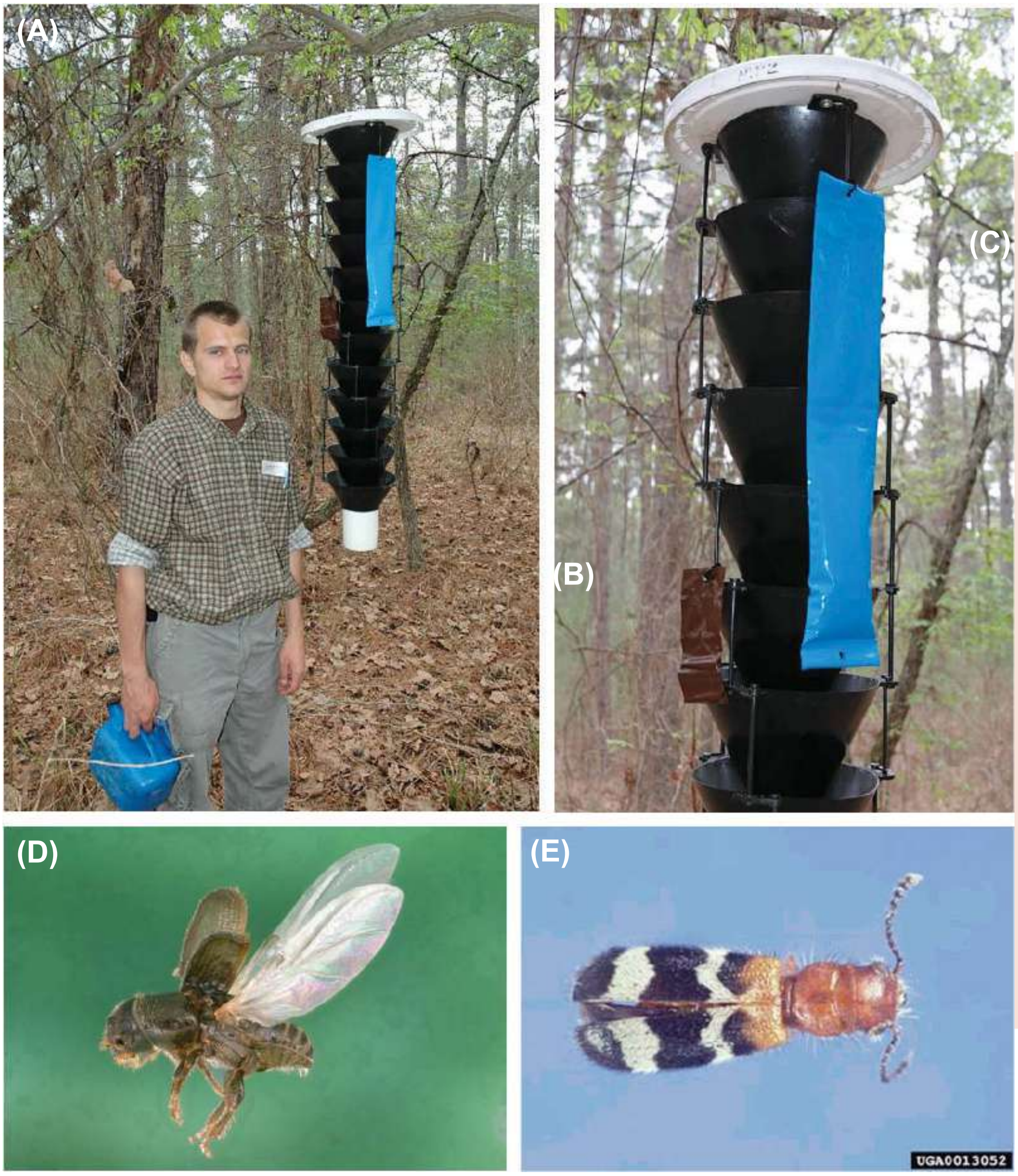

Figure 17.11—The Southern Pine Beetle Prediction System uses Lindgren funnel traps (A) placed in the field for 4 weeks starting when dogwoods bloom. The trap is baited with the SPB pheromone frontalin (B) and a dispenser of host odors (alpha- and beta-pinene) (C), an attractive bait combination that draws in flying adult SPB (D) and the clerid beetle, *Thanasimus dubius* (E), a major SPB predator. Both the number of SPB and number of clerids caught in traps are the variables used to forecast SPB infestation levels for the current year. (photographs (A), (B), (C) by Ron Billings, Texas Forest Service; photograph (D) by Erich G. Vallery, USDA Forest Service, www.forestryimages.org; photograph (E) by Gerald J. Lenhard, Louisiana State University, www.forestryimages.org)

than 2 decades. The traps are monitored for 4 consecutive weeks during the spring, beginning when dogwoods bloom. This seasonal event coincides with the long-range dispersal of SPB.

In 2007, the traditional host lure consisting of a rapid-release dispenser (amber glass bottle with wick) of steam-distilled loblolly pine turpentine was replaced with polyethylene bags of alpha-pinene (70 percent) and beta-pinene (30 percent). These commercially available host lures, in combination with synthetic frontalin, have proven equally effective for use in the SPB prediction survey (R. F. Billings, Forest Pest Management, Texas Forest Service, 301 Tarrow, Suite 364, College Station, TX 77840, unpublished data).

Responding insects are collected weekly for 4 consecutive weeks. Trap catch data—number of adult SPB (Figure 17.11D) and number of clerids (Figure 17.11E)—are sent to the Texas Forest Service for compiling and for making local, State, and regional predictions of SPB trends. The mean number of SPB/trap/day and the ratio of SPB to the total catch of SPB plus clerids (defined as percent SPB) in the current and previous year for the same trapping location are the variables used for predicting infestation trends and population levels for the remainder of the year. The SPB Prediction Chart (Figure 17.12) was developed and validated by comparing trap catch variables with actual detection records for each county, Ranger District, and State monitored. Upon completion of the annual survey, predictions are distributed to cooperators and are published on the Internet (Texas Forest Service Web page at http://texasforestservice.tamu.edu) for all to use, usually by the end of May.

17.5.2. Accuracy of the SPB Prediction System

An analysis of predicted and actual SPB infestation trends and population levels for participating States documents the accuracy of the prediction system (Billings and Upton, in press). From 1999 to 2005, the percent of correct predictions of SPB infestation levels averaged 82 percent for all States combined (range 71-100 percent); mean predictions for SPB population levels for States averaged 74 percent correct (range 43-100 percent). Despite system limitations, forest managers have come to depend on this early warning system for scheduling when and where to conduct aerial detection flights and to plan for suppression projects. This represents the first effective and validated prediction system for outbreaks of a bark beetle species anywhere in the world.

A recent survey of State forestry agencies shows that the SPB Prediction System has become the primary means of monitoring SPB populations during nonoutbreak years in three southern States—Arkansas, Texas, and Virginia. During years when SPB traps catch few or no SPB in spring surveys, the use of aerial detection flights may be greatly reduced or discontinued. In nine additional States—Oklahoma, Louisiana, Mississippi, Alabama, Georgia, Florida, South Carolina, Maryland, and Delaware—pheromone traps have become second only to aerial detection flights as the primary means to monitor SPB populations.

17.5.3. Extending SPB Monitoring into the Autumn

Based on the success of spring surveys to predict SPB infestation trends, the USDA Forest Service, Forest Health Protection, Region 8, is evaluating whether traps deployed

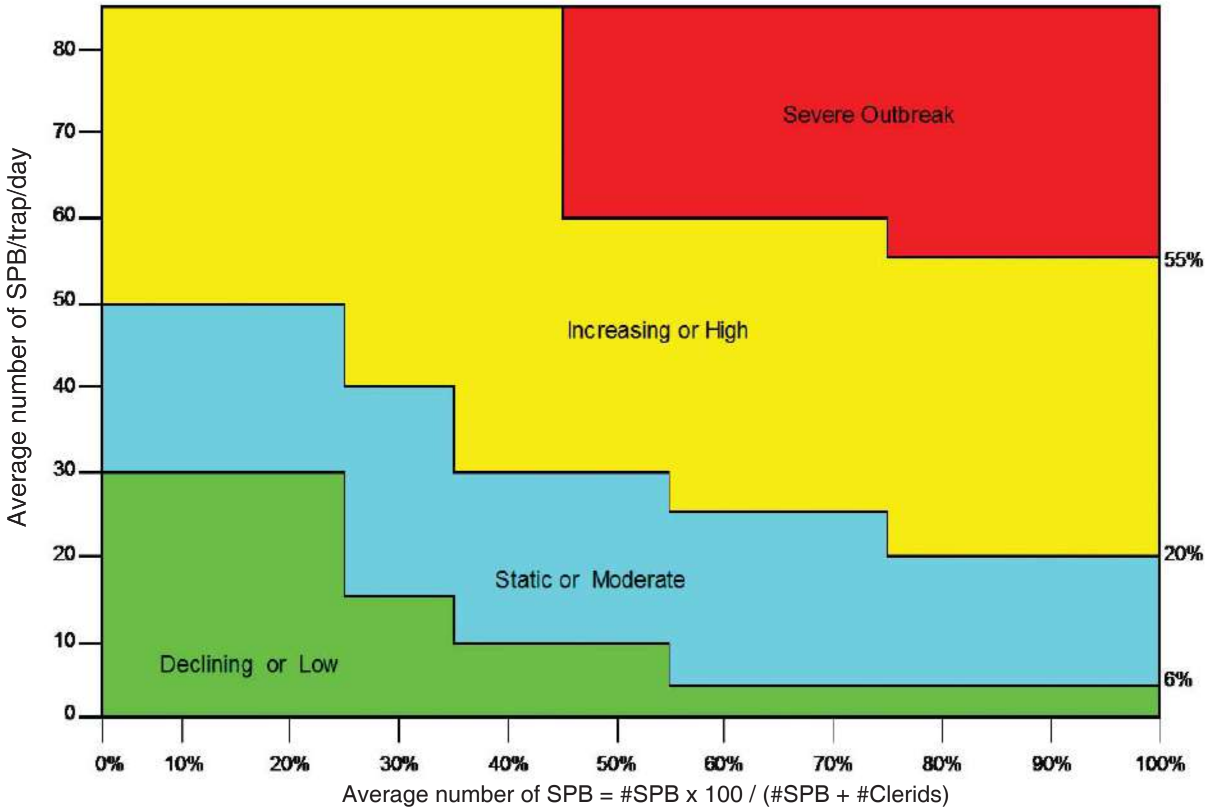

Figure 17.12—Southern pine beetle prediction chart, used to forecast SPB infestation trend and level for the current year, is derived by plotting the mean number of SPB/trap/day and percent SPB for the current year and comparing these data to that for the previous year (if available) for a given locality.

in November may be as effective as spring-deployed traps for prediction purposes (J.R. Meeker, USDA Forest Service, Forest Health Protection, 2500 Shreveport Road, Pineville, LA 71360). If so, fall surveys would provide even more lead time to prepare for pending SPB outbreaks. One limitation of fall surveys for predicting SPB infestation levels is that winter temperatures may play a critical role in determining SPB population trends the following spring (Ragenovich 1980, Tran and others 2007). By the same token, infestation trend predictions based on spring surveys may be rendered incorrect by adverse summer weather (excessively hot temperatures for prolonged periods) (Beal 1933). The long-term accuracy of fall predictions using pheromone traps remains to be determined.

17.6. SUMMARY

Monitoring SPB populations is a routine and essential phase of pest management for SPB, considered the most destructive pest of southern pine forests. Periodic detection flights over pine-forested landscapes in the South provide the primary means to detect new SPB infestations and pending outbreaks. Ground evaluation methods have been developed to provide pest managers with additional information on the status of SPB infestations detected from the air and the need for direct control. Methods for aerial detection and ground checking on State and private forest lands differ from those methods used on Federal lands, and also vary significantly among States. The goal in each case, however, is the same: to identify those SPB spots most likely to cause significant resource losses if not controlled and to facilitate subsequent control operations.

In recent decades, an effective system to predict SPB infestation trends and SPB population levels using pheromone traps has been developed and implemented to supplement aerial detection flights. This system is currently being implemented in 16 States through a network of traps deployed across the southern region each spring by State and Federal pest management specialists, providing another tool to better manage this destructive forest pest. Also, the feasibility of using pheromone traps deployed in the autumn to predict SPB infesation trends is being evaluated.

17.7. ACKNOWLEDGMENTS

Appreciation is extended to the State pest management specialists who contributed information on their States' specific methods for SPB detection and evaluation in the recent survey mentioned in this chapter. These specialists also voluntarily conduct the annual SPB prediction monitoring with pheromone traps in their respective States. These dedicated contributors are: Steve Mattox (Oklahoma Division of Forestry), James Northum (Arkansas Forestry Commission), William Upton (Texas Forest Service), Carlton Cobb (Louisiana Forestry Commission), Dr. Evan Nebeker (Mississippi Forestry Commission), Dana McReynolds (Alabama Forestry Commission), Clint Strohmeier (Tennessee Division of Forestry), James Johnson (Georgia Forestry Commission), Dr. Chris Asaro (Virginia Division of Forestry), Dr. Albert Mayfield (Florida Division of Forestry), Laurie Reid (South Carolina Forestry Commission), Rob Trickel (North Carolina Forestry Commission), Steve Tilley (Maryland Department of Agriculture), Glenn Gladders (Delaware Forest Service), and Jon Klischies (New Jersey Forest Service).

18

Conducting a Southern Pine Beetle Survey Using Digital Aerial Sketchmapping (DASM)—An Overview

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Abstract

This is an overview on conducting a southern pine beetle (SPB) survey using Digital Aerial Sketchmapping (DASM); for a detailed treatment of DASM visit the following Web site: http://www.fs.fed.us/foresthealth/technology/dasm.shtml. Sketchmapping – “A remote sensing technique of observing forest change events from an aircraft and documenting them manually on a map” (McConnell and others 2000). Recent advances in microprocessor speed and PC system performance now make possible the use of portable computers for aerial sketchmapping in aerial survey work. The USDA Forest Service Remote Sensing Applications Center (RSAC) and Forest Health and Technology Enterprise Team (FHTET) have worked with software vendor, Michael Baker Jr., Inc., to develop an application that will make survey and monitoring of SPB spots more accurate and efficient. The core of the DASM is GeoLink® software (Michael Baker Jr., Inc.). GeoLink incorporates a global positioning system (GPS) signal into a displayed background map window and enables the user to sketch points, lines, or polygons onto the virtual map display. GeoLink then translates these data into ESRI® shapefiles, a common geographic information system (GIS) data format. Advantages include automatic tracking of aircraft position on the map base through a link to a GPS receiver, ability to display many types of background maps for better accuracy in digitizing SPB spots, and the reduction of time spent digitizing data into the GIS.

Keywords

DASM
GeoLink
sketchmapping

18.1. INTRODUCTION

The purpose of an aerial detection survey is to accurately locate insect and/or disease spots and to determine their relative size and number in order to evaluate the need for control. This is accomplished for the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) by conducting periodic flights over pine forests in small, high-winged aircraft such as the Cessna 182 and 206. Suspected SPB spots (groups of dead and dying pine trees) are plotted onto hardcopy maps or aerial photographs (Figure 18.1). Once detected from the air, suspected spots are visited on the ground to confirm the causal agent and assess the need and priority for control (Billings and Pase 1979a). Hardcopy products are then provided to the local or district forester for data entry. The sketched features (points, lines, polygons) are then "heads-up" (on screen) digitized into a geographic information system (GIS). These data are then used to prepare reports at the forest, regional, and national level. Problems with this manual system include: numerous cumbersome maps to manage in the cockpit, the inaccuracy of sketched features, and the office time required to digitize sketched features. Inaccurately mapped SPB spots are particularly problematic since field crews must use the maps to locate spots on ground. Advances in GIS, global positioning system (GPS), and computer technology have led to the development of the Digital Aerial Sketchmapping System (DASM), which has helped solve some of the problems with the manual method. It is important to note that even with its inefficiencies and lack of accuracy, primarily with inexperienced surveyors, the manual system works.

18.2. BACKGROUND

Interest in the development of a digital aerial sketchmapping application led to a request in 1995 by the Pacific Northwest Region to the Forest Health and Technology Enterprise Team (FHTET) and the Missoula Technology Development Center (MTDC) to initiate an information-gathering project on the feasibility of developing a system. As part of this project, forest units throughout the National Forest System were surveyed to determine the needs of the sketchmapping community. Personnel from FHTET and MTDC visited the British Columbia Forest Service at William Lake, British Columbia, in June 1996 for a demonstration of their digital sketchmapping system. There were several disadvantages identified with this system, and in general, the system was slow and cumbersome. The Remote Sensing Application Center (RSAC) put together a list of requirements and began an extensive search for contractors that could meet these criteria (Thistle and others 1996). Based on the investigation, RSAC chose GeoLink® by Michael Baker Jr. Inc. of Jackson, Mississippi (Figure 18.2).

18.3. SYSTEM DEVELOPMENT

18.3.1. Software

The GeoLink software is able to display many different types of geospatial data as background maps; most SPB detection flights are conducted using digital orthophoto quarter quads (DOQQ) because of the need for accuracy. When collecting data using GeoLink, the aircraft's position is displayed as an icon on the map display along with features (point, line, polygons), type keys, and a user-

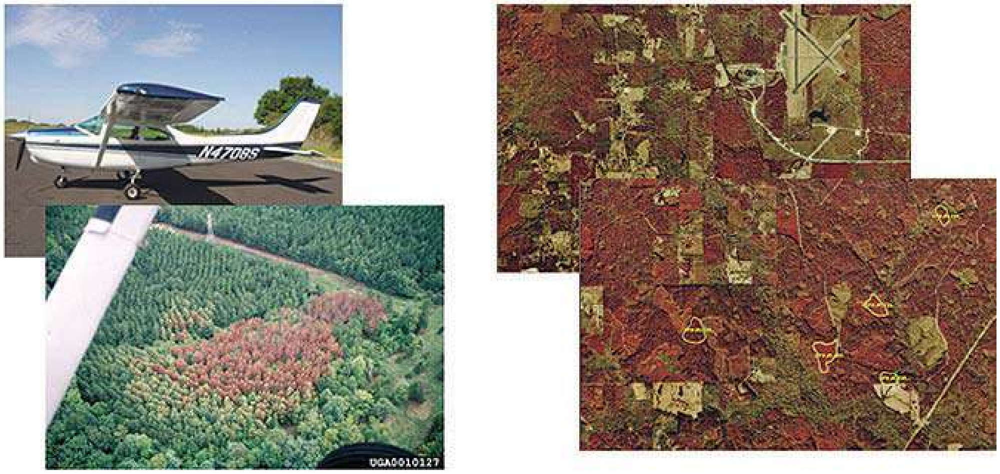


Figure 18.1—Sketchmapping forest pest infestations. Sketchmapping is a remote sensing technique of observing forest change events from an aircraft and documenting them manually on a map. (images by McConnell and others 2000, lower left photograph by Andrew J. Boone, www.forestryimages.org)

defined keypad for attributing features. The observer selects the particular type of feature to be sketched, sketches the feature on the screen, and then attributes the feature using the keypad. The screen remains frozen while the feature is being sketched and updates after the Enter key is pressed. When the aircraft icon advances to the edge of the window, the map display updates with the aircraft icon moving to the center of the window. Upon completion of the SPB survey, a translation step converts the sketched features into ESRI® shapefiles.

18.3.2. Hardware

There are three current hardware configurations being used with the DASM system. The first consists of a laptop PC (Figure 18.3A), a touchscreen manufactured by KDSPixelTouch™ (Ontario, CA), a GPS receiver, and a specially designed power distribution board that draws from the aircraft power system. The disadvantage to this laptop-based hardware setup is that it is cumbersome. It is awkward to use because of the many different components and cables in the confined space of a small aircraft. Also, the unreliability of the KDS touchscreen and the time it takes for repair are limiting. The second system is the Hammerhead™ pen tablet PC (Figure 18.3B), one of the new generation mobile PCs that show great promise for the DASM system. It is very simple from a hardware perspective, consisting of the PC, the GPS antenna/cable, and the power distribution box connecting the PC power cable to the aircraft power supply. The third configuration uses the Motion™ Tablet PC (Figure 18.3C). With a 12.1-inch screen, this Tablet PC provides ultramobile technology with high-end performance and light weight. The Motion™ computer offers Bluetooth capability (cordless functionality) and a high-resolution screen.

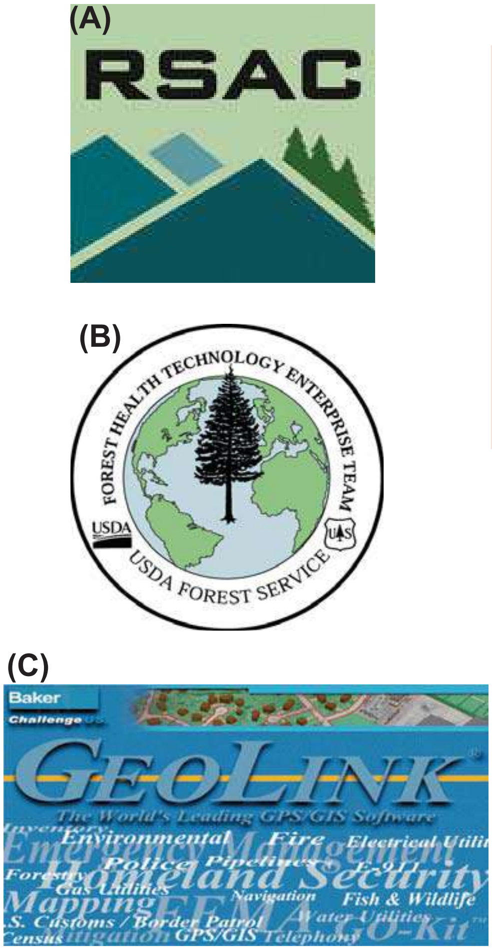


Figure 18.2—(A) The USDA Forest Service Remote Sensing Applications Center (RSAC) and (B) Forest Health and Technology Enterprise Team (FHTET) have worked with software vendor, (C) Michael Baker Jr., Inc., to develop an application that will make survey and monitoring of SPB spots more accurate and efficient.

Figure 18.3—Three current hardware configurations being used with the DASM system. (A) KDSPixelTouch™, (B) Hammerhead™Tablet PC, (C) Motion™ Tablet PC.

18.4. METHOD

18.4.1. Preflight Planning

Preflight planning is essential to a successful DASM project (Figure 18.4). You establish the survey area and prepare background maps, set your flight lines, and determine what data is to be gathered and what attributes will be associated with your spots. During preflight planning you can build a project to use within GeoLink that will contain the above information. This project can be reviewed by simulating a flight; this ensures that all data and settings are correct before the flight. ESRI GIS software is useful for preflight planning tasks. Safety issues are a top priority in preflight planning—no-fly zones, airports, tall structures, check-in points, "go/no-go" decision points. As the surveyor, you are not only gathering data but must become familiar with maps, charts, aircraft, and weather, and must be able to properly identify problem areas; and now, with DASM, you must also become familiar with computers and geospatial data. However, once you become familiar with the DASM system, it can be an asset to in-flight safety by accurately showing your position relative to restricted areas, hazards, and Federal Aviation Administration (FAA) Sectional charts. Preflight planning must be a top priority for a safe and successful survey.

Digital Imagery for SPB detection

Background maps can consist of vector and image (raster) maps. Displayed images may be in any of the supported data types including TIF, BMP, JPEG, and others. If you know the datum/projection of your imagery and whether it has a .tfw or .reg registration file, GeoLink will display the imagery. False color infrared DOQQs (Figure 18.5) are the preferred background map during SPB survey flights because the high resolution (2 m) of this imagery allows the surveyor to precisely digitize the spots. Also, the color infrared (CIR) may help one to differentiate between hardwood and pine species. Accuracy of the SPB spot location is critical because field crews will use the coordinates to find the spot on the ground. Administrative boundaries can also be displayed within a GeoLinks project.

During a GeoLink logging session, the entire map is redrawn each time the display refreshes a map, even if you are displaying only a small portion of that map on the screen. With such a large raster image in memory, very little remains for other computer functions. This situation can cause dramatic slowdown in display refresh rate and/or system crash. To avoid this, GeoLink detects when large raster images are loading and launches a utility called the SplitTiff Raster Optimization Utility. SplitTiff creates a new proprietary image file from the raster image,

Figure 18.4—Preflight planning.

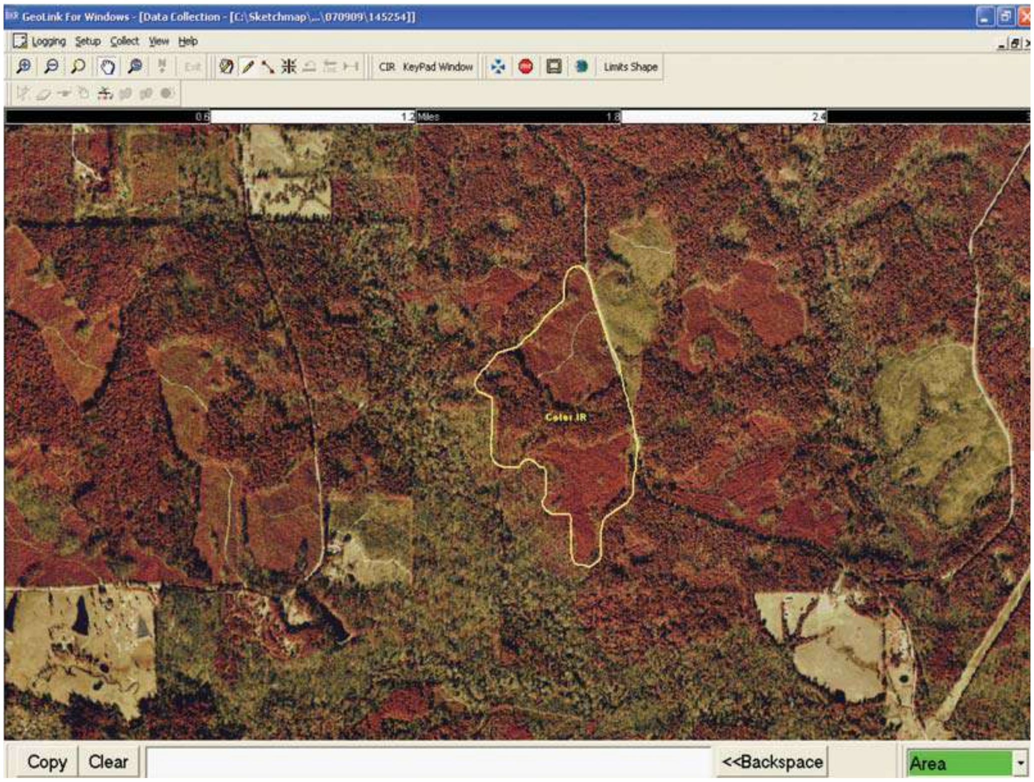


Figure 18.5—Color infrared imagery.

called a GeoLink Optimized Raster (*.gor) file. GeoLink loads only the required neighboring GOR files into RAM when a map is displayed. GOR files are separate from the source TIFF and TIFF World Files from which they were created. You can view them only in GeoLink, but you can copy and move them as you would other files.

Shapefiles

Vector shapefiles such as roads, streams, contour lines, flight lines, forest boundaries, compartments, stands, hazard areas, and no-fly zones can be overlaid on raster images to help you pinpoint SPB spot locations and help provide for a safe survey (Figure 18.6). During an active outbreak, SPB detection flights may be conducted over the same area several times in one season. The ability to display previous survey data is important in keeping track of new and already recorded SPB spots. GeoLink gives you the ability to display shapefiles with many different colors, shades, and text that will help you distinguish survey data. Surveyors often want to display large shapefiles over their raster map data. A SplitShape utility has been created to decrease the screen regeneration time for ArcView® shapefiles with many records. The SplitShape utility can either be run automatically by GeoLink when large shapefiles (500 features or more) are added to the background map list, or run manually to batch process files. The SplitShape utility creates a new file to go along with the original three files (.shp, .dbf, and .shx). The new file has an extension SLF (Shape Look-up File). This file must be transferred along with the original SHP, SHX, and DBF files to speed up display. Since the shapefile format has not been changed in any way, data can still be shared between GeoLink and the GIS systems easily.

Data Collection

Digitizing

Digitizing features within GeoLink is a four-step process (Figure 18.7): 1. The feature type to be digitized is selected; for SPB surveys, either points or polygons will be used; 2 Digitize the feature on the screen. Locate the feature on the ground and place the point or polygon on the screen using the stylus; 3 Fully attribute the feature; specify what you want that point or polygon to represent; 4 Click the Enter button to save the feature to disk. Each feature you digitize will have data (latitude, longitude, date, time, and attributes) associated with it.

Real time feature editing

It is easy to make errors when digitizing and attributing features while flying at 100 knots. One simple way to deal with errors is to tag the feature with a “del” (for Delete) attribute, then

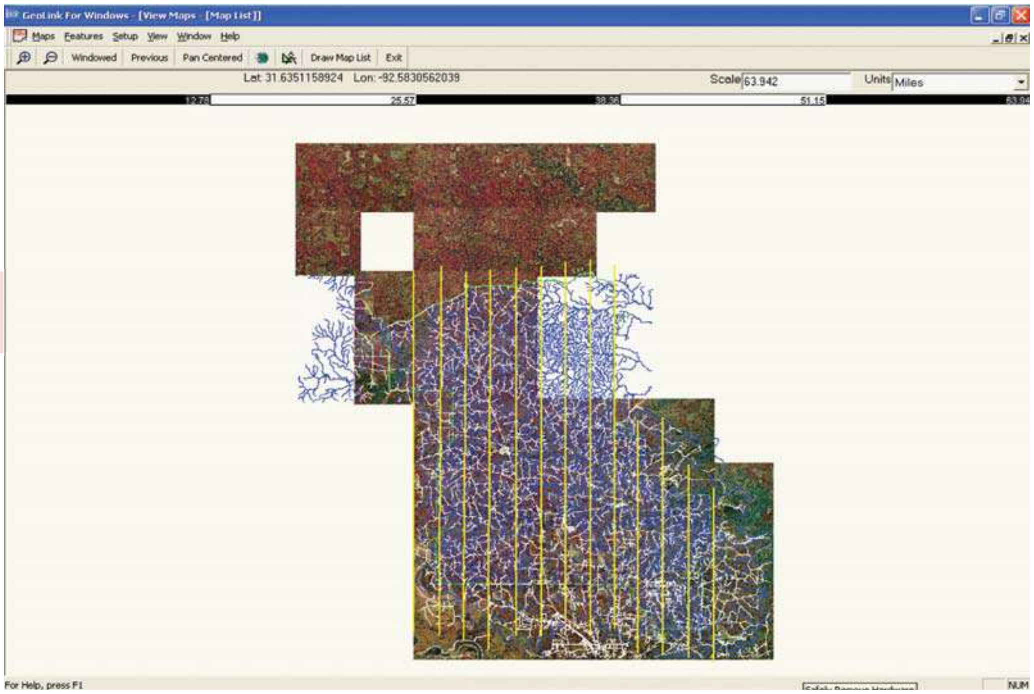
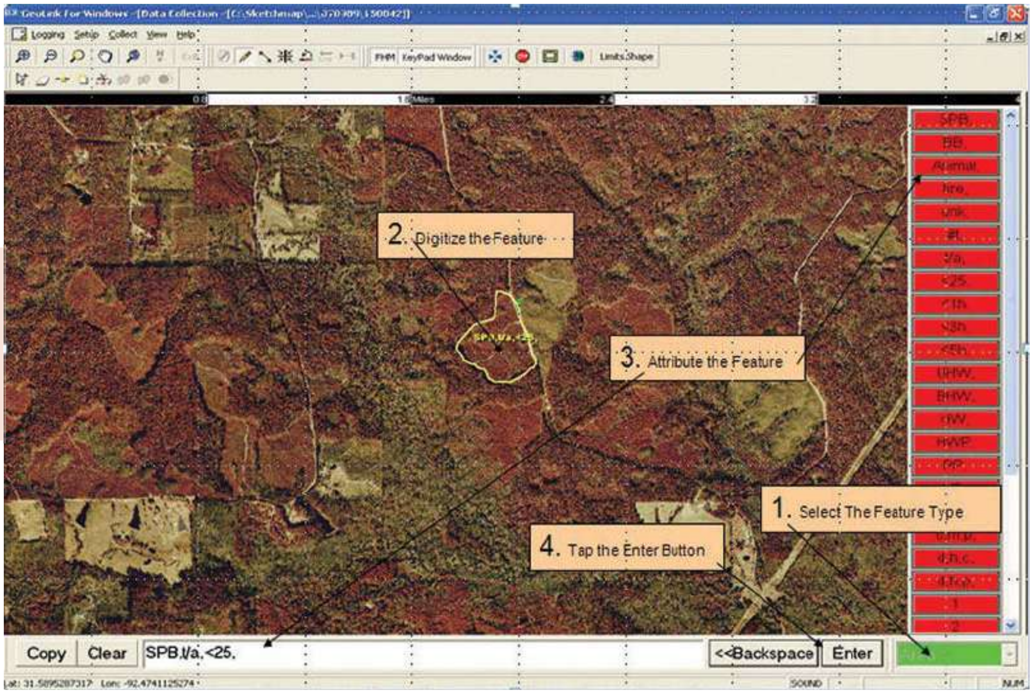


Figure 18.6—The use of shapefiles.



2. Digitize the Feature

3. Attribute the Feature

1. Select The Feature Type

4. Tap the Enter Button

SPB.t/a.<25.

Figure 18.7—Digitizing—A four-step process. 1. Select points or polygon. 2. Digitize feature. 3. Attribute feature. and 4. Click Enter.

redigitize the feature over top of the one just attributed with "del". In such a case, the first step in post-processing is to delete all features with the "del" for an attribute. Another way to correct digitizing errors, whether spatial or attribute, is to use the Real Time Feature Editing process in GeoLink (Figure 18.8). You can use this feature in either Simulate or Log mode and the functionality will be the same.

Translating the digitized features

Enter the Translate Mode by selecting Translate from the main toolbar (Figure 18.9). The Translate Mode is used to convert GeoLink's® proto-shapefiles collected during a log session into true ESRI® shapefiles. During the Translate process, the shapefiles are projected into the coordinate system you specify. It is recommended that you run the translation during the same day, since you can see the

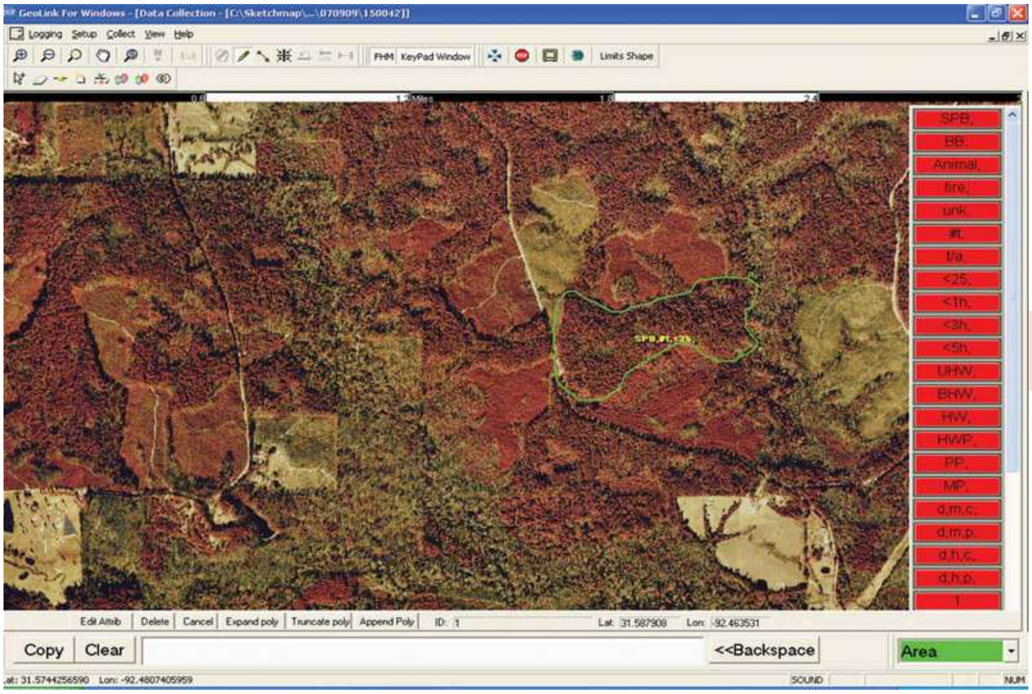


Figure 18.8—Real-time feature editing.

Figure 18.9—Translate window.

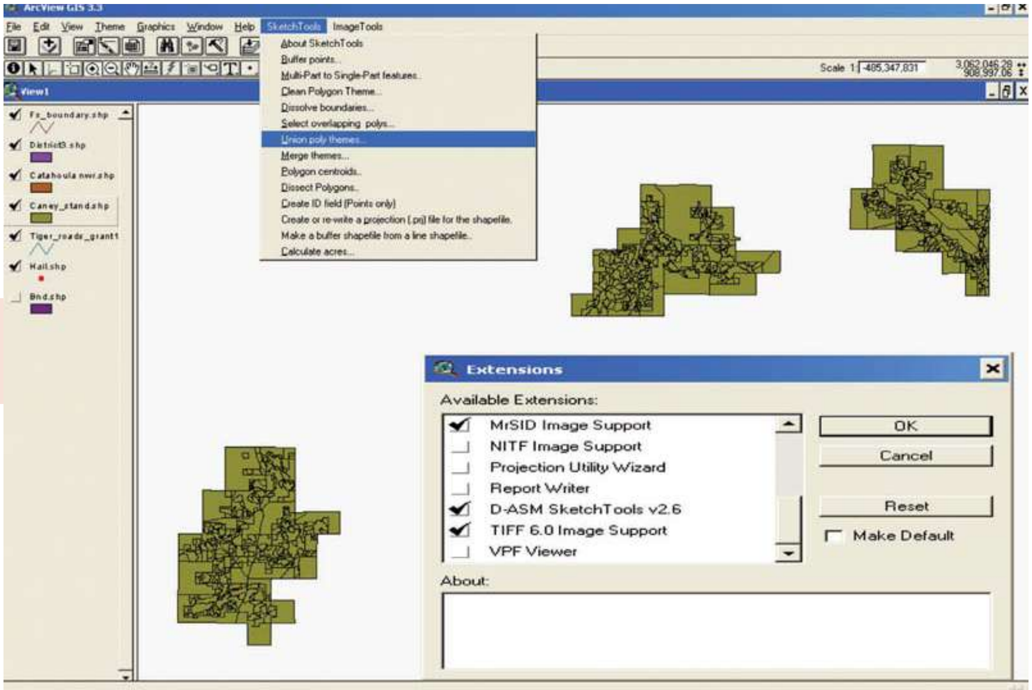
results while the mission is still fresh in your memory.

Post-Processing DASM Mission Data

The PC-Based DASM system developed by the USFS Forest Health and Technology Enterprise Team (FHTET) and the Remote Sensing Applications Center (RSAC) enables aerial surveyors to collect forest damage information in digital format. This new system changes not only how the data are collected, but also how the surveyor edits the data after collection. Using the traditional, paper map-based method, the surveyor would make changes to features drawn on the maps using pencil and eraser. The features and attributes would then be transferred by hand to another paper map to produce a clean, easy-to-read copy for digitization by GIS staff. The DASM systems output features in a digital file; editing and data QA/QC (Quality Assurance/Quality Control) that formerly was done with a pencil and eraser is now done on softcopy using GIS software. Clear communication between the surveyor and GIS staff about data format and content is essential. SketchTools, an ArcView® extension developed by RSAC (Figure 18.10) to facilitate post-processing in ArcView, is a series of utilities to help you process your points, lines, polygons, and associated feature tables.

18.5. DISCUSSION

SPB detection flights are conducted throughout the growing season to locate small outbreaks of southern pine beetle. The goal is to locate spots and treat them before they increase in size. Crews must find these SPB spots, which may be as small as three trees, based on the accuracy of the points specified on the survey map. A distinct advantage in using the DASM system is that the surveyor no longer has to keep track of his/her position on the map. This can be difficult in the flat, relatively featureless areas of the Southeast United States. The DASM system places the aircraft on the map base, so the surveyor can devote more time looking for SPB spots and accurately recording them with DASM.



Available Extensions:

- ☑ MrSID Image Support
- ☐ NITF Image Support
- ☐ Projection Utility Wizard
- ☐ Report Writer
- ☑ D-ASM SketchTools v2.6
- ☑ TIFF 6.0 Image Support
- ☐ VPF Viewer

☐ Make Default

Figure 18.10—Sketchtools—an ArcView® extension.

Using the DASM system, accuracy of the SPB-spot mapping has substantially improved, and ground crews are able to navigate directly to the spots by loading the coordinates obtained from the aerial survey into a GPS receiver. Previously, GIS technicians had to "heads-up" digitize the spots from the hardcopy photos and then print out maps that were used by the field crews to find spots. This process often took days; using the DASM system, spots can be located during a morning detection flight and field crews can be visiting the spots that afternoon.

With there being no glory in bouncing around in an aircraft trying to find SPB spots in the middle of summer in the South, the more technology can help, the better. In the hands of a well-trained, willing surveyor the DASM system can improve SPB surveys.

19

Southern Pine Beetle Field Survey

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Keywords

aerial survey
GIS
GPS
mobile mapping
southern pine beetle

Abstract

Southern pine beetle (SPB) is one of the most formidable insect pests impacting southern forests. Federal, State, and private forest managers have always dealt with this pest in some capacity. One of the primary requirements for controlling SPB is locating infestations on the ground. Once the infestation has been located, data is collected and used in management decisionmaking. Several methods have been used to accomplish these tasks. This paper describes traditional methods, as well as new technologies being used for SPB field surveying.

19.1 INTRODUCTION

One of the principal goals of the monitoring procedure used by the USDA Forest Service, Forest Health Protection (FHP), for the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is to provide information to pest management specialists in a timely manner. The survey data are also used in various types of reports. The aerial sketchmapping procedure (described in chapter 18); the database management system, SPBIS, (described in chapter 20); and the map/text reporter (described in chapter 21) address different aspects of the automation procedure. In this chapter the issue of automated survey data collection and transfer is addressed. Two issues are considered: 1. the use of digital technologies to collect data, and 2. the transfer of the data to the database management system. In the past, a major impediment to the timely use of SPB surveys information has involved the transfer of data from paper survey forms to the database management system, Southern Pine Beetle Information System (SPBIS). Paper forms were satisfactory for collecting data, but survey personnel often did not have sufficient time to enter data into SPBIS. Consequently, management decisions could not be based on the most current information. The procedure described in this chapter addresses automated data collection and transfer to SPBIS.

19.2. USING DATA FROM AERIAL SKETCHMAPPING

The data collected using aerial survey is vital to finding infestations on the ground. The quality of this data can vary greatly due to surveyor experience, type of aircraft, and environmental conditions, among others. The use of global positioning system (GPS) and other digital surveying technologies continues to make it easier to locate infestations. While digital aerial sketchmapping (DASM) is becoming more commonplace, traditional sketchmapping using paper maps is still used in many instances.

19.2.1. Data from Traditional Aerial Detection Methods

With traditional aerial sketchmapping the surveyor records infestation locations on a paper map while flying over a given area. This method, when used by an experienced surveyor, is effective in recording infestation locations. However, if the surveyor has limited experience or is not familiar with the survey area, the recorded locations can vary significantly from their actual ground location. This makes ground truthing infestations very difficult. With no definite coordinates, ground surveyors must rely on their knowledge of the area or the quality of the maps they have at their disposal. These factors dictate the efficacy at with which infestations can be surveyed.

19.2.2. Data from Digital Aerial Sketchmapping (DASM)

DASM provides solutions to many of the problems associated with traditional sketchmapping. A variety of background imagery can be used to help the surveyor orient himself to the survey area. This system employs a GPS that constantly monitors the position of the aircraft during the survey, allowing the surveyor to know his position in relation to the ground at all times. This feature alone helps to improve the accuracy of recorded infestation locations. Despite these advantages, it is still possible for an inexperienced surveyor to record infestations incorrectly. If the background imagery being used is outdated, the surveyor may have difficulty distinguishing locations on the ground due to landscape changes. While both traditional and digital sketchmapping have drawbacks, the DASM system allows surveyors who have a wider range of abilities to collect quality data.

19.3. NAVIGATION TO INFESTATIONS

19.3.1. Traditional Navigation Methods

Traditionally, paper maps of the survey area are used to find infestations on the ground. These maps vary greatly in scale, detail, and overall accuracy. Often hand-drawn directions are used to guide surveyors. When used by experienced surveyors, traditional methods can be very effective. Surveyors with little or no experience will require time to acclimate themselves to their surroundings. Paper maps are still a very useful surveying tool.

Topographical Maps

One type of map that is used to navigate to an infestation is a topographical map. These maps show relief in some measurable form, such as contour lines that show changes in elevation for an area. These maps allow the surveyor to determine the most efficient route to an infestation. In areas with little relief, a direct path is usually the best, depending on the land cover. Topographical maps are particularly useful in areas with frequent changes in relief. The survey can use natural contours to reach an area more efficiently.

Forest Service Maps

Forest service maps, either State or Federal, are available for all public lands. These maps are not updated on a regular basis and vary greatly in accuracy. In most cases these maps display major highways and landmarks within the boundary of the forest. They also show selected forest service roads and trails. If accurate, these maps can be used to learn an area and get the surveyor close to an infestation. Often when the surveyor gets close to an area he will find a variety of other access points into the woods such as skidder trails, fire breaks, and logging roads that are not marked on the map.

Aerial Photography

Aerial photography is also a useful tool for surveyors. Photos of a given area allow the surveyor to use natural and manmade landmarks to navigate. Photos also allow the surveyor to get an idea of how the surrounding landscape is composed. Any type of map or photo a surveyor can take into the woods will be useful in locating SPB infestations.

19.3.2. GPS Data Loggers

Currently there is a wide variety of data loggers designed to meet navigation and field data collection needs. Units vary greatly in cost and functionality. The units being used for SPB work by Forest Health Protection are the Trimble® GeoExplorer™ series.

Digital Imagery

Digital imagery can be a useful addition to the tools surveyors use to find infestations. Current digital imagery is readily available and can be manipulated to work in most digital mapping systems. Surveyors can use an image of the survey area to navigate and validate their position. The most commonly used types of digital imagery are color infrared or true color images.

Shapefiles

A shapefile is defined as "a vector data storage format for storing the location, shape, and attributes of geographic features." (Environmental Systems Research Institute Geographic Information System (ESRI® GIS) Glossary 2007). Shapefiles can also be a useful surveying tool. Shapefiles are currently available for a wide array of features on State and Federal lands. Features on private land are less common but can be easily created in a GIS.

Global Positioning System

Global positioning system is an integral tool in surveying SPB infestations. Global positioning system in conjunction with quality background imagery allows surveyors to determine their exact location on the ground, thus orienting them to the infestation. In recent years the quality of GPS receivers has increased while their cost has steadily decreased. High quality units are available for a variety of uses. The use of GPS has greatly increased the efficiency of locating infestations.

19.4. DATA COLLECTION AT AN INFESTATION

19.4.1. Automated Data Collection

The tools available for field data collection have continued to increase in recent years. Traditional data collection consists of a field technician manually recording observations. Advances in hand-held mobile device technology have increased the opportunities for automated data collection. Hand-held mobile devices are personal computers designed for field use. For mobile mapping applications, they integrate a user-friendly operating system, GIS software, and GPS capabilities to allow for efficient and accurate data collection. Mobile devices come equipped with many different software and hardware configurations to suit the needs of the individual user. It is important to consider the environment in which the mobile device will be used. Field conditions are more variable and often much harsher than those in an office environment. It is important to consider the functionality of the device in the field and, most important, protection of collected data. The memory capacity and processor speed of the device are also important. The device must have enough memory to sufficiently store data while being able to efficiently operate GIS software, which is often graphically intense. The software utilized by the device must also be compatible with the software on a desktop computer in order to facilitate data transfer. Mobile devices are constantly changing, becoming more compact yet more diverse in their capabilities.

This brief overview of the components of a mobile mapping system is intended to show that these technologies, while having several inherent drawbacks, will continue to improve. This chapter will discuss in depth one specific mobile mapping application in the field of forest entomology.

19.4.2. SPBIS Mobile Mapping System

Mobile mapping can be defined as "the ability to collect field data, with unique geospatial time tags and attributes, for integrating into or updating a GIS" (Rasher 2001). Mobile mapping allows for the collection of a variety of data types at any time and place. The differences between mobile mapping and automated data collection are subtle. Automated data collection can be done from a stationary position, while the term "mobile" implies that data is collected on the move. Mobile mapping systems are designed to facilitate automated data collection in the field. Three major components comprise a mobile mapping system: GPS, a GIS, and a hand-held mobile device for data collection. The sequential steps in surveying and monitoring the SPB are illustrated in Figure 19.1. The survey begins with aerial sketchmapping. The traditional method of aerial sketchmapping involves manually marking the location of SPB infestations on a paper map. Digital aerial sketchmapping is a new technology that utilizes GPS and GIS technologies to allow the surveyor to mark areas on a digital map, which are in turn converted into a data format that can be used in a GIS. Each location marked on the map has GPS coordinates associated with it. These data can then be uploaded into a hand-held device and used for navigation purposes. It is often difficult to locate infestations on the ground using traditional navigation methods. Global Positioning System coordinates allow the surveyors to reach the desired location more quickly. Once an infestation has been located, a survey form is completed. The current form consists of a single sheet of paper containing blank fields for each desired data type. The data are collected on the paper form and manually entered into the SPBIS database. It has been determined that the primary restriction in the current SPBIS data collection process is data entry. Entry of data into SPBIS is a time-

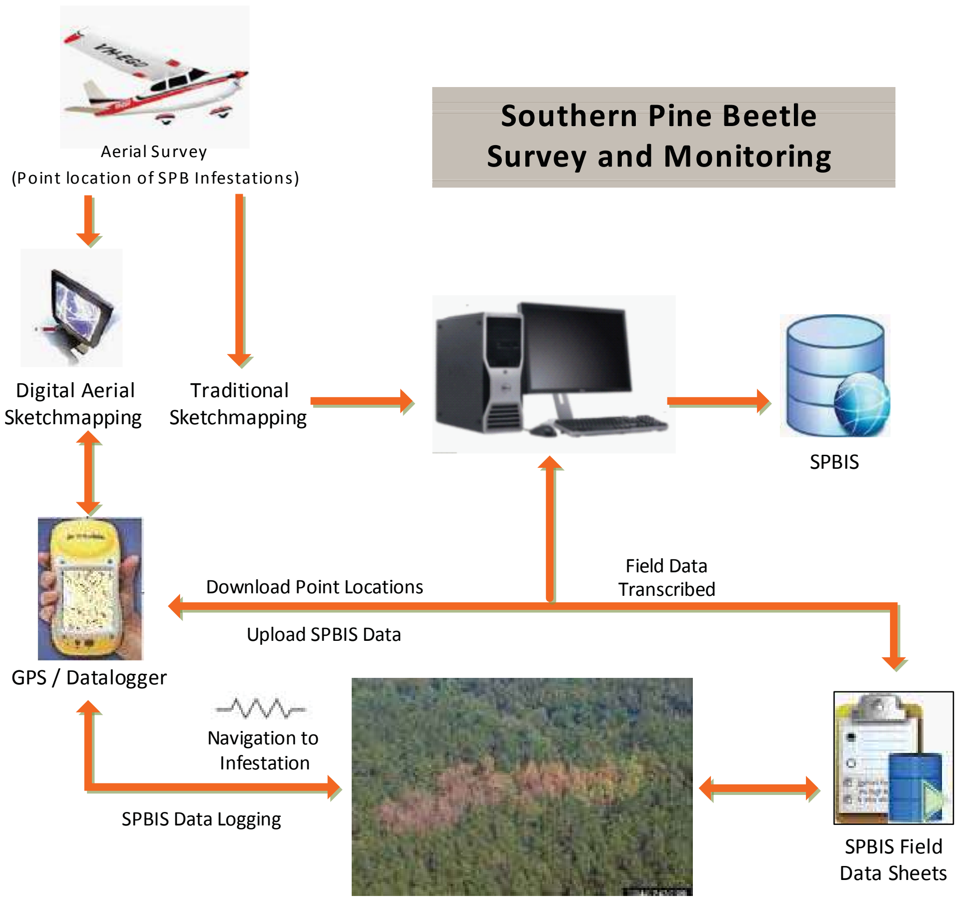


Figure 19.1— Schematic of the SPBIS Mobile Mapping System. (KEL image)

consuming process and is often neglected. When SPB outbreaks occur during the summer, district personnel have limited time in which to enter survey data into SPBIS. In order for SPBIS to be used as an operational management tool, data must be entered in timely manner. Given the current situation, SPBIS data are not used for operational forest management decision-making. The database serves as storage for historical outbreak records. The combination of a mobile GPS unit and a digital upload interface between the unit and SPBIS allows surveyors to collect data in a digital format and upload it directly into the database. This eliminates much of the need for manual data entry. The shortcomings of the SPBIS database will continue to be compounded if the development of a dependable system for data acquisition and processing is further delayed. With little or no data entry occurring, information for decisionmaking is limited. This severely limits the ability of managers to develop plans for prevention and suppression.

It is important to measure the size of an SPB infestation to determine total losses in a given area. Traditionally, infestation size was estimated by the surveyor. Acreages taken by this method vary greatly in accuracy. Global positioning system, along with mobile GIS, allows the surveyor to make an actual measurement of an infestation. While these measurements still have some degree of error due to signal quality, they are more accurate than an estimate. Polygons created within the mobile GIS can also be exported onto a desktop GIS and corrected for even greater accuracy.

Digital SPB Data Collection Forms

The SPBIS database is designed to keep a record of all survey information. All data are collected into a primary database file (DBF) table and a backup DBF table that is associated with a shapefile. Each field within the form has a column in the DBF table. Each column in the DBF table corresponds to a field in the SPBIS database by name.

The backup DBF table is the record that is uploaded into SPBIS. Several fields can be edited. Any time an infestation is edited, any previous information is overwritten. Radio buttons for adding an infestation, a head, or a breakout are located at the top of the first page of the form. One of these choices must be made in order for data to be recorded. If a choice is not made, no data will be recorded.

Southern Pine Beetle Infestation Data is the heading on the first page. The fields on the first page include the Region, Forest, District, Infestation Number, Head or Breakout Number, Parent Head or Breakout, and Species of Pest. The Region, Forest, and District fields each have drop-down menus that contain all the possible location choices. The Head or Breakout Number and Parent Head or Breakout fields have default values if the user enters no value. Secondary heads and breakouts rarely occur; therefore, default values must be available in order for the data to be uploaded into the database. The drop-down menu for Pest Species field contains three choices: Southern pine beetle, any of the several species of *Ips* spp beetles that attack pine, and Black Turpentine Beetle. These three pests are not the only species that will be encountered while conducting a survey, but they are the most prevalent.

Heads and Breakouts are the heading for the second page of the form. This page contains fields for the Compartment Number, the Stand Number, Wilderness Identification, Wilderness Name, Pine Basal Area, Total Basal Area, Infestation Locator Identification, Infestation Priority, and the Estimated Area. The Wilderness Identification field contains a simple yes or no option. If an infestation is in a wilderness area it greatly affects the treatments that can be applied. If the infestation is in a wilderness area, the Wilderness Name field is activated. It contains names of wilderness areas that correspond to the forest and district chosen on the first page. The Pine and Total Basal Area are determined for the stand in which the infestation occurs. The Infestation Locator is the name of the person who found the infestation. The Priority field contains three choices: High, Medium, and Low. An option is chosen based on infestation activity and the value of the material contained in the infestation and surrounding areas. The acreage that is determined by traversing the infestation with an activated GPS is entered into the Estimated Area field.

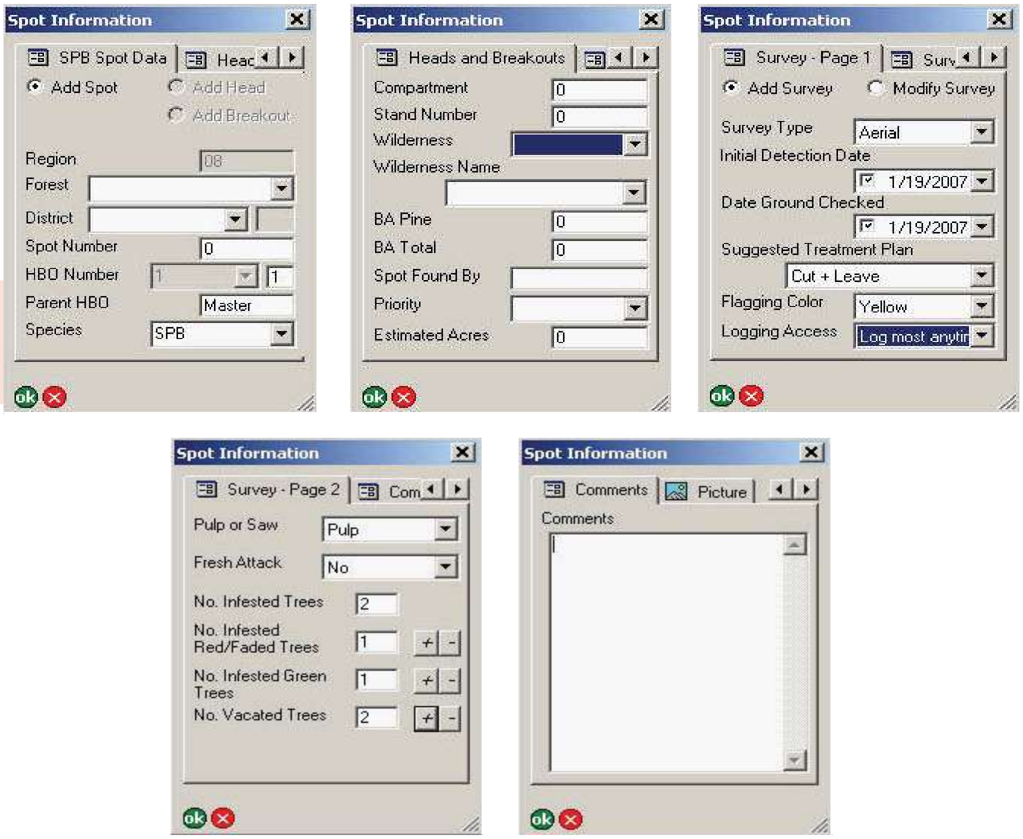
Survey: Page 1 is the heading for the third page. This page contains fields for the Survey Type, the Initial Detection Date, the Ground Check Date, the Suggested Treatment Plan, Flagging Color, and Logging Access. The Survey Type field contains the following choices: Aerial, Ground, and Video. These choices correspond to the manner in which the infestation was detected. The Initial Detection Date is the date the infestation was found, while the Ground Check Date is the date the infestation is first visited on the ground. These dates can be the same but often are not. The ground crew that conducts the initial infestation survey recommends the Suggested Treatment Plan. Treatment recommendations are based on current infestation activity and value of the stand in which the infestation is located. The Flagging Color field has a drop-down menu that contains several common flagging colors. Flagging Color is important to know for revisiting the infestation. The final field on this page is Logging Access. The initial ground survey crew also determines logging access based on the possibility that the infestation will be logged and its location. This field has a drop-down menu with the choices Poor, Fair, Regular, and Good. The Poor choice is made when the infestation is not a candidate for logging. Fair access is chosen when a logging decision cannot be made during the initial survey. Regular is chosen when the site can be accessed at any time. Good is chosen when the infestation can be easily accessed and the logs easily hauled from the site.

Survey: Page 2 is the heading for the fourth page. This page contains fields for Timber Type, Fresh Attack Determination, Number of Infested Trees, Number of Red or Faded Trees, Number of Green Infested Trees, and Number of Vacated Trees. The timber type choices include Pulpwood, Saw Timber, and Mixed. A choice is made based on the composition of the infestation. The Fresh Attack field contains a simple yes or no. This helps in determining what actions should be taken for control of the infestation. The subsequent four fields are used to determine the composition and size of the infestation. The Number of Infested Trees will equal the Number of Red and Faded Trees plus the Number of Green Infested Trees. Each field has an increment counter that allows the user to add one tree at a time while walking through an infestation. The final page of the form is for Comments. Any significant information concerning an infestation can be recorded here.

19.5. INTEGRATION OF DATA INTO SPBIS

19.5.1. Data Upload

Seamless upload of data into the SPBIS database is the most important aspect of this approach. One of the major problems with the current data collection system is data entry.



Spot Information

● Add Spot ○ Add Head ○ Add Breakout

Region	08
Forest	
District	
Spot Number	0
HBO Number	1 1
Parent HBO	Master
Species	SPB

Spot Information

Compartment	0
Stand Number	0
Wilderness	
Wilderness Name	
BA Pine	0
BA Total	0
Spot Found By	
Priority	
Estimated Acres	0

Spot Information

● Add Survey ○ Modify Survey

Survey Type	Aerial
Initial Detection Date	☑ 1/19/2007
Date Ground Checked	☑ 1/19/2007
Suggested Treatment Plan	Cut + Leave
Flagging Color	Yellow
Logging Access	Log most anytir

Spot Information

Pulp or Saw	Pulp
Fresh Attack	No
No. Infested Trees	2
No. Infested Red/Faded Trees	1
No. Infested Green Trees	1
No. Vacated Trees	2

Spot Information

Comments

Figure 19.2—Digital SPB data collection forms. (KEL image)

Manually entering data into the database is time-consuming and impractical at the degree required during SPB epidemics.

In order to streamline the data collection process, an application for uploading data directly from a mobile device was developed. An interface was developed between the SPBIS Oracle® tables and the backup database file (DBF) table associated with the digital SPBIS data form. This application was created in Visual Basic 6.0 and is embedded in SPBIS Version 5.0. The complex structure of the SPBIS database did not lend itself to the development of a simple data upload interface. Fields within the database are interconnected with one another. Therefore, fields within the DBF table of the data form must be connected to a corresponding field within SPBIS in order to have successful routing of data. The upload application reads data from each record on the mobile device in DBF form and writes them to five individual structured query language (SQL) statements that insert the data into the Oracle® tables. After data has been uploaded the Oracle® tables are queried to determine what control number (CN) Oracle has assigned each record so the origin or "parent" of each record can be tracked. The CN for a specific record is required if any modifications are to be made. The CN allows the database to search for the parent record and add newly collected data or overwrite existing data. The mobile unit is linked to the SPBIS via a Universal Service Bus (USB) connection. Once the unit and the database are in sync, data is automatically extracted from the mobile unit and stored in the database. Figure 19.2 shows the initial graphical user interface (GUI) and subsequent screen prompts, as they will appear on a desktop computer.

19.5.2. Data Download

Data can also be downloaded from the SPBIS database onto a GPS data logger. This allows surveyors to revisit infestations with previously collected data, which they can then modify or add to as needed. This allows the surveyor to keep all data concerning an infestation organized and prevents obsolete data from reaching the database. The data is transferred in the same manner as it is uploaded.

19.6. CONCLUSION

The collection of quality data concerning SPB infestations begins with an efficient and accurate field survey. While traditional methods are still used, modern technology allows surveyors to collect high quality data in a fraction of the time previously required.

19.7. ACKNOWLEDGMENTS

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20

Southern Pine Beetle Information System (SPBIS)

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Keywords

computerized record keeping
current and historical records
customized reports
database
historical database
monitoring
SPB infestation
southern pine beetle
summary reports

Abstract

The southern pine beetle (SPB) is the most destructive forest insect in the South. The SPB attacks all species of southern pine, but loblolly and shortleaf are most susceptible. The Southern Pine Beetle Information System (SPBIS) is the computerized database used by the national forests in the Southern Region for tracking individual southern pine beetle infestations. Historical SPB records are stored by Forest Health Protection (FHP) and have been used to document the effectiveness of SPB suppression techniques. The system is instrumental in forest plan implementation. It is a valuable tool for monitoring of forest management activities.

20.1. HISTORY OF THE SOUTHERN PINE BEETLE INFORMATION SYSTEM

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), is the most destructive forest insect in the South. The Southern Pine Beetle Information System (SPBIS) is an Oracle® database that was developed for the USDA Forest Service, Southern Region, Forest Health Protection (FHP). SPBIS was originally developed as a group of FORTRAN computer programs in the late 1970s at the Fort Collins Computer Center. In 1983, SPBIS was revised and placed on Apple® II computers at the district level. In 1988, a SPBIS version was released for the Forest Service Data General computers. SPBIS 2.0 was released in January 1999 and was designed to run on the IBM® RISC 6000 computers at Forest Service Regional, Forest, and District offices. SPBIS 2.0 used the Oracle® database management system, and Oracle® forms. The current version of SPBIS is 5.2; it is the result of numerous revisions to enhance ease of use. SPBIS is currently being managed by the FHP Alexandria Field Office in Pineville, LA.

20.1.1. Background of SPBIS Program

Data for the infestation files result from weekly input from field crews at the district level. Thus, SPBIS continuously reflects the up-to-date status of SPB suppression activities and also contains a history of suppression treatments at each district. Summary reports are generated by the districts, consolidated by the forest, and a regional report is issued every 2 weeks throughout the year.

SPBIS is a valuable functional tool for district personnel—particularly in SPB outbreak situations. It enables the staff to monitor the status of all infestations present in the district. At times there can be hundreds of infestations that are in some stage of suppression or monitoring, and the SPBIS system will produce reports that district personnel can use to prioritize control efforts for SPB infestations. Records of the suppression of SPB infestations were taken from the SPBIS system during the development of the Final Environmental Impact Statement (FEIS) for the Suppression of the SPB to demonstrate the effectiveness of the four suppression techniques.

20.1.2. Project Highlights

SPBIS is a district-based system for the storage and retrieval of information about the location, size, and status of individual SPB infestations, scheduled activities, and accomplishments. In 2004 version 5.0 included a complete reprogramming of the status report, additional validation routines, and increased functionality. Records from the previous years are maintained by FHP and have been used to document historic beetle activity trends/patterns, as well as the effectiveness of SPB suppression. The data have been used to support forest plan revision and implementation. In 2007 version 5.2 was released and is the current version in use today. Highlights of version 5.2 include the ability to email status reports as Adobe® Acrobat PDF file format directly to a recipient. The addition of geographic coordinate converter allows the user to enter X, Y coordinates in decimal degrees, degrees minutes and seconds, or Universal Transverse Mercator (UTM) at the survey record level, and the coordinates are saved as decimal degrees. This newest version also has the capacity to upload and download survey information on southern pine beetle spots using a Personal Data Recorder (PDR).

20.1.3. Technology and Skills

SPBIS is written in Visual Basic Code, Oracle® tables, Adobe® PDF, and SQL queries. The program uses Oracle relational Database Access method. SPBIS resides on a PC at each District and Forest Supervisor's Office. SPBIS is a menu-driven program and provides data entry forms with error-checking. FHP provides installation, assistance, and training for SPBIS to district personnel. The SPB status report is posted on the Corporate Database Warehouse as well as the Region 8 Web site.

20.2. SOUTHERN PINE BEETLE SUPPRESSION AND SPBIS

When SPB populations are low, the beetles will attack stressed or dying trees or trees infested by other bark beetles. Under those conditions, the SPB is not economically important. During outbreaks, the SPB attacks, colonizes, and kills even the most vigorous and healthy trees. Infestations or spots can involve large numbers of trees over hundreds of acres. During these epidemic periods, large-scale suppression projects are required.

The Southern Region is guided by the Record of Decision, signed April 6, 1987, for the Final Environmental Impact Statement for the Suppression of the Southern Pine Beetle. This document provides the legal mandate for suppression funding and specifies the acceptable suppression methods.

The job of locating and suppressing individual SPB infestations (spots) requires three separate field operations—survey and detection, either aerial or ground; ground checking the SPB spots detected in the survey; and direct control of the infestations.

Because host damage by the SPB occurs in well-defined patches, called spots, it is necessary to locate and enumerate these SPB spots in order to estimate their potential impact. Active spots are principally identified through detection flights (Hain 1980). Flights are conducted periodically throughout the active season, with flight timing dependent on expected level of beetle activity, season, objectives, and operational capabilities (Billings 1979). A spot is defined as more than 5 or 10 trees in size. Observers plot suspected beetle spots—pine trees with discolored foliage—onto maps or photographs. To determine if a spot is actively infested with the SPB it must be located on the ground and examined by a trained field crew.

Field crews follow the maps or photographs to the spot location and ground check the spots to confirm the cause of tree mortality and to determine the need for treatment. High-priority spots—those with the greatest number of SPB-infested trees—have a greater potential for additional tree mortality. These spots are marked for treatment first. In addition, it is important to determine the direction(s) in which the spot is moving. A direction is an area, known as the spot head, where the newly infested trees are located. These trees have crowns that are still green, and pitch tubes, where attacking beetles bore into the tree, are soft and sticky—indications that the trees are just coming under SPB attack.

Southern pine beetle-caused losses can be reduced through application of one or more recommended control tactics. These include cut-pile-and-burn, cut-and-leave, cut-and-remove, cut-and-hand-spray, and semiochemical. More details about the specific application and their appropriate uses are on pages 2-3 to 2-15 of the Final Environmental Impact Statement (FEIS) for the Suppression of the SPB (see chapter 16). No matter which control method is implemented for a given SPB infestation, time is of the essence in minimizing SPB losses. Beetle infestations can expand very rapidly. Saving a few days' time in the suppression operation can significantly reduce the number of trees lost. In the summer, no more than 4 weeks should elapse between ground check/marking and treatment.

20.2.1. Prioritizing SPB Spots

SPBIS is particularly useful for determining which SPB spots should be treated. Not every SPB spot must be controlled. Spots with few newly attacked and green-infested trees and many vacated trees (SPBs have emerged and left the trees) are unlikely to grow and, consequently, should not be suppressed. These spots are considered to be inactive and are recorded as such in the SPBIS database. Some SPB spots will only have a few infested trees. In this case, the spots will be monitored for several weeks to determine if they will continue to expand or go inactive.

20.2.2. Breakout SPB Spots

An infestation is known as a breakout and is recorded as such in SPBIS if the following criteria are met:

- When newly infested trees occur adjacent to an SPB spot that has been treated by one of the suppression methods, the infestation is a breakout (number of infested trees does not influence its classification as a breakout).
- The breakout occurs within 30 days of suppression of the original SPB spot and/or breakout spot treatment during the summer months (May through September), and within 45 days of completion of original and/or breakout spot treatment during the rest of the year (October through April).

If uninfested host trees are located between the treated spot and the infestation, the infestation is considered a separate spot and is recorded as such in SPBIS. Also, if a new infestation occurs outside the specified time frames, the infestation is considered a new spot and is recorded as such in SPBIS.

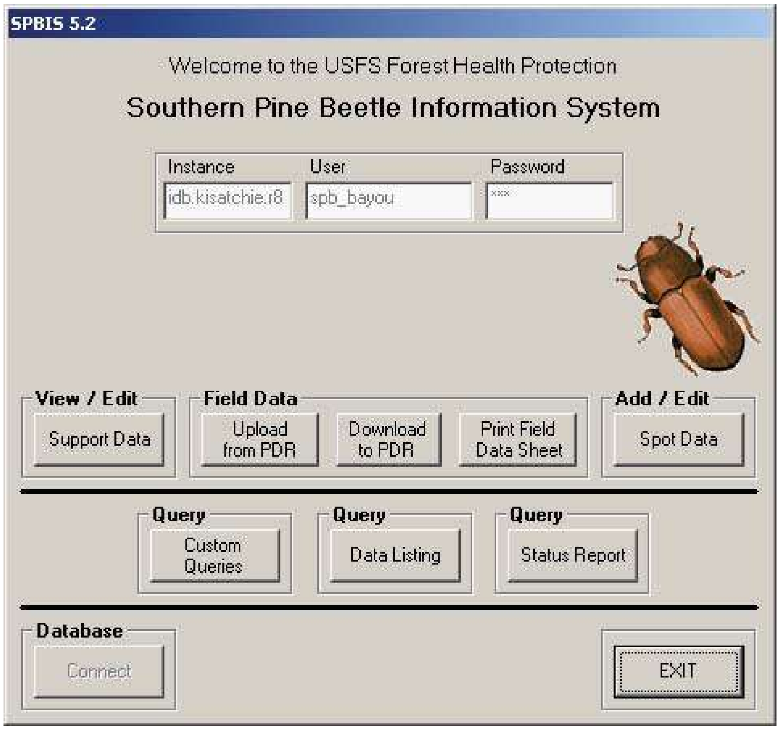
If two or more breakouts are found on different sides of the treatment area on the same visit, this is a multiple breakout. With a multiple breakout each spot will have the same survey date but different information pertaining to the particular spot.

A breakout can only occur after the original spot has been suppressed. The survey date on the breakout must come after the suppression date of the original spot or the suppression date of the previous spot.

Partial Treatment of a Spot

When a spot is only partially treated it is necessary to record the suppression data while continuing to track the remainder of the original spot. This can be accomplished by giving the partially treated area a new SPBIS number while referencing this spot to the original spot. The original spot number is included as the parent spot number on the data entry screen. This differs from the breakout code that is used when the entire original spot is suppressed.

Special management considerations are noted whenever conditions or special situations occur. Examples of special management considerations might be when an SPB infestation occurs in the association with a threatened or endangered species such as red-cockaded woodpecker, Louisiana pearl shell mussel, archeological sites, botanical areas, research natural areas, or recreation sites. The SPB FEIS and forest plan provide direction about appropriate SPB suppression tactics available for consideration. There is a section of the SPBIS form for inserting such site-specific information about the individual situation.


SPBIS 5.2

Welcome to the USFS Forest Health Protection

Southern Pine Beetle Information System

Instance idb.kisatchie.r8

User spb_bayou

Password ***

Figure 20.1—SPBIS Input Interface Screen.

20.3. USING SPBIS AS A TOOL FOR MONITORING AND SUPPRESSING SOUTHERN PINE BEETLE

The SPBIS database is a combination of Oracle® forms and SQL*Plus™ reports that use the Oracle Relational Data Base Access Method. The system is menu-driven, and forms provide easy data entry. The data entry/edit program automatically checks for errors as data are entered, and immediately notifies the user when data are invalid. Reports can be generated by menu or by using customized SQL*Plus queries.

Currently, the SPBIS database is physically located at the SPBIS Command Center (the FHP Unit, Alexandria Field Office, in the Kisatchie National Forest.) This single region-wide database holds all historical and current data for all districts in the Southern Region.

20.3.1. Definitions of SPBIS Screens

SPBIS 5.2, the newest version of SPBIS, has five main screens. The SPBIS Input Interface Screen (Figure 20.1) opens the program and enables the user to navigate to all sections of the program. The user must enter unique information specific to the forest and district in order to access the SPBIS program.

Once connected, the user can navigate to several screens. The user can view support data, upload and download SPB field survey information from the Personal Data Recorder (PDR), print blank data sheets used in the field for SPB collection when the PDR is not available, add new SPB data, and/or change existing data in the program. The SQL*Plus™ allow the user to create customized queries to extract specific data from the database and create a custom spreadsheet based on species, dates, and districts. A status report can be created with dates as the default, and the user can create status reports for all forests or particular forests within Region 8.

SPBIS Main Spots Table

The SPBIS Main Spots menu allows the user to add new data, modify and view existing data, and delete data already entered into the program. Once the user enters the forest and


SPBIS Main Spots Table; Instance = idb.kisatchie.r8

● View
○ New Spot
○ Modify
○ Delete

Record 1 of 3250

Manual Input

Region: 8

Forest: 03 Chattahoochie / Oconee

District: 08 Oconee

Species: SPB

Spot Number: 14

Suppressed On: 12/25/2003

☐ View HBO Records

Comments:

Figure 20.2—SPBIS Main Spots Table Screen.


SPBIS Heads Breakouts Table

● View
○ New Head
○ New Breakout
○ Modify
○ Delete
○ Surveys
○ Treatments

Record 1 of 1

Head Name: 1

Parent Breakout:

Compartment: 152

Stand: 17

State: GA

County: 237

Priority:

Active HBO Detected on: 4/26/2000

Total Affected Acres: 1

BA Pine: 100

BA Total: 100

Pine Species:

Found By: ma

Wilderness: ☐

☐ Tally Surveys and Treaments

Comments:

Figure 20.3—SPBIS Heads Breakouts Table.

district information into the Main Spots Table (Figure 20.2), the user is allowed to add, modify, and delete SPB information only for that specific forest and district. The user can view any forest and district information that has been entered into the program but cannot alter the information in any database other than the one assigned to him/her. Features displayed on the screen include total number of SPB spots entered into the SPBIS program, including historical and current data. There is a toggle bar that enables the user to quickly find a unique SPB spot, or the user can type in the unique SPB spot under the Spot Number field and the program will pull information pertaining to the SPB spot into the database. There is historical SPB data on some districts, some as far back as 1980. The Main Spots screen allows the user to enter data for SPB, *Ips* engraver beetles, and black turpentine beetle (BTB), *Dendroctonus terebrans* (Olivier). There is also information located on the screen that identifies the status of each SPB spot; for example, if an SPB spot has been suppressed, the suppression date appears in red.

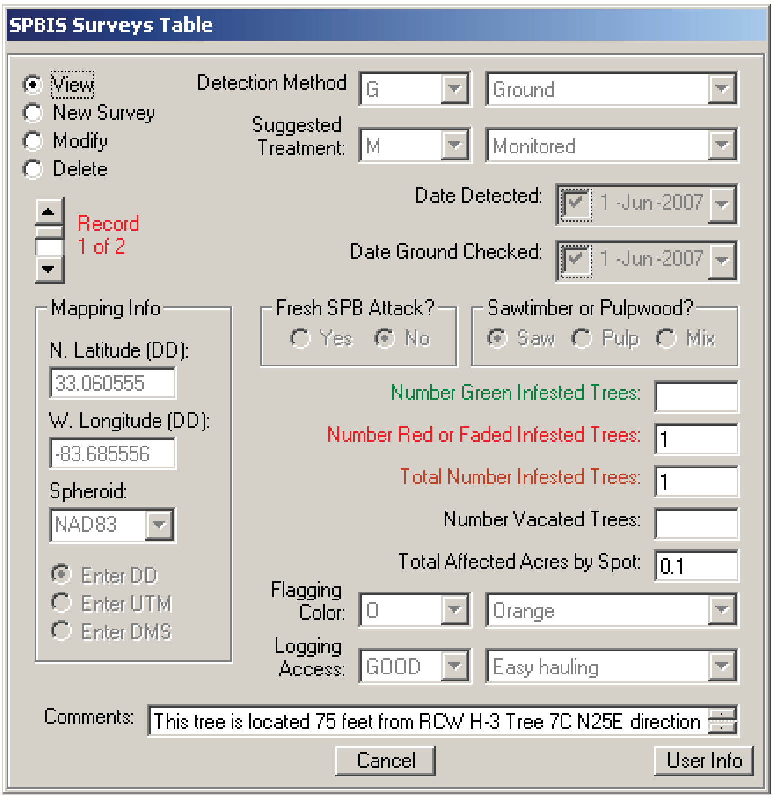
SPBIS Heads Breakouts Table

In order to see what information has been entered into the program the user must check the View Heads Breakout Records box located on the Main Spots Table. When the View HBO Records box has been checked, the SPBIS Heads Breakouts Table will appear (Figure 20.3). The SPBIS Heads Breakout table includes information for actual heads and breakouts on an SPB spot, as well as the compartment and stand location. Once the compartment and stand have been identified, the State and county will appear as grayed information. If the compartment and stand are not correct the State and county will remain blank. It is very important for the district to enter the correct compartment and stand number in order to properly identify the correct county location for the SPB spot. This menu also lists important information about the size of the SPB spot based on total affected acres, Basal Area Pine, and Basal Area Total, as well as Pine Species. The user can then select the Survey or Treatments screen to view. One unique feature SPBIS 5.2 has is the ability to view the Survey and Treatment screens while also viewing the Main Spots table and heads and breakouts table on the computer screen. In the past the user could only view one screen at a time.

SPBIS Surveys Table

An SPB spot can be detected by air, ground, or video. Once the SPB spot has been detected, district personnel will ground check the SPB spot and collect survey information from the spot. Using a PDR or SPBIS field sheet, the employee records the detection method used to find the SPB spot and the method of treatment suggested for the particular spot. The suggested treatments include cut, pile and burn; experimental; inactive or dead; cut-and-leave; monitored; cut-and-remove; cut-and-hand spray; or semiochemical. The dates of detection and ground check are entered into the SPBIS Surveys Table (Figure 20.4), as well as information identifying the SPB spot.

Entering the latitude and longitude is vital for future visits to the SPB spot. Latitude and longitude can be entered in Decimal Degrees,


SPBIS Surveys Table

● View ○ New Survey ○ Modify ○ Delete

Detection Method: G Ground

Suggested Treatment: M Monitored

Date Detected: ☑ 1 -Jun-2007

Date Ground Checked: ☑ 1 -Jun-2007

Record 1 of 2

Mapping Info

N. Latitude (DD): 33.060555

W. Longitude (DD): -83.685556

Spheroid: NAD83

● Enter DD ○ Enter UTM ○ Enter DMS

Fresh SPB Attack? ○ Yes ● No

Sawtimber or Pulpwood? ● Saw ○ Pulp ○ Mix

Number Green Infested Trees:

Number Red or Faded Infested Trees: 1

Total Number Infested Trees: 1

Number Vacated Trees:

Total Affected Acres by Spot: 0.1

Flagging Color: O Orange

Logging Access: GOOD Easy hauling

Comments: This tree is located 75 feet from RCW H-3 Tree 7C N25E direction

Figure 20.4—SPBIS Surveys Table.

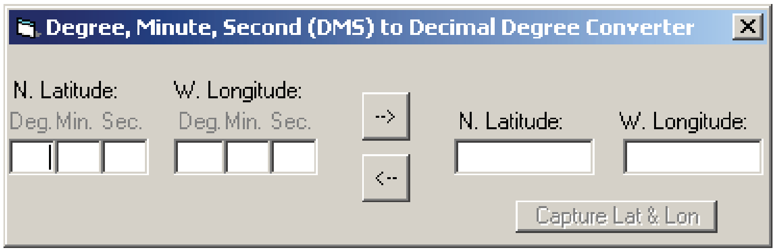

Degree, Minute, Second (DMS) to Decimal Degree Converter

Figure 20.5—SPBIS Conversion Screen for converting Degree, Minute, Second (DMS) to Decimal Degree (DD).

Degrees Minutes and Seconds, or Universal Transverse Mercator (UTM). If the latitude and longitude are entered in Degrees Minutes and Seconds or UTM, there is a program built into the system that will convert the figures to Decimal Degrees accessed at the Conversion Screen (Figure 20.5). Information such as green-infested trees, number of red- or faded-infested trees, total number of infested trees, and total number of vacant trees is also entered into the program, as well as flagging color used to identify the SPB spot from the road. Logging access is another category used to identify the condition of the SPB spot.

An SPB spot can be surveyed multiple times and each time can be documented. When more than one survey has been entered into the program, a toggle bar will appear in the left-hand column denoting there is more than one survey.

SPBIS Treatments Table

Once the spot has been suppressed, data can be entered into the SPBIS program using the SPBIS Treatments Table (Figure 20.6). This table records the actual treatment used to suppress the SPB spot, and the day/month/year the spot was marked, sold, treated, and suppressed. The program also records the salvage volumes of both sawtimber and pulpwood, as well as number of trees treated and total affected acres.

If an SPB spot has been sold and a breakout occurs before the spot can be suppressed, supplemental volume can be entered into the program. Information used by a district can be added into the program, such as Sale ID, Cutting Unit ID, and Permit Number.

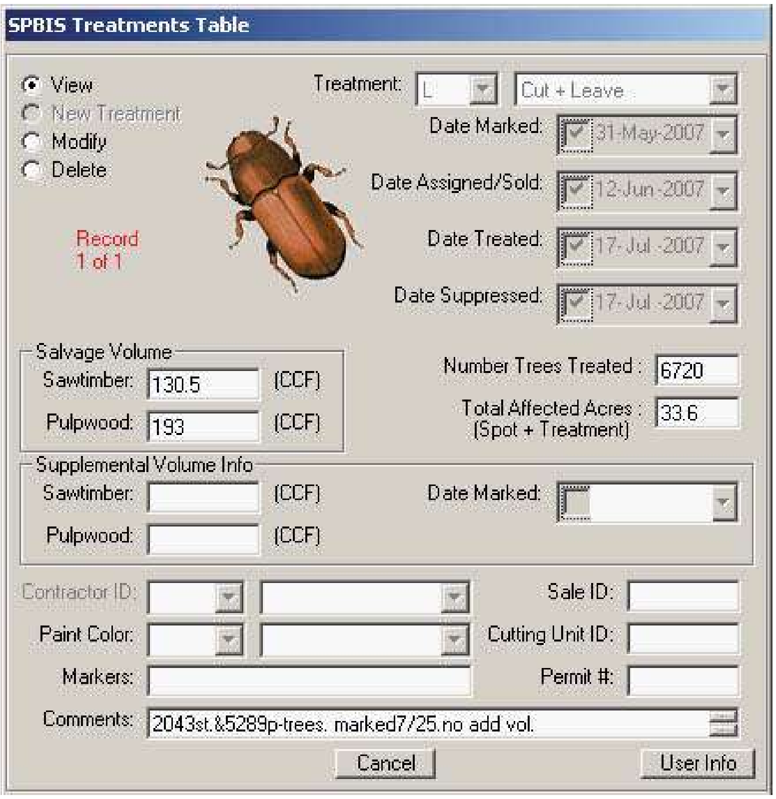
Perhaps the most important SPBIS-produced report is the Southern Pine Beetle Southern Region Status Report. It is used to monitor SPB, *Ips*, BTB or a total of all three beetle species on each district. This report can be customized by identifying a particular forest and showing activity on each district within the particular forest, or a general report can be obtained reporting activity on all forests in Region 8. This report is sent to the Forest Service Washington Office as well as the Regional Office in Atlanta, GA. The report is generated using a date range, and information can be obtained from the general forest or the wilderness area in the particular general forest. Printer options include printing to the default printer or selecting a particular printer, printing to PDF file, or emailing the status report. There are 33 lines on the status report with information ranging from cumulative spot total to estimated total acres affected. Information such as total number of inactive spots, total number of spots suppressed, and total number of spots requiring control can be obtained. There is also a section on the status report which captures number of trees treated by cut-and-leave, volumes removed by cut-and-leave and cut-and-remove, acres accomplished with cut-and-leave and cut-and-remove, and total acres inactive.

20.3.2. Miscellaneous Forms

Another feature of SPBIS is the Special Management Consideration screen. This screen allows the district to keep track of special management issues, such as threatened and endangered species, and heritage resources. There is also a section detailing customized queries. The program has seven different query types to select from, and once a certain query type is selected there are specialized queries within the query type to better customize a report.

20.4. FUTURE OF THE SOUTHERN PINE BEETLE INFORMATION SYSTEM

The next version of SPBIS will have embedded capability in the report functions to generate Google Earth™ KML files (Figures 20.7-20.10). These report companion KML files will geographically represent the locations and summary data of database queries such as the biweekly Status Reports "02. Total Number of New Spots Detected", any of the individual Spot Queries aka Braintrust Queries, and the ubiquitous data listing function.


SPBIS Treatments Table

● View
○ New Treatment
○ Modify
○ Delete

Record 1 of 1

Treatment: L | Cut + Leave
Date Marked: ☑ 31-May-2007
Date Assigned/Sold: ☑ 12-Jun-2007
Date Treated: ☑ 17-Jul-2007
Date Suppressed: ☑ 17-Jul-2007

Salvage Volume
Sawtimber: 130.5 (CCF)
Pulpwood: 193 (CCF)

Number Trees Treated: 6720
Total Affected Acres: (Spot + Treatment) 33.6

Supplemental Volume Info
Sawtimber: (CCF)
Pulpwood: (CCF)
Date Marked: ☐

Contractor ID:
Sale ID:
Paint Color:
Cutting Unit ID:
Markers:
Permit #:
Comments: 2043st.&5289p-trees. marked7/25.no add vol.

Figure 20.6—SPBIS Treatments Table.

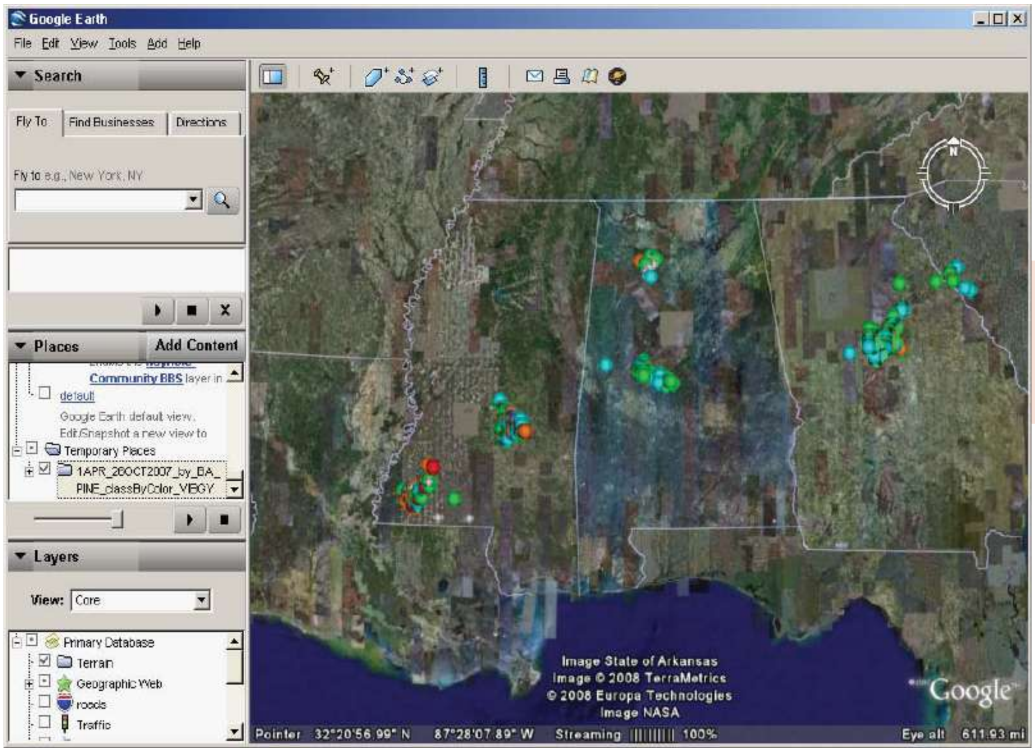
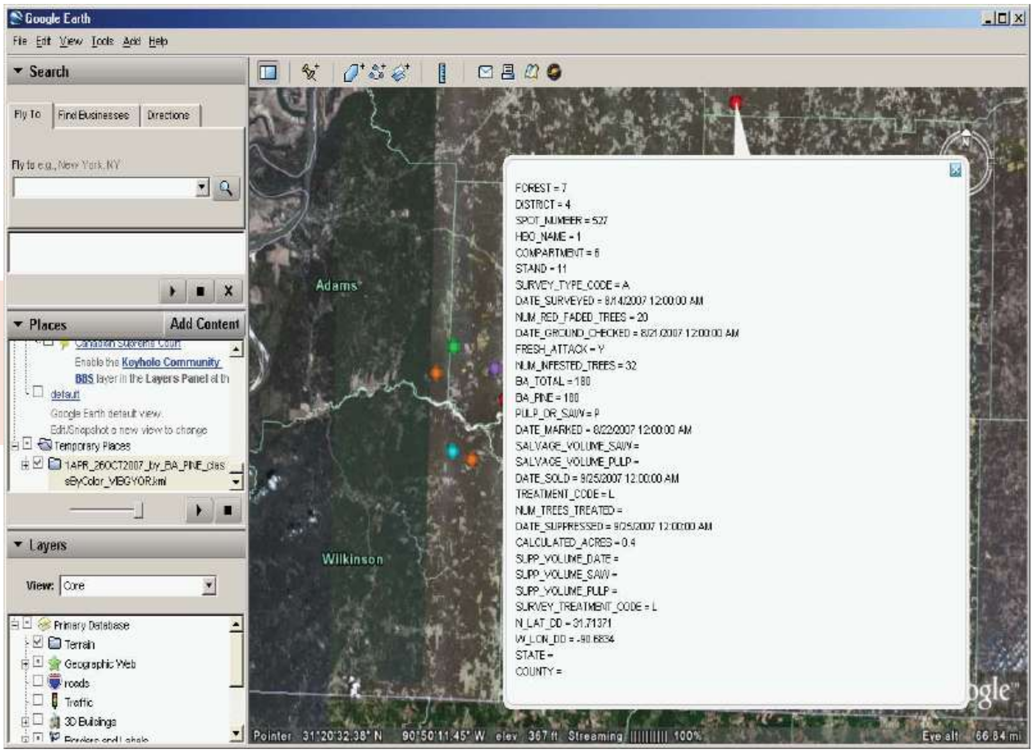


Figure 20.7—A future SPBIS option: embedded SPB spots generated by Google Earth^{TM} KML files.



FOREST = 7
DISTRICT = 4
SPOT_NUMBER = 527
HBO_NAME = 1
COMPARTMENT = 6
STAND = 11
SURVEY_TYPE_CODE = A
DATE_SURVEYED = 8/14/2007 12:00:00 AM
NUM_RED_FADED_TREES = 20
DATE_GROUND_CHECKED = 8/21/2007 12:00:00 AM
FRESH_ATTACK = Y
NUM_INFESTED_TREES = 32
BA_TOTAL = 180
BA_PINE = 180
PULP_OR_SAW = P
DATE_MARKED = 8/22/2007 12:00:00 AM
SALVAGE_VOLUME_SAW =
SALVAGE_VOLUME_PULP =
DATE_SOLD = 9/25/2007 12:00:00 AM
TREATMENT_CODE = L
NUM_TREES_TREATED =
DATE_SUPPRESSED = 9/25/2007 12:00:00 AM
CALCULATED_ACRES = 0.4
SUPP_VOLUME_DATE =
SUPP_VOLUME_SAW =
SUPP_VOLUME_PULP =
SURVEY_TREATMENT_CODE = L
N_LAT_DD = 31.71371
W_LON_DD = -90.6834
STATE =
COUNTY =

Figure 20.8—A future SPBIS option: display of SPB spot query data as a pull-down on a Google Earth™ KLM file.

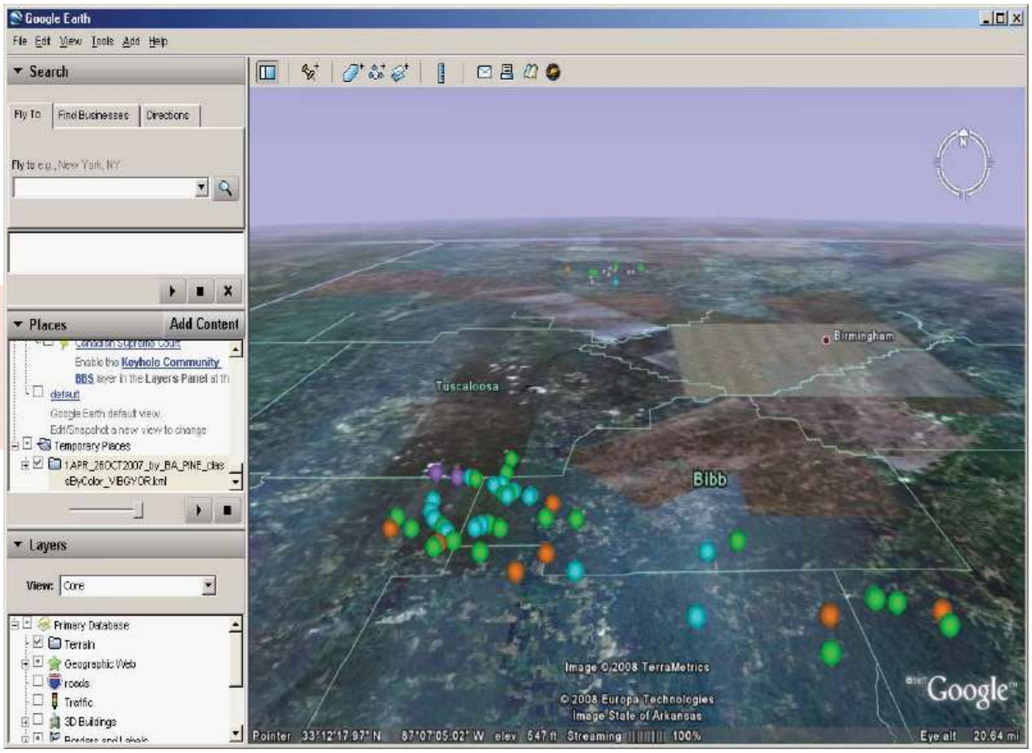


Figure 20.9—A future SPBIS option: SPB spots displayed as a "color ramp" view on a Google Earth™ KLM file.

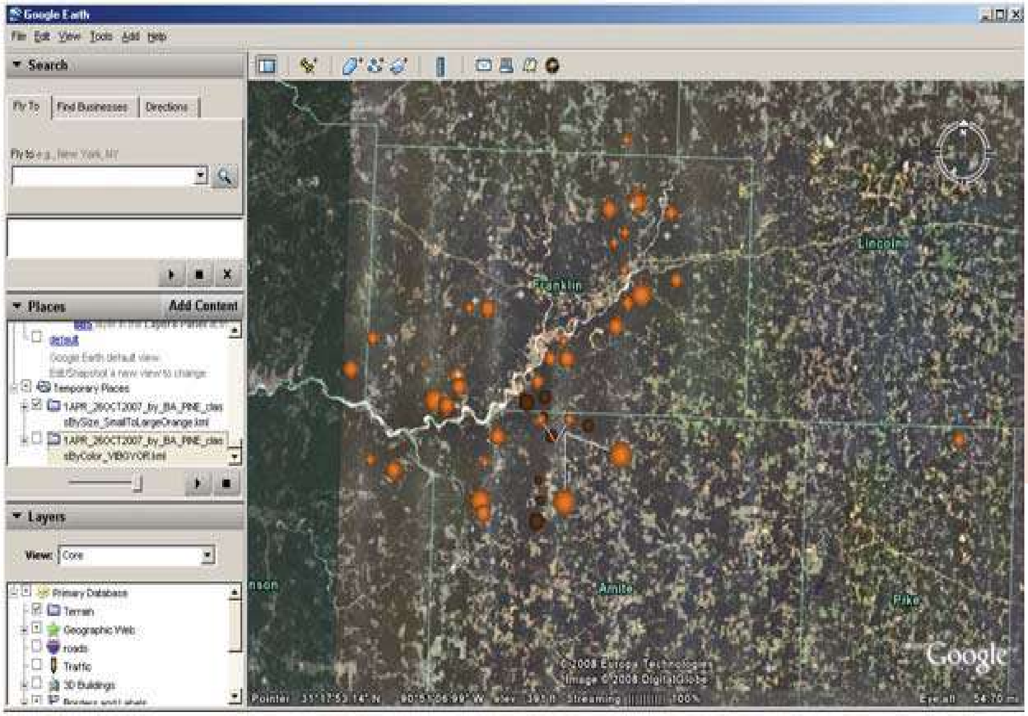


Figure 20.10—A future SPBIS option: SPB spots displayed as gradationally sized point icons on a Google Earth™ KLM file.

20.5. ACKNOWLEDGMENTS

I wish to acknowledge and thank Dr. Alex Mangini, Entomologist, Forest Health Protection, Pineville, LA, for his assistance in the final preparation of this manuscript. I would also like to thank Dr. James Meeker, Entomologist, Forest Health Protection, Pineville, LA; and Richard Spriggs Biological Science Technician, Forest Health Protection, Asheville, NC, for their review of this article and Tony Courter, System Analyst/Programmer, Forest Health Technology Enterprise Team, for the information and illustrations he provided for the section on the future of SPBIS and also his review of this article.

21

Operational Use of Southern Pine Beetle Survey Information

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Abstract

Survey and monitoring activities are generally undertaken to identify where and to what extent insects and diseases are impacting the resources and conditions of the forest environment. Often the usefulness of a survey is directly related to how quickly the data can be collected, organized, interpreted, and viewed. The USDA Forest Service, Forest Health Protection (FHP), conducts surveys and monitors southern pine beetle (SPB) populations on public lands throughout the range of the insect in the Southern United States. This task is complex and involves aerial detection, data collection on the ground, database management, and application of the survey information. In this chapter we describe the technology used to facilitate operational use of SPB survey information. A Web-based computer system, the SPB Map/Text Reporter (SPB-M/TR), is used for this purpose. The SPB-M/TR is a Web-based geographic information system (Web-based GIS) designed to facilitate operational use of SPB survey information for suppression, prevention, evaluation, and reporting purposes. The SPB-M/TR organizes, summarizes, and interprets the SPB survey information collected from the public forest land in Region 8. The SPB-MT/R extracts SPB survey data from the SPBIS (the Southern Pine Beetle Information System) database and uses it in combination with spatial data from the Ranger Districts to build interpreted reports and maps. Access to the SPB-M/TR is through the Internet.

Keywords

decision support
spatial data
SPB survey
SPB monitoring
Web-based GIS

21.1. INTRODUCTION

Survey and monitoring activities for the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), are generally undertaken to identify where and to what extent the insect is impacting resources and conditions of the forest environment. Often the usefulness of a survey is directly related to how quickly the data can be collected, organized, interpreted, and viewed. The survey and monitoring system developed by the USDA Forest Service, Forest Health Protection (FHP), for the SPB is one of the most sophisticated approaches used for any forest insect or disease (Figure 21.1); i.e., it is a model system that can be tailored for use on other pest species. Three technical components of this survey and monitoring system are particularly noteworthy and have been described elsewhere in this book: digital aerial sketchmapping (chapter 18), automated field data collection (chapter 19), and the SPBIS database management system (chapter 20). In this chapter we examine the final component of the sequence of digital technologies developed to automate SPB survey and monitoring (Figure 21.1). Our specific objectives are: 1. to describe the Web-based computer system developed to organize and summarize SPB survey information, the SPB Map/Text Reporter (SPB-M/TR), and 2. to describe the technical approach used in developing the system. The SPB-M/TR facilitates real-time use of SPB survey information for operational forest pest management purposes and automates summary of survey results for reporting purposes.

21.2. AUTOMATED ORGANIZATION, SUMMARY, AND DISPLAY OF SOUTHERN PINE BEETLE SURVEY AND MONITORING INFORMATION: THE SPB-M/TR

In this section we provide a general overview of SPB survey and monitoring. This introduction is intended to illustrate the complexity of the enterprise as it relates to effective and efficient collection and use of field data. With this background we next consider how the SPB-M/TR facilitates use of survey information for planning, problem-solving, and decision support in an SPB integrated pest management (IPM) context.

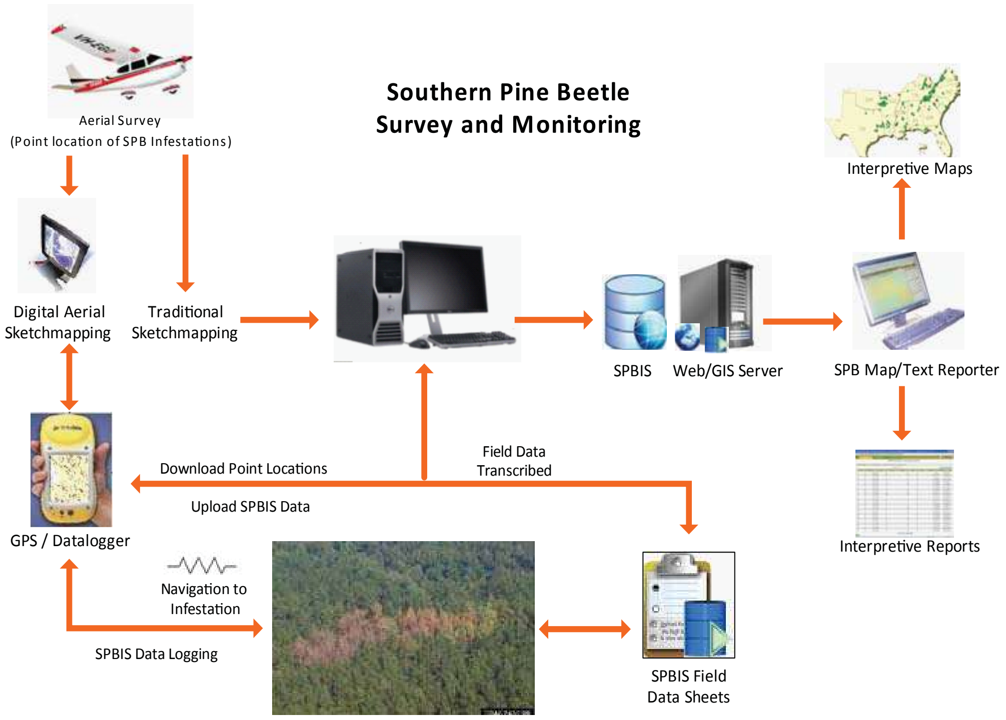


Figure 21.1—Schematic diagram of the activities associated with survey and monitoring the SPB. The Southern Pine Beetle Map/Text Reporter facilitates real-time use of SPB survey information for operational forest pest management purposes and automates summary of survey results for reporting purposes. (KEL image)

21.2.1. General Overview of Southern Pine Beetle Survey and Monitoring

The sequence of activities associated with survey and monitoring of the SPB involves an aerial detection flight, ground reconnaissance and data collection, SPBIS database management system with specified survey data, forest managerial response to an interpretation of the information from the survey, and development of a summary report. This general sequence of activities is also used for survey and monitoring the SPB on private forest lands as well (chapter 17).

Typically, an initial aerial detection survey is conducted during the spring season on Ranger Districts and other public forest lands within Region 8 by the USDA Forest Service. The procedures and technologies outlined in chapters 18, 19, and 20 are used. In most years, the number of infestations observed on the detection flight is small, and district and FHP personnel conduct the ground surveys, collect the required data, and enter it into SPBIS. Actions regarding management of the individual infestations are usually straight-forward, and sufficient staff is available to carry out the specific chores associated with the survey and response. Also, summary reporting can be accomplished on a timely basis.

However, periodically SPB outbreaks occur that include broad expanses of public forest land, often distributed across multiple States within Region 8. When the outbreaks of this magnitude occur, the forest management response becomes an enormous and complicated task that requires efficient planning, organization, and execution. Under this circumstance, each of the digital technologies developed for SPB survey and monitoring are taxed and the decisionmaking component becomes of paramount significance. The SPB-M/TR specifically addresses the issues of information management, which includes logistical decisionmaking, performance monitoring, and reporting.

21.2.2. Functionality of the Southern Pine Beetle Map/Text Reporter

The SPB-M/TR is a flavor of a computer application referred to as a management information system (MIS). Specifically, an MIS is a computer-based application that translates data into information useful in supporting decisionmaking, performance monitoring, and report generation. An important feature of the MIS is that it is designed to address structured problems; i.e., the solution to the problem can be specified in advance (Coulson and Saunders 1987, Coulson and others 1999c). The specific details of the SPB-M/TR architecture are described below. Essentially, this system is a composite of computer hardware resources, specialized software (e.g., ArcIMS® [Internet Map Server] using ActiveX™, ASP, and JavaScript® for customization), and a database management system (SPBIS).

The distinction between data and information is important. Data are measurements that define an ecological phenomenon, process, or relationship of interest. In the context of survey and monitoring, one important data type consists of the measurements that define SPB infestations,—tree species, tree age, tree density, number of infested trees, and so on. Information is data that have been given meaning by way of relational connection. Forest managers use data about SPB infestations and interpret it in order to make decisions about an appropriate action to be taken. For example, a 100-tree infestation detected in May and occurring in a 50-year-old loblolly pine plantation (*Pinus taeda* L.) would be considered significant information by a forest manager. The interpretation of the four types of data by the manager results in information that would likely result in a decision to apply a suppression tactic and thereby prevent further damage to the forest resource.

The functionality of the SPB-M/TR was defined through a series of knowledge elicitation workshops. We interviewed Forest Service personnel who were directly involved in responding to the large outbreak of the SPB that occurred in Texas and Louisiana during the mid-1980s. When large outbreaks occur, the logistical response is directed in large part to four types of activities: 1. reacting to the aerial survey results, 2. decisionmaking relative to application of suppression tactics for the SPB, 3. task monitoring and scheduling, and 4. accomplishment reporting. The knowledge elicitation workshops defined how the Forest Service personnel addressed each of these activities. This information was used to define the functionality of the SPB-M/TR. Following are examples of the type of information provided by the Forest Service relative to the four activities identified above.

Logistical Response to Aerial Surveys

The first task associated with survey and monitoring the SPB is the aerial detection survey. The digital sketchmapping procedures used for collecting data (coordinates) on the spatial location of infestations were described in chapter 18. These data are entered into SPBIS and subsequently accessed by the SPB-M/TR. During outbreaks, the number of infestations detected is usually too large for all of them to be immediately ground checked by Forest Service personnel. Consequently, specific infestations are selected for priority ground checking, based on judgments relating to the severity of their impact and/or clustering. Examples of the criteria that Forest Service personnel use in setting the priority, extracted in the knowledge elicitation interviews, include: the size of the infestation (large infestations often expand rapidly and cause significant tree mortality), proximity to sensitive areas (e.g., Red-cockaded Woodpecker [*Picoides borealis*] colonies, campgrounds, scenic areas, and so on), proximity to private property, and spatially clustered infestations. These data are displayed as interactive maps using ArcIMS (Internet Map Server). This visual display component of SPB-M/TR is important, as it allows the forest manager to see features and land-use activities spatially associated with the infestations. Eventually, all infestations are ground checked.

Decision Support for Suppression of SPB Infestations

The second task associated with survey and monitoring the SPB is the actual data collection from the infestations identified on the detection flight. The procedure used is described in chapter 19. The data collected for each infestation has been specified by FHP. The survey specialist enters the data into a digital data logger. Subsequently the data are downloaded directly to SPBIS (chapter 19). The SPB-M/TR extracts specified data from SPBIS, and it is used by the forest manager for decisionmaking purposes. Again, access to spatial data and to the mapping component of the SPB-M/TR is a extremely valuable tool in the decisionmaking processes. The knowledge elicitation interviews defined the specific kinds of data the forest manager needed. Examples included instructions such as: show the locations of the largest infestations, show the location of the infestations with the largest infested trees, show the location of the infestations next to sensitive areas, and show the infestations that are most accessible by forest roads. These types of data are used by the forest manager in decisions regarding which infestations to treat with suppression tactics, which to ignore, which to monitor in the future, and so on.

Task Monitoring and Scheduling

During outbreaks of the SPB, the response by the Forest Service is continuous from the early spring, when infestations are initially detected, throughout the fall, when growth declines. Keeping track of the various activities associated with the surveys and actions taken and not taken is a significant challenge. The SPB-M/TR addresses this issue as well. Examples of the types of questions identified in the knowledge elicitation interviews include the following: show the infestations that have been treated, show the infestations that have not been treated, show infestations identified for salvage, and show infestations near sensitive areas. This type of information management provides a continuous and real-time record of the Forest Service response to the outbreak.

Accomplishment Reporting

The response to outbreaks of the SPB consumes tremendous resources and accountability, and accomplishments are typically closely monitored by the Forest Service. In addition, the outbreaks affect private forest lands, and responding to concerns by landowners and citizen groups relative to actions and activities of the Forest Service is also a significant challenge. The SPB-M/TR addresses this issue as well. Initially, the reporting capability was directed specifically to biweekly reports for Forest Service administrative personnel. The report contained both text material (e.g., number of infestations detected, number treated, number not treated, volume salvaged, and revenue for timber sales) as well as map information illustrating the location of the infestations. The SPB-M/TR also provided for annual map and text summaries of actions associated with the response of the SPB outbreak.

21.3. TECHNICAL APPROACH USED IN DEVELOPING THE SPB-M/TR

The SPB-M/TR was developed as a Web-based geographic information system (Web-based GIS) application designed to facilitate access to spatial and tabular data as well as advanced mapping of SPB survey information over the Internet. The overall approach of the SPB-M/TR is divided into three tiers (Figure 21.2):

- A Data tier containing the SPBIS database
- A Web/GIS server tier that provides the GIS components (ArcIMS) and the communication mechanism that performs the process of transferring data across the network
- A Client tier that consists of the application that allows end-users to request, visualize, and process the data

21.3.1. SPBIS Database (Data Tier)

The survey data resides in the SPBIS database management system described in chapter 20. The SPB-M/TR queries the SPBIS database and extracts the data as a comma delimited file (.cvs) and converts it into a GIS shapefile (digital storage format for geographic locations and data attributes). The GIS shapefile, which contains the SPB survey data, is stored in the Web/GIS server.

Web/GIS Server Tier

The SPB-M/TR includes two main Web interfaces that enable online access to the GIS layers and SPB data attribute information. The application uses ArcIMS 9.3 (Environmental Systems Research Institute, ESRI®) as the main component to serve the spatial data and Active Server Pages (ASP) as an interface to access the attribute data and to check user authorization (authentication). ASP and Java scripts are included within HTML documents to confer the capacity of generating Web contents on demand.

Authentication

User access to the SPB-M/TR requires authorization to be able to login the system. A valid ID and password are required to access the SPB-M/TR. If the user is valid, the application Web server creates a session to navigate the SPB-M/TR (Figure 21.3).

Client Side (Application Description)

The SPB-M/TR is organized into three main search modules (query modules): SPB Survey Module, SPB Monitoring Module, and Advance Search Module. Each one of these modules allows the user to retrieve attribute data from the SPB SPOT layer that contains the SPBIS data displayed as a map (Figure 21.4).

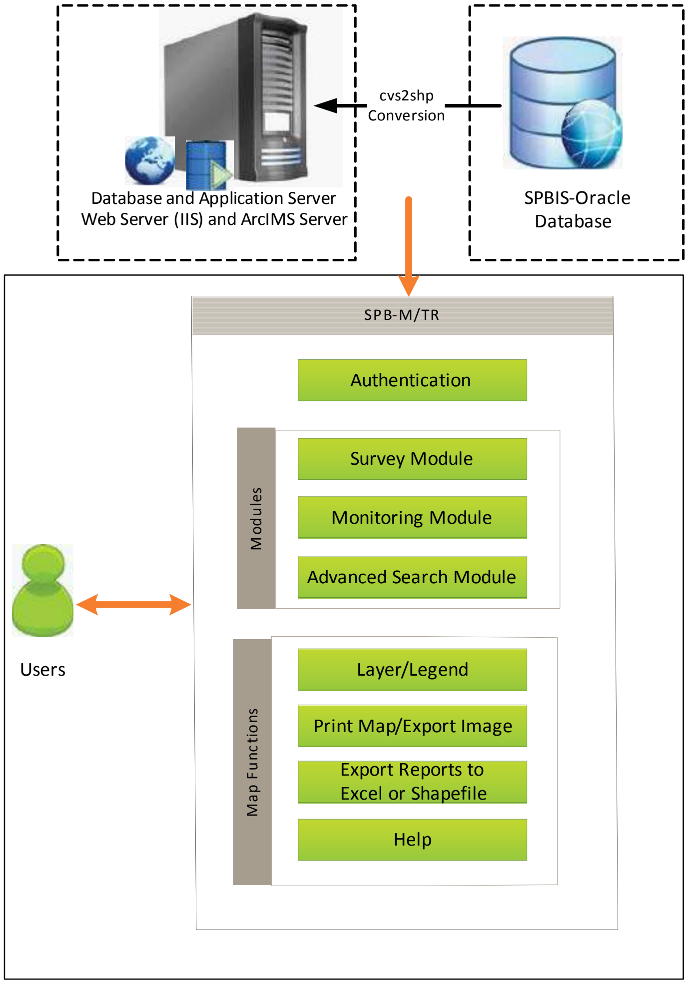


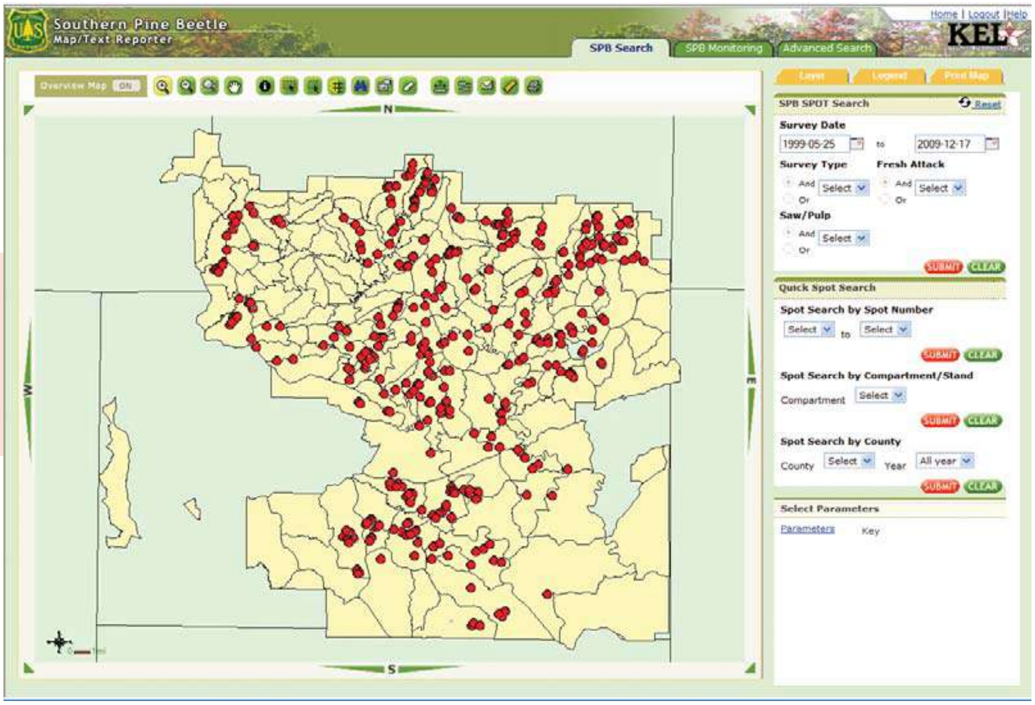
Figure 21.2—The three-tier architecture used to develop the SPB-M/TR. The overall approach is divided into: SBPIS database, Web/GIS server, and Client tiers. (KEL image)

The SPB Survey Module queries data pertaining to the logistic response to the survey, such as show the infestations by: Survey Date, Survey Type, Fresh Attack, Spot Number, Compartment/Stand, County, and Year. The SPB Monitoring Module uses the treatment and suppression data from SPBIS. Users can query the infestations by: Suppression Date, Treatment Type, Number of Trees Treated, Sold Date, and Calculated Acres, among others. The Advance Search Module allows building a customized query using SQL (Stuctured Query Language). The user can extract any type of SPBIS data in combination with attribute data from other GIS layers in the system such as roads, streams, compartments/stands, and sensitive areas. Examples of the types of queries users can create include: show the location of the infestation next to sensitive areas, show the location of infestations that are

User Name: kel

*Fogot your password?Click for Password Assistance.

Figure 21.3—Authentication screen to access the SPB-M/TR. (KEL image)



Survey Date 1999-05-25 to 2009-12-17

Figure 21.4—SPBIS data displayed as a map within the SPB-M/TR. The data can be queried using the search modules in the system. (KEL image)

most accessible by forest roads, and show the locations of infestations that are within 100 m from a stream.

Map Functions (Toolbar Functions)

The Web interface provides the users with helpful toolbars to interact with the mapping system. Layer and Legend tabs let the user modify the visualization of the maps using different spatial data layers such as roads, streams, compartments, and stands. Interactive map functions such as Zoom, Pan, and Full Extent allow the user to view the displayed maps in greater detail or to choose different areas for display. Feature functions such as Identify, Select, Find, and Saved Query provide the user an interactive way to query the data. Advanced functions such as Measure and Add Marker allow customization of the maps; the Print and Export functions are important for creating the reports in different formats, such as tabular text, Excel files, PDF maps, and shapefiles.

21.4. CONCLUSIONS

The survey procedure developed by the USDA Forest Service, Forest Health Protection, for the SPB is a contemporary approach that integrates fundamental technologies associated with automated aerial detection, ground data collection, database management, and information management. The first three of the component technologies, developed specifically for SPB survey and monitoring, were described in chapters 18, 19, and 20. In this chapter, we focused on the methodology that facilitates use of the survey information for planning, problem-solving, and decisionmaking; i.e., SPB-M/TR. The SPB-M/TR system greatly expedites survey and monitoring activities directed to the SPB. It also facilitates the operational use of the digital sketchmapping technology, the automated data collection system, and SPBIS database management system. Most important, the SPB-M/TR system provides real-time access via the Internet to SPB survey information in a map/text format tailored specifically for IPM purposes.

The SPB-M/TR was developed specifically for SPB survey and monitoring. However, the application addresses a fundamental problem associated with all survey and monitoring programs for forest insects and diseases, namely, the timely use of the information for management purposes. The approach used in developing the SPB-M/TR deals directly with two common issues associated with survey and monitoring programs in general; i.e., 1. Structuring survey data so that it can be used by forest managers for planning, problem-solving, and decisionmaking purposes, and 2. Having real-time access to the summarized survey data. The technical approach used for the SPB-M/TR can be applied to other forest and insect disease management problems. The approach can be tailored for use in survey and monitoring programs for other forest insect and disease pests. The output from the SPB-M/TR can be used with related forested management problems; e.g., the relation of bark beetles and fire management.

Section III

III. Silviculture and Management

Section III addresses silviculture and management of the southern pine beetle. The section includes three chapters: the first deals with risk and hazard assessment, the second with silviculture, and the third with forest restoration. Each of these chapters involves management of the forest environment. *Management*, in the context of southern pine beetle, means simply to take charge of or care of the forest environment. Managing the forest environment is a “place-based” activity involving discrete human activities enacted on a spatially explicit land area. The first chapter in this unit addresses evaluation of forests for their vulnerability to impacts by the southern pine beetle and involves integrating three concepts: risk, hazard, and exposure. *Risk* is a measure of the total loss expected to occur as a result of southern pine beetle activity in the forest. *Hazard* refers to the conditional state of the forest and is an aggregate of multiple variables; e.g., pine species present and edaphic characteristics of the site (soil type, texture, pH, etc.), climatic conditions where the site is located. *Exposure* is a function of the distribution and abundance of the southern pine beetle. The second chapter in the unit involves silviculture approaches that can be used to minimize impacts by the southern pine beetle. *Silviculture* is defined simply to mean the theory and practice of controlling forest establishment, composition, and growth. Silvicultural tactics are generally concerned with prevention of southern pine beetle-caused losses in stands rather than suppression of populations. The third chapter in this unit deals with restoration and addresses specifically establishment of new forests following damage by the southern pine beetle. This task involves critical examination of forests that have been damaged to define why outbreaks occurred and to prescribe a reforestation (or alternative use) policy that will avoid this circumstance in the future. Simulation models that integrate the interaction of historical patterns of forest succession, fire patterns, and herbivory by the southern pine beetle are useful for this purpose.

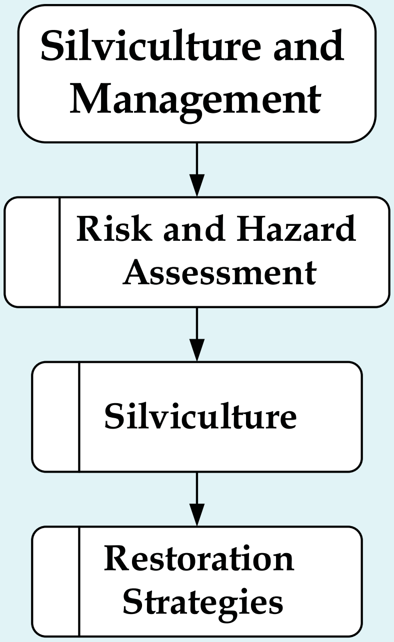


Figure III.1. Diagrammatic representation of the organization of Section III of *The Southern Pine Beetle II* dealing with silviculture and management. This section contains three chapters that address risk and hazard assessment, silviculture, and restoration strategies.

22

Risk Assessment for the Southern Pine Beetle

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Keywords

damage
hazard
risk
southern pine beetle

Abstract

The southern pine beetle (SPB) causes significant damage (tree mortality) to pine forests. Although this tree mortality has characteristic temporal and spatial patterns, the precise location and timing of damage is to some extent unpredictable. Consequently, although forest managers are able to identify stands that are predisposed to SPB damage, they are unable to avoid damage entirely. Instead they must manage this uncertainty using risk assessment tools. This chapter discusses the development and utility of these tools for managing the SPB.

22.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is the most destructive pest of Southeastern U.S. pine forests. The SPB is estimated to have caused $900 million worth of direct economic damage between 1960 and 1990 (Price and others 1998) and other less tangible effects to watershed, ecological, and sociological forest functions. Southern pine beetle damage has a characteristic spatial and temporal pattern that makes risk assessment an important tool for management. Periodic outbreaks comprise large numbers of discrete infestations (contiguous patches of tree mortality) that cause localized damage to some forest areas but not others. In addition, the location and timing of SPB infestation are to some extent unpredictable. These characteristic patterns of damage ensure that some forest managers will be affected by the SPB while others may not.

The values attributed to forest products and function, the spatial and temporal patterns of SPB damage, and the unpredictability of damage form the central ideas of this chapter and key concepts involved in a discussion of SPB risk. Another major theme of this chapter is that risk assessment (the process of estimating and communicating risk) is part of a larger decisionmaking process that should allow practical and effective forest management decisions to be undertaken. The scale of the SPB problem, including the geographic range of the SPB and the number of different stakeholders it affects, suggests that estimates of risk should be readily interpretable and communicable to a wide variety of forest managers and for diverse management goals. The following section objectively defines risk and its interpretation based upon these concepts.

Estimating and managing SPB risk requires an understanding of the interaction between the SPB and measurable properties of the forest. Over many decades, foresters have reported the common association of dense pine stands and slow tree growth with SPB outbreaks. Such observations have gradually developed into a more objective, scientific study of the interaction between the SPB and the forest. This chapter reviews this scientific literature, with the aim of identifying consistent factors that indicate SPB risk. Here the primary focus is to address the following, basic questions:

1. Which silvicultural, climatic, or biotic factors lead to an increased likelihood of SPB damage?
2. Given this information, how much SPB damage is likely to occur in a particular location during a given timeframe?
3. How readily can this scientific literature be interpreted, communicated, and used for effective decisionmaking?

The interpretability and communicability of risk represents a difference between ecological research designed to investigate risk factors and the dissemination of these results to practicing forest managers. One measure of the success of SPB risk research is the extent to which scientific results are used in practice. Accordingly, the chapter concludes by assessing how results from the current scientific literature have been transformed into state-of-the-art, decisionmaking tools.

22.2. WHAT IS RISK?

Everyday definitions of risk involve two fundamental concepts: damage (or loss) and uncertainty. For example, Webster's dictionary defines the noun, "risk", as "possibility of loss or injury", and suggests several synonyms including hazard and threat. For scientific or procedural purposes, a more precise definition of the term, risk, is useful. This extra precision is important for a number of reasons:

1. It enables risk analysts and managers to effectively communicate with each other and understand how estimates of risk have been calculated, what risk estimates actually mean, and how they can be used to aid decisionmaking.
2. A clear, unambiguous definition serves as a useful paradigm for guiding the collection of data and designing analyses to assess risk.

A common and widely adopted scientific definition of risk is that it is a quantification of expected damage (or loss) defined in time and space. In a variety of risk assessment fields, the concept of risk is further defined in terms of two principal components: the probability of an adverse event occurring and the damage caused by this event. For forestry applications risk has been defined as:

$$\text{Risk} = P_a \times A_d \qquad (1)$$

where P_a is the probability of an adverse event occurring and A_d is the amount of damage caused by the event (Bredemeier and others 2000, Mott 1963). For example, the total risk from the SPB to a unit area of forest can be conceptualized as the probability of the area becoming infested and (or multiplied by) the amount of damage that is likely to occur as a result of this infestation. Despite the simplicity of this framework, it should also be noted that more work is needed in order to use it to assess risk practically. For example, both the probability of an adverse event occurring (P_a) and the damage caused by an event (A_d) need to be defined precisely in time and space dimensions. In the case above, definitions and units would need to be provided for the spatial extent of a stand (e.g., 1 ha), the temporal scale of the analysis (e.g., 1 year), and measurement of damage (number of trees killed). These definitions ensure that the results of the risk assessment are scaleable (can be applied to different temporal or spatial scales), comparable to risk estimates for different areas or observations, and therefore interpretable.

Unpredictability is clearly a key concept for defining risk and also presents one of the biggest challenges to understanding exactly what risk is. Fundamental to this issue is the differentiation of risk and uncertainty. Haimes (1998) delineates risk and uncertainty as follows:

“Risk refers to a situation in which the potential outcomes can be described in objectively known probability distributions. Risk is a measure of the probability and severity of adverse effects. The term, uncertainty, refers to a situation in which no reasonable probabilities can be assigned to the potential outcomes. Uncertainty is the inability to determine the true state of affairs of a system.”

For the SPB, both the probability of an infestation occurring (P_a) and the damage caused by an infestation (A_d) are unpredictable. However, this unpredictability can be represented by objectively defined probabilities or probability distributions. This probabilistic approach conforms to an intuitive understanding of risk—although it may not be possible to predict the occurrence of an event exactly, it can be defined (summarized) well enough that it becomes useful for decisionmaking.

22.2.1. Risk Assessment

Risk assessment is the process of estimating and communicating risk. It is argued that risk estimates, or indices, are ultimately a decision support tool, and that the risk assessment process should involve an understanding of specific decisionmakers and their outstanding risk assessment questions. Equation 1 defines risk using two components that are both probabilistic (conceptually at least). Since risk assessment is primarily used in situations where future events are unpredictable, fully formulated, explicit indices of risk should use probability distributions to describe the likelihood of damage occurring. For example, one might calculate as a risk output or index a probability density function that summarizes estimates of SPB-induced tree mortality for a specified time period and spatial unit.

However, in practice this is not always technologically possible, and more implied estimates of risk might be appropriate. For example, either one of the components of equation 1 could be used as a risk estimate. In this case, the risk endpoint implies risk rather than describing it explicitly. For example, deterministic values that represent the average amount of damage or loss that might occur in the future, or categorical and relative measures of the likelihood of an event occurring (e.g., high, medium, or low risk) might also be more feasible, or appropriate, implied indices of risk. In all cases, the success of a risk index is dependant on a strong definition of what it actually means.

Risk assessments are usually required to be procedurally straightforward. For example, a forester might assess risk by measuring certain properties of a stand, enter these variables into a risk model, and obtain an estimate of risk. However, irrespective of the accuracy of the model, the utility of the risk assessment also depends on the cost and inconvenience of collecting the necessary variables. In other words, risk models intended for practical applications need to balance predictability with ease of collecting the data required by the model (Lorio 1980b).

The output of risk assessments should also address questions most relevant to a forester. For example, models that provide categorical and relative outputs of risk (high, medium, or low) provide useful information for determining which areas of the landscape are more likely to suffer damage, and therefore identify where risk reduction methods (e.g., thinning) should be prioritized. They are unable, however, to determine whether a risk reduction method is actually beneficial based on a cost/benefit analysis. Similarly, forest managers might want to rescale risk outputs according to the amount of land that they currently manage and a timeframe that is most appropriate to them. For example, one landowner might be interested in the expected losses occurring within a 50 ha parcel over a 10-year period, while another might be interested in losses for a 100 ha plot over a 20-year period. Feasibly, both questions can be addressed using the same basic pieces of information (i.e., the conceptual model outlined in equation 1), but only if this information is scaleable (appropriate spatial and temporal units are included) and easily interpretable (the meaning of risk indices are well defined).

It can be concluded that risk assessment and the development of practically useful risk models and indices is subtly different from ecological research. Nevertheless, ecological understanding of the factors that predispose forests to the SPB is essential for providing effective and reliable risk assessment models. The other essential components of the risk assessment process are:

1. Identification of outstanding and important risk questions
2. Development of data collection methods and models capable of addressing these questions
3. Communication of well-defined, easily interpretable risk outputs

Section 22.3 critically reviews the current research into which stand and site variables predispose forests to the SPB. This review focuses upon research that provides models and summaries that directly address SPB risk. Section 22.3 concludes with a summary of how versions of these models are used to provide effective SPB decision support tools.

22.3. A REVIEW OF SPB RISK ASSESSMENT

It is possible to assess SPB risk at a variety of spatial or temporal scales. For example, the focus of an assessment might be an individual tree, an individual stand, or a specific region (e.g., national forest, county). Similarly, at each of these spatial scales, risk might be reported for any given time frame (e.g., a month, a year, 50 years). It can be seen that these scales are hierarchical, such that identifying individual tree risk should allow one to calculate stand risk, which in turn could be used to calculate regional risk. In large part, the spatial and temporal scale at which risk is reported should be driven by specific, practical management questions. However, reporting the spatial and temporal dimensions of risk outputs is an important component of any assessment and allows results to be readily interpreted and rescaled for different units of time and space.

Three major trends stand out from the current risk assessment literature. The first is that most studies concentrate on the spatial scale of the risk to a stand of trees. This is probably driven by the fact that data collected for SPB risk assessment is often the result of a practical requirement to visit infested stands, and because stand level measurements are the basic building blocks of forestry. Second, current risk models usually infer a measure of the likelihood that a stand will become infested during an outbreak, given the current silvicultural and environmental condition of the stand. As such, relatively few models deal with the damage that can be expected following an infestation, yet this is clearly an important component of overall risk (see equation 1). Third, current risk models most often report relative, categorical outputs of risk; for example, high, medium, or low. Correctly interpreted, these outputs allow forest managers to identify which stands are more likely to be infested than others, but do not provide absolute estimates of damage or losses. Categorical estimates of risk are subjective—high risk from one study may not be equivalent to that of another—and are difficult to interpret for different spatial or temporal scales than used in the original study.

The following sections present a detailed and critical review of the current SPB risk assessment literature. A number of terms, including risk, hazard, and susceptibility, are commonly used throughout this literature. For the purposes of this review, they are all treated as indices of risk irrespective of the terminology, but will be discussed in terms of the three main trends outlined above and their consequences for forest management. In other words, the aim of the review is to organize and critique current risk models according to the component of risk they attempt to represent, the spatial and temporal scales for which the measurement is most relevant, and the utility of the risk outputs for risk management. This review is also limited to studies that directly attribute stand and site variables to any of these indices rather than studies that detail key ecological information about the SPB but cannot be directly used to assess risk.

22.3.1. Stand Level Risk

Infestation Probabilities

A number of researchers have developed models that attempt to determine stand and site characteristics that predispose stands to SPB damage. Although differences in methodology make it difficult to directly compare the results of these models, tree vigor (represented by measurements of basal area and radial growth), landform, and soil characteristics are key components to all these models. Disturbance of the stand (lightning, mechanical damage, or wind disturbance) is also shown to be positively associated with infestations (Daniels and others 1979, Hedden and Belenger 1985, Ku and others 1980a). Tables 22.1 and 22.2 provide a list of models (discriminant analysis and logistic regression methods respectively) and the stand variables that contribute to SPB damage. It should be noted that most researchers provide a variety of models with different complexities that explore how the predictive accuracy of the models is affected by the inclusion or exclusion of certain variables. This process is useful because in practice, certain stand variables may be unavailable or difficult to measure. As previously discussed, risk assessment involves more than finding the most predictive combination of stand variables; it must also address the practical ease with which variables can collected.

Although an understanding of the factors that predispose stands to the SPB is an important qualitative output from the risk literature, in isolation it may not lead to fully informed decisionmaking. A complete decisionmaking process requires knowledge of the correlation between stand level variables and infestation incidence. For example, in practice it is important to understand how changes in a stand variable (for example, basal area) might affect the likelihood of SPB damage. This would allow a manager to address whether risk reduction methods are worthwhile. Is the cost of a treatment or management action offset by its benefit? This information is provided by an evaluation of the predictive ability of a particular risk model. Interestingly, the SPB literature highlights a major dichotomy in this understanding. Some researchers claim up to 80 percent predictive accuracy of their models. However, others report that infestations occur in less than 5 percent of even high-hazard stands. The resolution to this apparent inconsistency lies with the methodologies used to collect the data to assess risk. Understanding the reasons for this dichotomy is important for interpreting the results from these stand-level infestation models and for developing future risk assessment methodologies.

Modeling the factors that predispose stands to SPB damage requires two essential pieces of information:

1. Stand and site measurements for infested stands
2. Site and stand characteristics of stands that did not become infested

Without both pieces of information, logical, scientific methods cannot be developed that assess the probability of infestation occurrence. A fundamental problem for SPB researchers is that forests ecosystems are extensively managed (there are lots of forest to inventory), and forestry activity (hence the potential for measurement and inventories) tends to be focused around areas that have a current SPB problem. In other words, for the SPB (and many other disturbances), there is a natural tendency to make detailed observations about forest conditions only if a problem occurs. Accordingly, three different methods for sampling (obtaining details for both infested and uninfested stands) the forest might be proposed:

1. Delineate a complete, contiguous area of forest (for example, a national forest) and build stand and infestation inventories for all stands.
2. Collect information for all infested stands and an equal number of randomly selected noninfested stands.
3. Sample a given number of stands by selecting them randomly from a larger forested area.

Each sampling method has advantages and disadvantages, and also affects the methodology required to analyze data and interpret the results. Methods 1 and 2 have both been used by SPB researchers to construct risk models, and it is the difference between these methodologies that leads to difficulties in interpreting the predictive ability of the resulting risk models.

Table 22.1—Discriminant Analysis Models for Stand Risk Rating (continued on next page)

Author (location)	Model	Notes
Kushmaul and others (1979)	DS = 2.33550 – 0.01906 (PINEBA) + 0.01484 (RAD) – 0.00829 (UNDER) – 0.00613 (SOIL) – 1.71662 (BARK).	73% accuracy for infested plots and 75% for uninfested plots
Louisiana, Mississippi, and Texas Gulf Plain	DS < –0.13514 = Infested	N = 35
		(15 infested and 20 noninfested plots)
	DS = 3.06135 – 0.018342 (PINEBA) – 0.00705 (AGE) – 0.00002 (DENSITY) – 0.00880 (SITE) – 0.04085 (TOTALBA) DS < –0.12736 = Infested	Correctly classified 80%of the infested and 70% of the uninfested plot subsets
	DS = 0.93080 – 0.02004 (PINEBA) + 0.01827 (RAD) DS < –0.12917 = Infested	Correctly classified 93%of the infested plot subset, 65% of the uninfested subset.
	Where: SOIL = Surface Soil Depth PINEBA = Pine Basal Area (ft^2/acre) BARK = Bark thickness (cm) TOTALBA = Total Basal Area (ft^2/acre) DENSITY = Stand Density (stems/acre) AGE = Age of Pines (years) SITE = Site Index (base age 50) RAD = average 10 year radial growth UNDER = Understory %	
Ku and others (1980a, 1980b)	DS = -1.50 (TOTALBA) + 3.3 (AGE) + 64.3 (RAD) + 0.93 (HARDBA).	75% accuracy
Arkansas	DS > 100 = Low susceptibility 1 < DS < 100 = Medium susceptibility DS < 1 = High Susceptibility	N_{subset} =268
	Where: HARDBA = Hardwood Basal Area (ft^2/acre) TOTALBA = Total Basal Area (ft^2/acre) RAD = Average Radial Growth in cm (10yr) AGE = Stand Age (years)	
Porterfield and Rowell (1980 unpublished)	DS = 1.02559 - 0.00043 (VOLUME) + 1.33776 (SAW) - 2.14726 (BARK) + 0.01878 (RAD) + 0.03205 (SLOPE) - 0.00791 (PINEBA)	79% accuracy
Texas to Virginia	DS < 0.0442 = Infested	N = 1021 547 infested and 474 uninfested plots 74% accuracy N_{subset} = 119 (69 SPB-infested, 50 noninfested)
	Where: RAD = 10 years radial growth (mm breast height) VOLUME = Total Volume in ft^3 (> 4.6 inches DBH) SLOPE = Ground Slope (%) SAW = pines > 9.6 ft3 as proportion of VOLUME PINEBA = Proportion of total BA in pine BARK = Average Bark Thickness (nearest 0.1 inch)	

Table 22.1 (continued)—Discriminant Analysis Models for Stand Risk Rating

Author (location)	Model		Notes
Hicks and others (1980)	DS = -0.51161(BT) + -0.51526(PBA) + -0.40455(AH) + 0.17528(LAF) + 0.13538(SI) + 0.17002(ADBH) +0.12525(RGI)+ 0.18884 (TSD)+ 0.10389(SST) + 0.10514(SUBST) + 0.08937 (WR) + 0.07829 (HBA)		79% Accuracy
	Unknown DS classification		
	Where:	HBA = Hardwood basal area	
	BT = Bark Thickness (cm)	SI = Site Index (m)	
	PBA = Pine basal area (m^2/ha)	SST = Surface Soil Texture	
	RGI = Radial growth Increment (last 5 years)	TSD = Topsoil Depth	
	LAF = Landform	SUBST = Subsoil Texture	
	AH = Average height (m)	WR = Water regime	
	ADBH = Average DBH (cm)		

Method 2 has been the most commonly used sampling methodology for SPB research, probably because it requires the least sampling resources. For example, Kushmaul and others (1979) used discriminant analysis to classify whether a stand became infested based on site and stand characteristics. The resulting model was then tested on an independent subset of the data (data not used to build the model) to determine the number of times that the model correctly predicts the fate of a stand based on its characteristics (predictive ability). For this study, the models yielded prediction accuracy of 70-80 percent, suggesting that the model is very good at determining which stands are likely to become infested. Consequently, a naïve, practical interpretation of these results suggests that stands with certain characteristics are very likely to become infested by the SPB.

Closer inspection suggests this conclusion is not valid. First, the model classifies stands as either infested or noninfested—two choices. It follows that one would expect to get 50 percent of classifications correct purely by chance. A 70 percent or an 80 percent classification has a different practical interpretation if compared to a null model of 50 percent accuracy. However, the most serious interpretative problem with sampling method 2 is that the data (and model) misrepresents the ratio of infested vs. uninfested stands occurring within the forest. Even during SPB outbreaks, the landscape comprises many

Table 22.2—Logistic regression models for determining infestation probabilities of stands

Author (location)	Model	Notes
Daniels and others (1979) (unknown location)	$P = 1/ (1 + e^{-(-8.599 + 0.044 (BA) + 3.309 (PINEBA))})$	Undisturbed non-plantation stands
	$P = 1/ (1 + e^{-(-9.998 + 0.088 (BA) + 4.801 (PINEBA))})$	Disturbed non-plantation stands
	Where:	No goodness of fit specified
	P = Probability of infestation	
	BA = Total Stand Basal Area	
	PINEBA = Proportion of total Basal Area in Pine	
Zarnoch and others (1984) (Central Louisiana)	$P = 1/(1 + e^{[4.900 - 0.030 (AGE) - 0.004 (SIZE)]})$	
	Where:	No goodness of fit specified
	P = Estimated probability of SPB infestation over 8 years	
	AGE = Age of Substand	
	SIZE = Size of Substand (Acres)	

more uninfested stands than infested ones, and this affects the interpretation of the results. Interpreted correctly, these results suggest that if infested and uninfested stands are preselected from the landscape in equal numbers, the predictive accuracy of the model is 70-80 percent. This interpretation (which is correct, given the data and the analysis) does not actually address a practically useful risk assessment question. A more appropriate question, and one that can be used to make effective decisions, should directly address the probability that a stand with given attributes becomes infested in a given time period.

Other researchers have identified and addressed the problem of uneven sampling with updated analyses. For example, Hicks and others (1980) used a discriminant analysis and estimates of the sampling bias between infested and uninfested stands to determine actual infestation probabilities for stands with different attributes. In addition, the logistic regression methodology reported by Daniels and others (1979) and Reed and others (1982) uses a methodology designed to overcome these sampling problems. However, although analyses can be modified to account for unrepresentative samples, outputs will always be sensitive to the relative sampling frequency of infested to uninfested stands. The methodology of Mason and Bryant (1984) provides the most obvious solution to this problem by delineating entire portions of the landscape and collecting data for all stands—sampling methodology 3. Although not without its own problems (for example, the expense of data collection and determining an appropriate spatial scale for a study), the advantage of this method is that it encourages regular, ongoing inventories of the forest useful for assessing risk to any forest disturbance agent. In the near future, remote sensing may provide more efficient and detailed forest measurements and help overcome some of these problems and solve a fundamental problem for SPB risk assessment.

Table 22.3 shows infestation probabilities calculated by a number of researchers. In summary, these rates are between 0.01 and 5 percent even for high-risk stands. For example, Hicks and others (1980), using data from East Texas between 1975 and 1977, estimate infestation probabilities less than 0.01 (1 percent) even for stands with high basal areas (>27 m^2/ha). Daniels and others (1979) report slightly higher infestation rates during an outbreak in 1975 (undisclosed location), but for stands with a basal area between 20 and 35 m^2/ha still only estimate infestation probabilities of between 0.01 and 0.02 (1-2 percent). Reed and others (1982), estimate year by year infestation probabilities for East Texas ranging from 0.0043 to 0.0479 (0.4-4.8 percent) between 1966 and 1976 (note that parts of East Texas were under permanent outbreak conditions during this period). These estimates are based on methodologies that account for biases in sampling, and suggest that even during outbreak years the probability that any single stand will become infested is relatively low, even if the stand has attributes that predispose it to an infestation. The estimates in Table 22.3 are also scaleable in time and space. In other words, they can be used to estimate, for a typical outbreak year, the total risk for a collection (ownership parcel) of any number of stands. If outbreak frequency data are included, then they can be used to estimate the likelihood of an infestation occurring for any spatial extent and for any time period (for example, the harvest cycle of a stand—see section 22.3.2). It should also be noted that although low infestation probabilities may reduce the perceived problems (risk) caused by the SPB, when these numbers are rescaled for entire forests comprising many stands and extended time scales, these probabilities become much more significant.

In addition to providing practical risk information, it is argued that the magnitude of the probabilities in Table 22.3 conforms to current knowledge of the SPB. It is generally believed that the SPB most readily attack and infest stressed and weakened trees. This stress might be caused by a number of factors; for example drought, mechanical damage (Hedden and Belenger 1985), lightning strikes (Coulson and others 1999b, Flamm and others 1993), or flooding. In addition, it is clear that these potential hosts will only become infested if they can be successfully located by beetles (Paine and others 1984). Finally, any weakened and successfully attacked tree must be close to other potential hosts (others subject to stress) if a multi-tree infestation is to develop. So, ecologically, the occurrence of infestations may involve the co-occurrence of a number of fairly rare events. Mathematically low probability events multiply to produce even lower probability events, facts that may be important for assessing the predictive success of these models. It is therefore probably not surprising that the predictive accuracy of these models is

Table 22.3—Summary of stand-level infestation probabilities during outbreaks

Author	Location, Year	Infestation Frequency	Units	Basal Area or Risk Range
Lorio and others (1982)	Kisatchie National Forest, Louisiana	13.4	Infestations per 1000 ha	High risk
		6.8		Medium risk
		3.2		Low risk
	East Texas, 1973-1978	9.9	Infestations per 1000 ha	Very High risk
		5.8		High risk
		3.9		Moderate risk
		2.7		Low risk
		1.8		Very Low risk
Hicks and others (1980)	East Texas, 1975	0.002	Infested area/Total Host Area	All host types
	1976	0.004		All host types
	1977	0.002		All host types
	All Years by BA	0.000	Probability of infestation per ha	0.0 -9.2 (m^2/ha)
		0.000		9.3-18.4 (m^2/ha)
		0.001		18.5-27.5 (m^2/ha)
		0.001		>27.5 (m^2/ha)
Daniels and others (1979)	Unknown, 1975	0.008	Probability of infestation (Undisturbed stands)	11.48 (m^2/ha)
		0.014		22.96(m^2/ha)
		0.023		34.4 (m^2/ha)
		0.037		45.93 (m^2/ha)
		0.015	Probability of infestation (Disturbed stands)	11.48 (m^2/ha)
		0.048		22.96 (m^2/ha)
		0.131		34.4 (m^2/ha)
		0.313		45.93 (m^2/ha)

low. The resolution of forest data is driven by the practical difficulties of measuring extensive forest ecosystems—it is difficult to account for every tree in the forest. In addition, the small size and cryptic behavior of the beetle make it difficult to measure, yet its presence or absence is undoubtedly the most important factor that contributes to an infestation occurring (Paine and others 1984). Arguably, models based on aggregate, stand-level data should not be expected to be highly predictive. And from a risk assessment perspective, researchers should be reassured that even small amounts of extra information (predictive accuracy) can contribute to effective decisionmaking if it is objective, logically sound, and easily interpretable.

Infestation Growth Risk Models

Assessing the probability that a stand will experience an infestation is one component of stand-level risk. The expected amount of damage caused by an infestation completes a full assessment. The ultimate size of an infestation is driven by the potential for spot growth, which in turn may be driven by stand, site, and climatic variables similar to those that drive the initiation of infestations. But as Daniels and others (1979) point out, causal relationships important in the initiation of outbreaks (infestations) may be different from those involved in the subsequent spread of outbreaks (infestations). However, like infestation dynamics, the growth and ultimate size of infestations are to some extent unpredictable. The goal of spot growth models, especially for risk assessment, is to understand the relative importance of various site factors to spot growth and to estimate the losses likely to accrue in a stand that has become infested.

In contrast to assessments of stand infestation, there have been fewer studies on the growth or sizes of infestations. This is puzzling, since the data required to model infestation growth should comprise mostly information (excepting the role of beetle immigration and emigration) collected solely within infestations rather than for the entire forest area. It could also be argued that infestation growth and tree mortality are ultimately responsible for economic or other losses. In East Texas, the working definition of an infestation is 10 trees, but some infestations may grow to become three or four orders of magnitude larger. Understanding the factors that drive infestation growth determines overall stand damage. This level of understanding is more important for some risk assessment questions than for others. For example, over regional scales, a large number of infestations may occur. In such cases, the variability of within-stand damage may average out such that average infestation size becomes a meaningful concept. In contrast, for small private foresters who have incurred a single infestation, there may be considerable motivation to understand the amount of damage that might occur should a stand become infested.

Hedden and Billings (1979) used data collected over 3 years in East Texas to develop a model that was highly predictive in assessing the fate of infestations (Table 22.4). The model uses the number of active trees at first visit to determine the probability that an infestation will contain fewer than 20 active trees after 30 days. They also developed a model to estimate the number of trees killed per day as a function of the initial number of infested trees at the first visit, total basal area, and the total number of infestations detected for that year (Table 22.4). From a sample size of 62 spots, this equation gave an R^2 value of 77 percent. The model suggests that the total number of infestations in the landscape has a large effect on infestation growth. All other things being equal, spots showed different expansion rates for different years, with three times as many trees killed per brood during a severe outbreak year than during the collapse of an outbreak. Models without this variable failed to account for differences in the aggressiveness of spot growth for different years.

One potential criticism of this study lies in the use of initial infestation size (number of trees killed at first visit) to predict spot growth. It could be argued that if an infestation has grown large relatively quickly, then by definition it is situated in a stand suitable for spot growth and more likely to continue growing large. The interpretation provided by the authors is that the initial size of the infestation is important because it reflects the size of the resident beetle population available to sustain spot growth without dependency on immigration from surrounding infestations. It should also be noted that this difficulty arises largely as a result of the time lag between the initiation of an infestation and spot detection through changes in the color of foliage (Billings and Kibbe 1978)—another characteristic of the system that contributes to difficulties studying SPB.

Reed and others (1981) used the same data as Hedden and Billings (1979) to develop a new model (Table 22.4) that explained 77 percent of the variability of spot growth. Extending the work of Hedden and Billings (1979), they coupled this with a model that estimates the probability of an infestation becoming inactive after 30 days. These two equations can be used to simulate and predict ultimate spot size. At the beginning of the simulation, the growth equation can be used to predict the size of the spot after 30 days. The second equation can then be used to determine if, after this time period, the spot is predicted to remain active. To simulate an infestation over any period, the procedure is repeated for as long as the spot remains active.

Schowalter and Turchin (1993) addressed some of the problems of the delay between infestation initiation and measurements of spot growth by introducing beetles to stands to control for the timing of infestation initiation and initial beetle population size. Their main conclusion is that the pine basal area of the stand significantly influenced the growth of the infestations. More specifically, they found that tree mortality was significantly related to the average nearest pine distances of the stand, and the number of trees killed in each stand was highly variable. In all cases, introduced beetles attacked trees in the stand, but sometimes these attacks were unsuccessful and did not lead to infestation growth.

In addition to simple statistical models, mechanistic population models have been developed that explore the interaction between stand characteristics and infestation growth. For example, the Arkansas Spot Dynamics Model (Stephen and Lih 1985) takes basic information about the location, silvicultural characteristics of the stand, and the conditions of a current infestation (counts of infested trees) to project average growth of the infestation. Validation of the model using data from 70 infestations suggested that predictions after 90 days are subject to a 13.3 percent error. Currently, the model is in the process of being validated

Table 22.4—Summary of simple spot growth models

Author	Model
Hedden and Billings (1979)	Probability that an infestation will contain < 20 trees after 30 days = 1 / (1+exp(-11.13 +3.53 $\log_e$ (AT)) Trees killed per day = -1.78627 + 0.02475(IAT) + 0.02765(TBA) + 0.14229(POP) Where: IAT = Number of trees under attack at first visit TBA = Total Basal Area in m^2/ha and the total number of infestations detected for that year POP = Total number of surrounding infestations in the landscape
Reed and others (1981)	Probability of spot becoming inactive (next 30 days) = 1 / (1 + exp(-1.04 + 0.06AT)) Natural logarithm of trees killed per day = TK/D = 3.435 + 0.965 $\log_e$ (AT) – 2.847 ($\log_e$ DBH) – 22.137 (TBA/DBH^2) + 0.0736 (TBA) + 0.558 (POP) Where: TK/D = Predicted natural logarithm of trees killed per day AT = Natural logarithm of the number of attacked trees at the start of the simulation period DBH = The mean DBH of the stand (cm) at the start of the year TBA = Total basal area of the stand (m^2/ha) at the start of the year POP = Number of spots per 405 ha (1,000 ac) of host type for the entire region during the year being examined AT = Number of affected treed at the beginning of a 30-day period.

using a much larger data set and further developed to allow it to be easily distributed to forestry professionals.

Another SPB spot growth model, TAMBEETLE, has been developed and described by Coulson and others (1989). This model differs from the Arkansas model in that it is a spatially explicit, stochastic model of population dynamics. Conceptually, the model tracks beetle populations within each tree using temperature-driven growth, fecundity, and survival rates, and simulates the emergence and reemergence of the within-tree beetles, and using this information evaluates the probability that attacking beetles will be numerous enough to overcome the defenses of neighboring trees. Note that this process is conceptually very similar to the one suggested by Reed and others (1981), except that it accounts for much more biological detail (especially the relationship between temperature and population processes), incorporates known mechanistic submodels, and runs on a time-step of 1 day instead of 30 days. Currently, the major problem with TAMBEETLE is that there are no published reports that detail the accuracy of the model.

22.3.2. Regional Scale Risk Assessment

The previous sections reviewed models that could be used to analyze risk at the scale of individual stands. In most of these studies, data were obtained for a single outbreak and for a particular region where the outbreak occurred. Southern pine beetle outbreaks can be conceptualized as having a frequency component (how often outbreaks occur within a region) and a severity component (how many

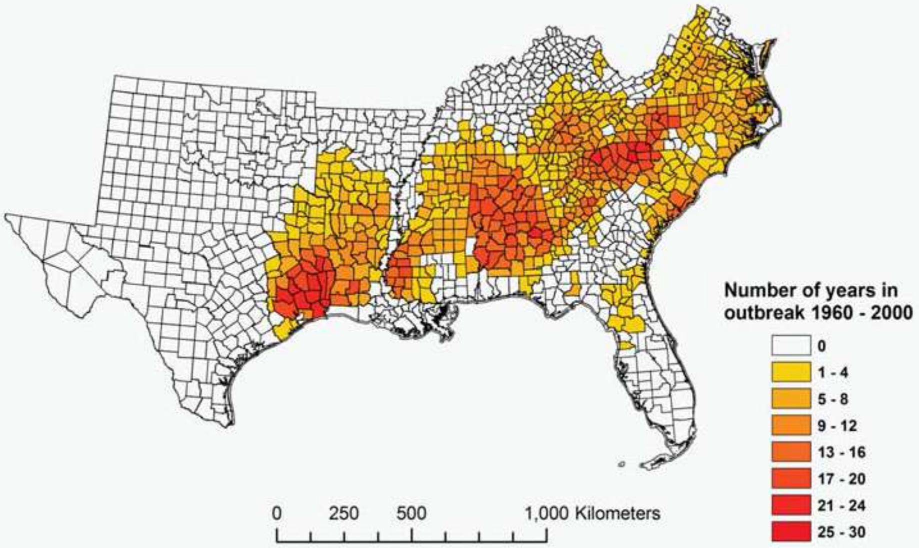

Figure 22.1—Frequency of SPB outbreaks by county between 1960 and 2000.

stands were infested as a result of that outbreak). So if strictly interpreted, because they are likely to be driven by the severity of that outbreak, infestation probabilities (and probably to some extent spot growth—see section above) are specific to a particular outbreak in a particular region. If all SPB outbreaks had the same frequency and severity, regional-scale risk would not be important. But empirical evidence suggests that this is not the case. Figure 22.1 shows the frequency of outbreaks across the range of the SPB, and it is possible that the severity of outbreaks also varies considerably across the range of the SPB. These patterns of outbreaks may be driven by factors such as climate, host availability (including the number of high-risk stands), and the structure (e.g., fragmentation) of the forested landscape.

The factors that contribute to regional SPB risk have added importance because of large-scale, human-induced changes in both climate and the state of the forest. For example, climate change may affect the range of both the SPB and its hosts, thus exposing new forest stakeholders to SPB risk. In addition, the forest is becoming more fragmented. This fragmentation concerns the physical juxtaposition of forest patches but also parcels of ownership and permeation by humans (Riiters and Wickham 2003). Physical fragmentation may directly affect SPB population dynamics, the initiation and growth of infestations, and ultimately the pattern of SPB damage, while ownership fragmentation may also be significant because it has the potential to affect an individual's interpretation of damage. For example, consider how a 100-tree mortality event might affect an individual who owns 1,000 trees vs. an individual owning 10,000. In the first case, 10 percent of a forest manager's trees (potential income) are lost, whereas in the second case only 1 percent are lost. It follows that the interaction between the pattern of SPB damage—including and especially the unpredictability of mortality—and pattern of forest ownership is an important factor for SPB risk research.

Regional-scale risk assessment requires an understanding of how climate, forest, and other relevant factors affect the larger scale spatial and temporal patterns of SPB damage. For example, quantifying the effects of regional climate and vegetation patterns on the severity and frequency of SPB outbreaks would allow extrapolation of stand-level infestation probabilities for any region of the SPB range and may also be important for assessing risk in the light of regional changes in forest structure and composition. Similarly, an understanding of the contagion of infestations would allow stand-level infestation probabilities to be estimated throughout the course of an outbreak, based on the location of a focus stand relative to existing infestations.

Most regional risk studies have focused on the effects of climate change. For example, Gumpertz and others (2000) use a logistic regression analysis to investigate the frequency of infestations in North Carolina, South Carolina, and Georgia. A number of regional-scale forest, physiographic, and climatic variables were used in the model, including estimates for the volume of timber grown in the county (pole timber and sawtimber); the proportion of habitat classified as xeric, mesic, or hydric; a number of average climatic variables for the county; the amount of land in one of five ownership classes; and three locational parameters: mean elevation, latitude, and longitude. The model accounts for and found significant spatial and temporal autocorrelation effects, suggesting that the locations of outbreaks in the previous year were good predictors of where outbreaks were likely to occur in the next year. Because of the large number of explanatory variables used in the analysis, the coefficients of the model are probably unable to provide conclusive information about which of these is most important. However, validation of the model based on 5 years of new data successfully predicted the occurrence of outbreaks and non-outbreaks 64 percent and 82 percent of the time, respectively. Furthermore, the authors argue that many of the independent variables do have some ecological relevance. For example, the amount of sawtimber in a county was considered a more useful explanatory variable than the amount of pole timber because the SPB preferentially attacks larger, more mature trees.

Gan (2004) performed regional-based risk assessment that explores the influence of selected county-level variables on total SPB damage. A panel data approach was used to model the proportion of timber killed in each county of the Southern United States over a 23-year period. Since the main focus of the work was to investigate the effects of climate change on beetle distribution and SPB risk, all but one of the independent variables used were related to current or lagged weather measurements. The model provided a good fit to the data (an R^2 of 97.5 percent), and suggests that both current and lagged weather variables are important factors that contribute to SPB damage. The author concludes that SPB risk might be increased by an average of 2.5 – 5 times for a range of predicted climate change scenarios.

22.3.3. Risk Models in Practice

One measure of the success of risk models is the extent to which they are actually used to aid practical decisionmaking. This criterion is not absolute (conceivably, poor models might prove useful for extended periods before their problems are realized). However, risk assessment is a practical process, and as many authors have noted (Kushmaul and others 1979), for a model to be practically useful, it must attain a balance between predictive ability and the amount of effort required to obtain the inputs (information) necessary to produce outputs. A review of current, procedurally used models (and who uses them) may indicate appropriate levels of detail relevant for different user groups, and identify characteristics that lead to utility.

One of the most common, practical uses of stand risk models is to help allocate Federal funds in cost-share programs that offer financial rewards to foresters who engage in good management practices. For example, in East Texas, thinning operations qualify for cost sharing if (among other factors) landowners own between 10 and 5,000 acres and if stands have greater than 70 percent loblolly, shortleaf, or slash pines, and two risk models are also used to determine qualification for cost-share programs. The first is a Texas Forest Service-defined grid (approximately 8.5 x 8.5 km cells) covering East Texas that rates geographically driven SPB risk (TFS uses the term Hazard) as Very Low, Low, Moderate, High, or Extreme (see Figure 22.2). Billings and others (1985) describe the methodology used to develop these grid block ratings, which are periodically updated to reflect changes in the forest landscape. A stand must be located in a Moderate, High, or Extreme Hazard stand in order to qualify for cost-share. The second model is site-specific and based on basal area and landform. If these conditions are met and the stand is reduced to no more than 80 square feet per acre (approximately 18.5 m^2/ha), then owners can claim up to $75 per acre for precommercial thinning or $50 per acre for pulpwood first thinning to offset the costs of the operation (Texas Forest Service document TFS 3/06/5000 should be consulted for more details).

Similar cost-share programs are administered by states across the range of the SPB. The aim is to provide incentives to individuals to reduce hazard across broad landscapes. The two-step evaluation process used by the Texas Forest Service suggests that risk is conceptualized as a property of both the local area that a stand is situated in, based on analysis of the forest landscape and past infestation history, and the potential for damage based on measured

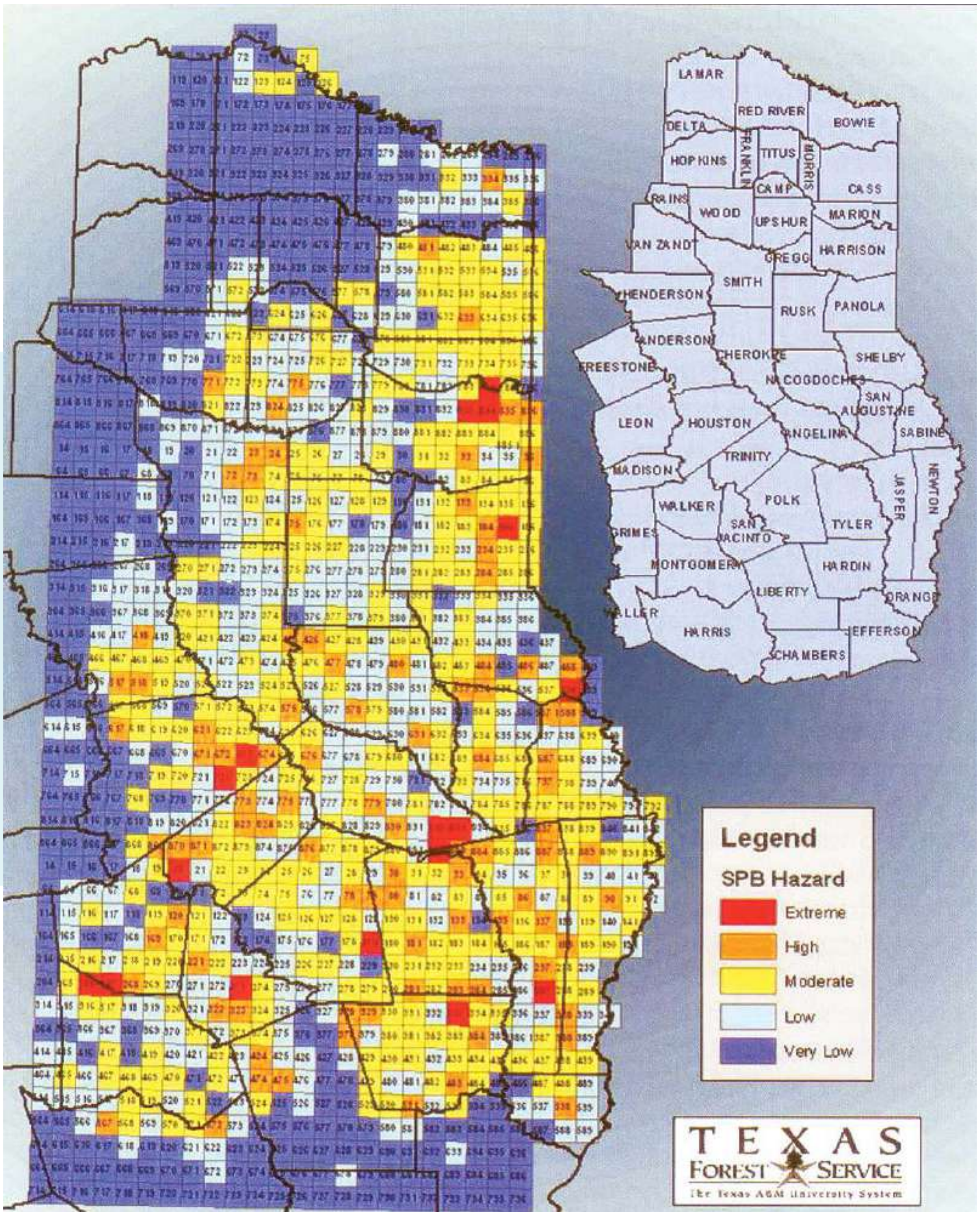

Figure 22.2—Map of categorical risk in East Texas used for determining eligibility to Texas Forest Service cost-share thinning program. The map is for 1996 and derived using work outlined in Billings and others (1985). Ratings from the map form the first component of assessing eligibility for funds (stands must be located in at least a moderate-hazard block). The second component is based on a more detailed appraisal of a particular stand. (Taken from document TFS 3/6/5000)

characteristics of the specific stand. Both models have strong ties to the scientific risk literature but have also been presented in a way that makes them easy to use and understand. For both the Texas Forest Service and small private foresters (nonindustrial private foresters) who use the model, the goal and purpose of the risk analysis is very clear: to determine whether a stand reaches a predetermined risk criteria that qualifies it for Federal dollars. Irrespective of its predictive accuracy, it could be argued that the benefit of this model is that it facilitates effective communication between landowner and the Texas Forest Service, which in turn leads to efficient decisionmaking.

During outbreaks, especially on Federal lands where full-time foresters are available, the focus of SPB management turns to the control of infestations rather than prevention. While infestation probabilities may be relatively small (see previous section), the scale of the forest landscape ensures that large numbers of spots may be detected in relatively short periods of time. So as an outbreak develops, the net result is an overwhelming number of infestations, often in remote areas. In addition, the extended time periods between outbreaks may result in foresters with limited SPB experience or expert knowledge having to visit, assess, and ultimately make decisions about these infestations. These decisions center on control of infestations, salvage of dead timber, and restoration of the damaged stands, all of which are dependant on future infestation growth. These decisions might involve estimates of direct economic damage, whether there is a possibility that an infestation will grow and cross an ownership boundary, presenting possible legal problems, or whether the infestation is likely to impact especially high value or highly protected trees such as red-cockaded woodpecker colonies or seed orchards. Under these situations, widely distributable, quantitative, and easy-to-use infestation growth models provide valuable decision support tools.

Two such models are widely used—the Texas Forest Service spot growth model (Figure 22.3) and the Arkansas Hog Model. The advantage of the former, based on work by Hedden and Billings (1979), lies in its simplicity. Using the basal area of the stand and the number of actively infested trees as the only input variables (both rapidly available by observation), it estimates the expected number of trees killed after 30 days. In addition, the model itself is simple to

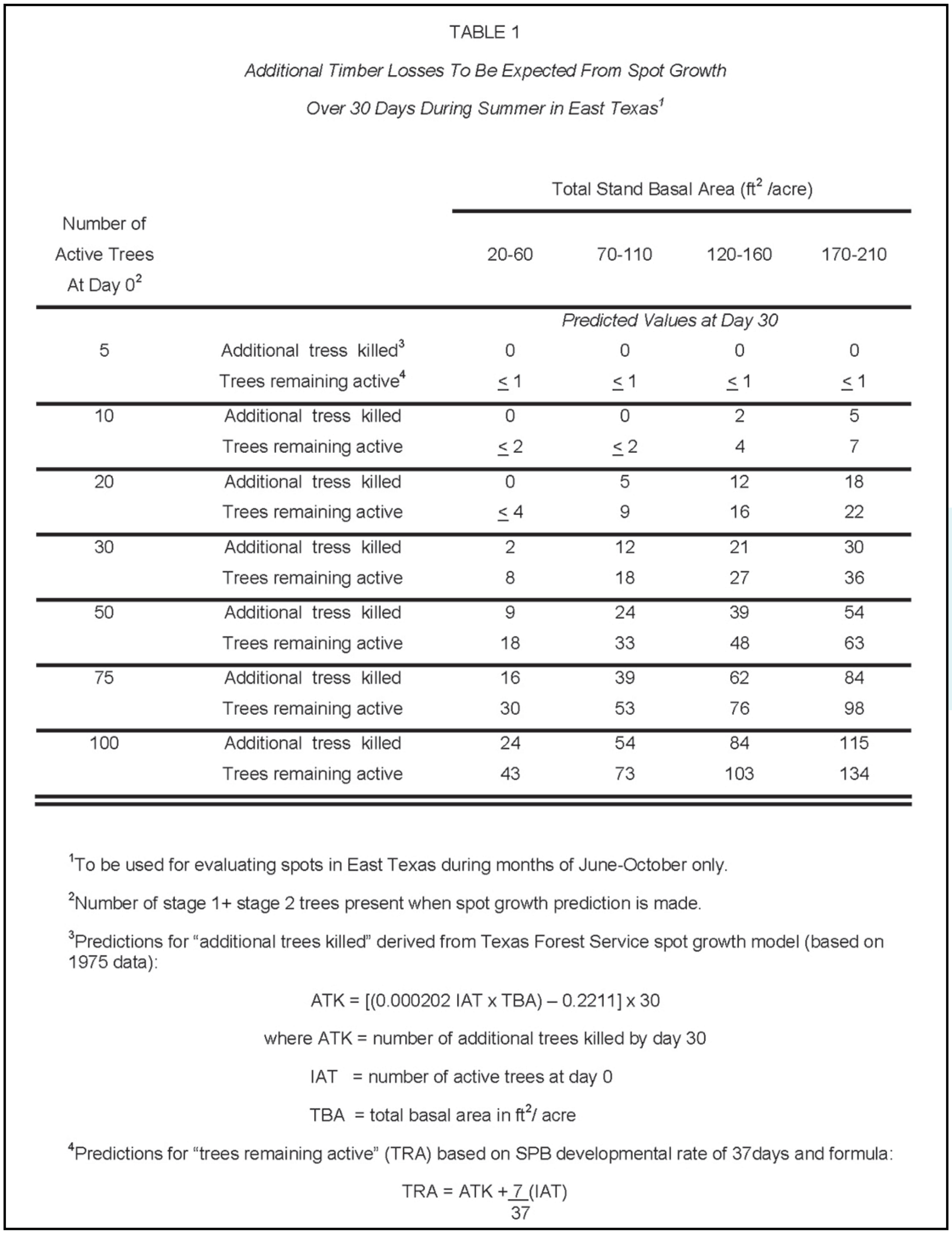

TABLE 1

Additional Timber Losses To Be Expected From Spot Growth

Over 30 Days During Summer in East Texas[1]

Number of Active Trees At Day 0[2]		Total Stand Basal Area (ft^2 /acre) 20-60	70-110	120-160	170-210
		Predicted Values at Day 30			
5	Additional tress killed[3]	0	0	0	0
	Trees remaining active[4]	≤ 1	≤ 1	≤ 1	≤ 1
10	Additional tress killed	0	0	2	5
	Trees remaining active	≤ 2	≤ 2	4	7
20	Additional tress killed	0	5	12	18
	Trees remaining active	≤ 4	9	16	22
30	Additional tress killed	2	12	21	30
	Trees remaining active	8	18	27	36
50	Additional tress killed	9	24	39	54
	Trees remaining active	18	33	48	63
75	Additional tress killed	16	39	62	84
	Trees remaining active	30	53	76	98
100	Additional tress killed	24	54	84	115
	Trees remaining active	43	73	103	134

[1] To be used for evaluating spots in East Texas during months of June-October only.

[2] Number of stage 1+ stage 2 trees present when spot growth prediction is made.

[3] Predictions for "additional trees killed" derived from Texas Forest Service spot growth model (based on 1975 data):

$$ATK = [(0.000202\ IAT \times TBA) - 0.2211] \times 30$$

where ATK = number of additional trees killed by day 30

IAT = number of active trees at day 0

TBA = total basal area in ft^2/ acre

[4] Predictions for "trees remaining active" (TRA) based on SPB developmental rate of 37days and formula:

$$TRA = ATK + \frac{7}{37}(IAT)$$

Figure 22.3—Excerpt from Texas Forest Service Leaflet (Circular 249) describing how to calculate risk (spot expansion) for stands with currently active infestations.

use and easy to distribute to foresters faced with active infestations. The limitations of the model are that it is specific to East Texas, although other models could easily be created for other regions, and that it presents a rather simplistic approach to estimating the likely trajectory of the infestation. The Arkansas Hog Model is by contrast a more complex, mechanistic-based model of population growth that provides estimates of infestation growth for any region in the South and can be distributed as a stand-alone PC-based or Web-based program (Stephen and Lih 1985). Again, inputs to the model are relatively simple, easily observable site characteristics, and outputs are average projections of infestation growth based on a validation of the model against independent data.

Probably the most ambitious and largest practical forestry risk assessment exercise is currently being conducted as an ongoing process in order to assess risk for the entire contiguous United States and Alaska (at a resolution of 1 km^2) and for every major forest pest and disease including the SPB. The stated goal of this risk assessment, undertaken as an ongoing process by the Forest Health Monitoring (FHM) Program of the USDA Forest Service, is to provide a strategic assessment for risk of tree mortality due to major insects and diseases. Specifically, one of the major objectives of the program is to "construct a risk modeling framework such that the resulting products may be easily linked with other risk mapping efforts (e.g., threat of wildland fire)" and in accordance with five general principles:

1. An integrative process that includes multiple risk models
2. A transparent and repeatable risk assessment process
3. Scalability allowing risk to be assessed at different spatial scales as more data and models become available
4. A procedurally efficient and straightforward risk assessment process that ensures the project is both realistic and provides outputs that are readily interpreted by a variety of stakeholders
5. A standardized approach that allows comparisons across geographic regions and for different threats

Crucially, the project provides an explicit definition of risk based on the principle that any forest experiences a background level of tree mortality and that levels above this constitute unacceptable damage. They define damage as follows:

"…our threshold value for mapping risk of mortality is defined as the expectation that, without remediation, 25 percent or more of standing live BA greater than 1 inch in diameter will die over the next 15 years (between years 2005 and 2020) due to insects and diseases."

Their definition of total risk and the risk index that they actually use is:

"…risk is often composed of two parts: the probability of a forest being attacked and the probability of resulting tree mortality, referred to as susceptibility and vulnerability, respectively (Mott 1963). Assigning the probability of insect and disease activity to specific locations requires data that is frequently lacking. Therefore, a probabilistic assessment was not undertaken for the 2006 risk mapping project, and we define risk as the potential for harm due to exposure from an agent(s)."

The risk assessment outputs are maps detailing the expected basal area loss per 1 km x 1 km grid (see Figure 22.4 for the map detailing SPB damage). These maps provide a visually appealing overview for forest managers interested in the aggregate health of the forest from a national, State, or county scale. The upfront definition of risk and the resolution of the maps are ideally suited to strategic decisionmaking and allow the results to be readily interpreted. For example, the maps show potential for damage based on site characteristics rather than full expectations of damage. But since the maps are designed to show the likelihood of damage over a 15-year period (a time scale long enough that infestations are likely to occur), it could be argued that this measure is an effective surrogate for actual risk, and the decisionmaking process is likely to benefit from this simplicity. Although the resolution of the FHM study is not designed to be particularly useful for individual landowners, eventually the decisions made using such outputs are likely to cascade down to individual stakeholders. For example, the cost-share program discussed earlier requires effective decisionmaking in order that adequate Federal funds can be allocated to the administering States.

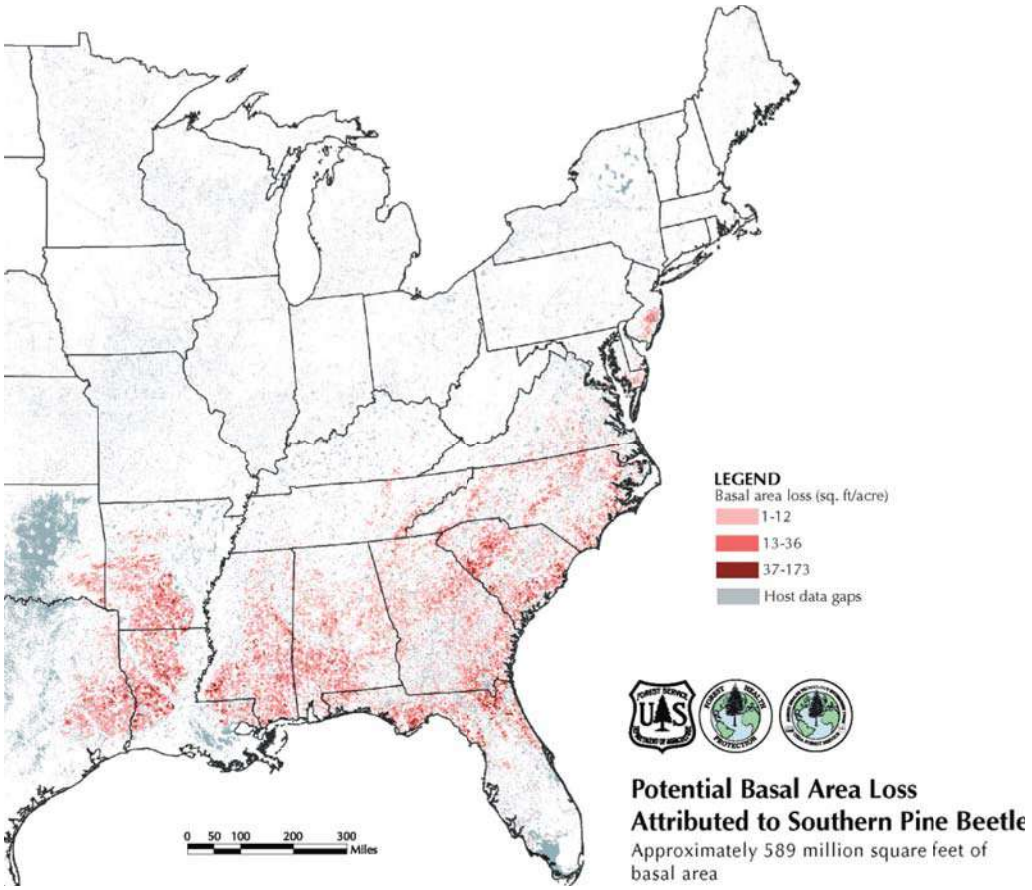

Figure 22.4—Strategic map of expected losses to SPB over a 15-year period at a resolution of 1km x 1km. (map courtesy of Krist and others, in press)

22.4. CONCLUSIONS

Forest management is driven by the value of forest ecosystems that can be impacted by a number of disturbances, including the SPB. Management of the SPB is complicated by its wide geographic range and unpredictability, and the extensive nature of forest ecosystems. This review suggests that it is not possible to predict exactly where SPB damage will occur, but knowledge exists that can be used to identify which areas of the forest are most likely to be damaged, and how much damage can be expected. The goal of risk assessment is to assimilate this knowledge and provide outputs that characterize this uncertainty and enable forest managers to effectively manage the SPB.

A large body of research has shown that certain site and stand characteristics predispose trees to attack. These include the silviculture of the stand (particularly the density and radial growth of trees), damage events (for example, lightning, logging damage), and site characteristics such as slope and drainage. Understanding the role of each factor allows management options to be identified that can be employed in order to minimize risk. Effective decisionmaking also requires estimates of the total amount of damage that one might expect under different management scenarios. These estimates allow an assessment of whether the cost of management actions will be offset by reductions in risk. They also inform forest managers of the potential problems caused by the SPB—it could be argued that SPB damage is more palatable if risks are known up front. One finding of this review is that more emphasis is currently placed upon minimizing SPB damage rather than providing outputs that allow complete risk management.

During outbreaks, the probability of even high-risk stands becoming infested is relatively low (between 0.01 and 5 percent per outbreak). These low infestation probabilities suggest that relationships between measurable stand conditions and infestation probabilities are relatively weak. Models for the growth of infestations (i.e., the severity of an infestation) are less common, but also suggest inherent unpredictability. Explanations for this, and the practical consequences for individuals tasked with managing the forest, have been discussed in previous sections. This unpredictability also has considerable implications for those in charge with managing and contributing to the risk assessment process. In many ways, this unpredictability emphasizes why objective, communicable risk assessments are so important. It is argued that without organized, well-funded approaches to risk assessment, individual forest managers are unlikely to be able to attain an unbiased, objective, and accurate view of SPB risk:

1. Outbreaks are periodic and relatively rare, so that most individuals will experience few during a lifetime.
2. Individuals are most likely to gather experience and knowledge from observations in their own stands. As the literature shows, it is inherently possible that a poorly managed stand will escape SPB damage and conversely that a well-managed stand will incur damage.
3. An objective assessment of risk depends upon balanced information of both infested areas and those that escaped infestation.
4. The unpredictability of the SPB ensures that accurate and objective assessments require considerable amounts of data. It is unlikely that an average forest manager will have the resources to make these unbiased observations.

Considering the unpredictability of the SPB, it could also be argued that without these risk assessments and the objectivity they provide, it would be difficult to formulate effective plans for managing SPB damage. For example, since the initiation and growth of an infestation in one area of the forest may lead to damage elsewhere, the SPB is most commonly viewed as a problem that affects human communities rather than just isolated individuals (Coulson and Stephen 2006). Although preventative management (e.g., basal area reduction) cannot guarantee zero damage, it may considerably reduce total damage at the regional scale. In other words, although the unpredictability and spatiotemporal patterns of the SPB may always lead to winners and losers, a community-level approach to SPB management can at least attempt to minimize the number of individuals affected by the SPB. In addition, the SPB is just one of many threats to forests. Like the SPB, most of these (e.g., fire, hurricane, and other biotic agents) are unpredictable and ideally suited to risk assessment. As defined in this chapter, risk involves not just the pattern of SPB damage, but also concepts and quantifications of the damage, both economic and sociological, caused by the SPB. As human interests encroach further into forested areas, they may also affect the values attributed to these forests and the amount of risk people are willing to accept. This is likely to drive increasingly critical decisionmaking that involves an objective, comparable evaluation of all potential forest threats.

These factors make the development of objective, scientific SPB risk assessments essential. The challenge for ecologists and risk assessors is to develop novel models and assessments that address the current and changing needs of forest managers. This depends on continued efforts to collect appropriate data, and the development of modeling methodologies that assimilate this information into useful risk indices and decisionmaking tools.

23

Silvicultural Considerations in Managing Southern Pine Stands in the Context of Southern Pine Beetle

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Abstract

Roughly 30 percent of the 200 million acres of forest land in the South supports stands dominated by southern pines. These are among the most productive forests in the nation. Adapted to disturbance, southern pines are relatively easy to manage with even-aged methods such as clearcutting and planting, or the seed tree and shelterwood methods with natural regeneration. In addition, most species of the southern pines can be managed using the uneven-aged selection method, which maintains continuous canopy cover on the site. Because southern pines grow so rapidly across a wide variety of conditions, stands can quickly become overstocked to the point where competition results in reduced growth, decline in vigor, and mortality—including mortality from infestations of southern pine beetle (SPB). Thinning is an effective silvicultural practice designed to avoid the problems associated with overstocked stands, and can be used in immature sapling stands through mature stands of large trees. When a stand is properly thinned, the crowns obtain more sunlight, root systems get a larger share of soil moisture and nutrients, and trees maintain acceptable rates of growth and individual vigor. The best silvicultural defense against SPB is to manage forest stands so that individual trees are vigorous and stands are not overstocked. Active forest management is important, based on timely thinning treatments and other silvicultural practices appropriate for the local species and site conditions that optimize current stand developmental dynamics, manage species composition, and promote tree vigor and forest health.

Keywords

disturbance
overstocking
silviculture
southern pines
southern pine beetle
thinning
tree vigor

23.1. THE SOUTHERN PINE FOREST RESOURCE

The Southern United States has about 535 million acres (216.5 million ha) of land, of which 214.6 million acres (86.8 million ha) is forested; of that, 202.7 million acres (82.0 million ha) is considered to be commercial timberland capable of producing wood products (Smith and others 2004). This area of forest is about 60 percent of that which existed at the onset of European colonization in 1630 (Conner and Hartsell 2002). Slightly more than half of the commercial timberland in the South is in hardwood-dominated forest types, and the balance—about 96 million acres (38.9 million ha)—is found in southern pine or oak-pine forest types (Smith and others 2004).

23.1.1. Distribution of Southern Pines

The southern pines consist of four major species: loblolly pine (*Pinus taeda* L.), shortleaf pine (*P. echinata* Mill.), slash pine (*P. elliottii* Engelm.), and longleaf pine (*P. palustris* L.). Thirty percent of the forest land area in the South—some 66 million acres (26.7 million ha)—is dominated by two major southern pine forest types. About 52 million acres (21.0 million ha) is in the loblolly-shortleaf forest type, and 14 million acres (5.7 million ha) is in the longleaf-slash forest type; another 30 million acres (12.1 million ha) is classified as oak-pine forest type, in which the southern pines are found in mixtures of varying percentage with oaks (Smith and others 2004).

The loblolly-shortleaf forest type includes pure stands of loblolly pine of natural or planted origin, and mixed stands of loblolly and shortleaf pine primarily of natural origin, in the Piedmont, Atlantic Coastal Plain, the upper Gulf Coastal Plain east of the Mississippi River, and the upper West Gulf Coastal Plain west of the Mississippi River. The type also includes stands dominated by shortleaf pine of natural or planted origin, or by loblolly pine plantations, in the Ouachita and Ozark Mountains in Arkansas, Oklahoma, and Missouri.

The longleaf-slash pine forest type is generally found in pure stands of either slash or longleaf pine of natural or planted origin, with minor occurrence of naturally regenerated stands with both species present.

Oak-pine stands are a minor and varying component of virtually all these pine-dominated forest types across the South. They are usually of natural origin, and there is often consideration given in these mixed stands to managing either for the hardwood component or, more commonly especially on forest industry ownership, to manage for the pine component so as to simplify species composition and to increase pine growth and yield.

23.1.2. The Major Species of Southern Pines

Loblolly pine is found in 14 States, growing from southern New Jersey to East Texas. Its natural range includes the Atlantic Coastal Plain, the Piedmont Plateau, parts of the Cumberland Plateau and Appalachian Mountains, and across the eastern and western Gulf Coastal Plain (Baker and Langdon 1990). Loblolly is the preferred species for plantation forestry in the South, and millions of acres of native mixed pine, pine-hardwood, and hardwood-pine stands across the South have been converted to genetically improved and intensively managed loblolly pine plantations for use in timber and fiber production.

Shortleaf pine is the most widely distributed of the four southern pines; it is found in 22 States, typically in mixture with other pines (especially loblolly) or hardwoods. However, in the Ouachita Mountains of Arkansas and Oklahoma, the species is the only dominant naturally occurring pine (Guldin 2007, Lawson 1990).

Slash pine has the smallest native range of the four species, found from southern South Carolina, through the hills of south Georgia and virtually all of Florida, and west along the lower Gulf Coastal Plain to southern Louisiana. It is not native to the trans-Mississippi, but has been widely planted and direct-seeded in western Louisiana and eastern Texas on cutover longleaf pine sites (Lohrey and Kossuth 1990).

Longleaf pine is native along the lower Atlantic and Gulf Coastal Plains from Virginia to East Texas, and once occupied an estimated 92 million acres (37.2 million ha) of the South. Today, it is much less widely distributed over roughly 3.2 million acres (1.3 million ha) due to cut virgin stands, fire exclusion, and reforestation of cutover areas with loblolly and slash pine (Boyer 1990, Landers and others 1995). However, earnest efforts are under way to restore longleaf pine ecosystems, especially on Federal and State lands such as national forests and lower Coastal Plain military bases.

The four southern pines are occasionally found in association with minor pine species such as spruce pine (*Pinus glabra* Walt.) in the lower Gulf Coastal Plain, pond pine (*P. serotina* Michx.) in the lower Atlantic Coastal Plain, and the pines having a more northerly distribution that are found in the Appalachians: table mountain pine (*P. pungens* Lamb.), Virginia pine (*P. virginiana* L.), pitch pine (*P. rigida* Mill.), and eastern white pine (*P. strobus* L.). Throughout the South, pines are found in intimate mixture with hardwoods, especially the oaks and hickories that comprise the potential natural vegetation communities (Keys and others 1995) that would eventually dominate the forests of the South in the absence of disturbance.

23.1.3. Natural Disturbance in Southern Pine Ecosystems

The southern pines are early-successional species adapted to disturbance events of varying size and scale, especially at larger scales. The climate of the South features a variety of large-scale disturbance events, any one of which can result in the devastation of an existing stand and create open conditions for establishment of a new age cohort of pines. Tornadoes, hurricanes, ice, drought, and fire are all prominent to varying degrees as major and minor disturbance events in the southern forest.

But the importance of the native southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) should not be overlooked in any discussion of disturbance ecology of southern pines. Outbreaks of the SPB can, if unchecked and under the proper conditions, grow to cover thousands of acres, and even if controlled can affect hundreds of acres of pines in any part of the region at any time.

Fire Ecology of Southern Pines

Fire, whether as a result of natural or anthropogenic occurrence, is the single most important ecological element in southern pine stand dynamics and development. Presettlement descriptions of southern pine forests commonly described mature pines with virtually no midstory, and understory plant communities dominated by grasses, annuals, and perennials such that one could easily ride a horse through the woods and not be impeded by vegetation (Hedrick and others 2007).

Before European settlement, there were two dominant sources of ignition of fires in forests of the South—lightning strikes and anthropogenic activity. Lightning is a common disturbance agent in southern forests. A thunderstorm passing through a forested landscape can produce many lightning strikes, any one of which can result in wildfire (Coulson and others 1999b). In addition, pines struck by lightning undergo a physiological response to that event that attracts SPBs to the tree—an important trigger in the epidemiology of infestations (Coulson and others 1983, Coulson and others 1999b).

Anthropogenic use of fire is important both in presettlement and post-settlement times. Native Americans used understory burning to promote hunting and community defense (Guyette and others 2006). Early settlers adopted the practice as well to promote forage for feral and domesticated livestock. No doubt both the Native American and European cultures appreciated the benefits that understory burning provides for control of the ticks and chiggers that infest humans who live and work in southern forests.

Fire is especially important in southern pine ecosystem dynamics. Each of the four southern pine species has developed interesting and unique adaptations to prescribed fire that can result in favorable conditions for seedling establishment and development.

Shortleaf pine is the only one of the four whose saplings will reliably resprout if the crown of the sapling is topkilled (Figure 23.1), a trait that was described as an adaptation to fire early on (Mattoon 1915). Thus, in sapling-sized shortleaf pine stands, a new age cohort develops after fire through resprouting and some added seedfall if a seed source remains nearby.

On the other hand, loblolly and slash pine saplings are quickly and effectively killed by fire, which may explain why these species are thought to be the more mesic of the southern pines. For example, slash pine is found naturally only in the wetter areas of the Atlantic Coastal Plain (Lohrey and Kossuth 1990), and loblolly pine has a reputation also of a species that thrives naturally on moist to wet sites (Baker and Langdon 1990).

Both loblolly and slash pine are abundant and regular seed producers, producing adequate or better seed crops at least half the time. The loblolly-shortleaf pine type in the western Gulf Coastal Plain is arguably the most prolific pine type in North America (Figure 23.2), producing

Figure 23.1—Shortleaf pine sapling resprouting after being topkilled by prescribed fire. Poteau Ranger District, Ouachita National Forest. (USDA Forest Service photograph by Richard Straight)

Figure 23.2—Natural regeneration of loblolly and shortleaf pine beneath a mixed loblolly-shortleaf pine overstory, Crossett Experimental Forest, Ashley County, Arkansas. (USDA Forest Service photograph by James M. Guldin)

adequate or better seed crops 4 years in 5 and having bumper crops with more than a million seeds per acre (Cain and Shelton 2001).

Essentially, the regeneration dynamics for Coastal Plain loblolly-shortleaf pine mixtures and for slash pine are for mature trees to produce enough seed on a sufficiently frequent basis to establish seedlings within any new opening in the forest shortly after it is created, and to have those saplings grow fast enough to survive the next surface fire.

One might speculate that these respective strategies of resprouting vs. reseeding work together in mixed loblolly-shortleaf pine stands of natural origin, and may suggest a reason why shortleaf is retained in the mixture. If a newly established loblolly-shortleaf pine cohort has the opportunity to grow fast enough to escape the next fire, the species mixture would favor loblolly pine, whose saplings grow faster than shortleaf pine. But if a surface fire occurs in a mixed pine sapling stand, the loblolly will be killed and would require a nearby seed source to reseed the area, whereas the shortleaf saplings would simply resprout—a dynamic that might confer an adaptive advantage to shortleaf in circumstances where loblolly would normally outgrow shortleaf.

Longleaf pine has a different strategy entirely, featuring extended irregularity in seed crops and the famous grass stage. While in the grass stage, the seedling emphasizes root growth rather than shoot growth, and the terminal bud is protected from surface fire by the physiognomic pattern of bud scales and needle architecture. In those early years, grass stage seedlings require occasional surface fires to prevent grasses and other understory herbaceous and woody vegetation from suppressing the pines. Those fires also serve to control brown spot needle blight (*Mycosphaerella dearnessi* Barr.) that infects pine needles and that, if uncontrolled, can prevent seedling emergence from the grass stage (Boyer 1979). After several years and under proper conditions, longleaf seedlings break the grass stage and initiate height growth rapidly (Figure 23.3).

Other Disturbance Agents in Southern Pines

Four other disturbance agents are sufficiently important to warrant special mention in southern forests: windstorms, ice storms, drought, and SPB. It is likely that all featured some degree of interaction with fire in presettlement forests, but there is little direct evidence of this.

Windstorms include two very different events. The first and by far the most devastating on a regional basis are hurricanes, which generally occur from June through October. With winds near the eye of a Category 4 hurricane in excess of 130 mph, the devastation wrought upon landfall in Atlantic and Gulf Coastal Plain forest types is tremendous. Stands in the path of the center of the hurricane are virtually certain to be completely lost, and stands in a wider band are also subject to considerable windthrow and breakage. In natural conditions, the degree to which scattered trees survive the storm and subsequent disturbances such as wildfire may determine the future species composition of the area.

Equally devastating on a local basis are tornadoes, which generally occur from April through June. More common in the western part of the region than the eastern, these storms develop during extreme transitions between cold fronts and warm fronts. The windspeeds found in tornados exceed those in hurricanes, with a midscale F3 tornado producing winds of 158-206 mph. Although the area affected by tornadoes is much smaller regionally than hurricanes, the damage from tornadoes can be dramatic locally (Figure 23.4), exceeding hundreds of acres of damage in an F3 event with a majority of trees broken or uprooted along the path of the storm.

Drought is the most insidious of the common disturbance events, and generally contributes to a malaise in forest growth and development that can result in significant effects if sufficiently prolonged. For example, there was a drought of several years' duration in southern forests west of the Mississippi River in the early 1950s, and reports are that mortality of white oak (*Quercus alba* L.) was widespread; recent data suggest that the effects of such droughts can last for decades after the drought has ended, and can predispose forest stands to other disturbance events (Dwyer and others 1995).

Ice storms can be especially damaging in the more northerly distributed forests of the South, especially in mountainous regions. Ice and glaze events are relatively common, and while they generally do not cause widespread devastation across the landscape, stands during certain periods of development seem especially vulnerable (Bragg and others 2003). Accumulations of ice are especially likely to damage pine stands younger than 25 years old, that are densely stocked with low live crown ratios, and that have recently been thinned (Figure 23.5).

The SPB is the single most damaging insect in southern pine forest types. It is known for episodic outbreaks in high-hazard stands that, if unchecked, can expand to cover thousands of acres. Outbreaks of the SPB tend to be more common in the lower Coastal Plain than in the upper Coastal Plain and Piedmont, although recent outbreaks in the southern Appalachians and the Cumberland Plateau suggest that where there are pines in a high-hazard condition, the beetle will find them.

Figure 23.3—Planted longleaf pine saplings between age 5 and 8 at different stages of release from the grass stage. Winn Ranger District, Kisatchie National Forest. (USDA Forest Service photograph by James M. Guldin)

Stand Development in Southern Pines

All four species are generally considered intolerant of shade as mature trees, but shade tolerance is more pronounced at younger ages especially in loblolly and shortleaf pine, both of which can tolerate more overstory shade when young than can longleaf and especially slash pine.

The southern pines also share the interesting attribute of being able to respond to release from adjacent or overtopping competition at relatively advanced ages. This enables the pines to maintain site occupancy under partial disturbance events such as ice storms or wind events. The four species also show

Figure 23.4—Stand conditions after an F3 tornado on 27 November 2005 in a mature even-aged shortleaf pine stand, Winona Ranger District, Ouachita National Forest. Note how the residual stem density approximates the seed cut in the seed-tree reproduction cutting method. (USDA Forest Service photograph by James M. Guldin)

good ability to differentiate in height, which helps minimize extended periods of sapling stagnation. However, stagnation can occur to a certain degree in densely stocked naturally regenerated sapling stands, especially in shortleaf pine stands.

Reproduction cutting methods are designed to loosely emulate a continuum of intensity of natural disturbance. Clearcutting, with its total removal of all overstory vegetation, approximates the most severe stand-replacement disturbances, such as the main path of a tornado or the flare-up of a canopy-destroying wildfire. But few ecological conditions in nature are so severe that all living trees are removed. More commonly, some trees remain following disturbance, and they provide seed to reforest the disturbed area. Reproduction cutting methods that rely on natural regeneration imitate this dynamic directly.

The even-aged seed tree and shelterwood methods approximate disturbance events sufficiently severe that a new regeneration cohort is established across the entire stand. They differ in the number of residual trees remaining on the site and in the provision of shelter by residual trees. In the seed tree method, few overstory trees remain, and microecological conditions for seedlings are essentially the same as if the area were clearcut. In the shelterwood method, more overstory trees remain, and their presence slightly ameliorates the microecological condition for developing seedlings.

The uneven-aged methods approximate disturbance events that open up only part of a stand. Thus, the new regeneration cohort will be found only in those portions of the stand within which the openings are found, rather than across the entire stand. The group selection method emulates disturbance events such as beetle spots or locally heavy windstorms that remove small groups of overstory trees within a stand; regeneration then occurs in that group opening. The single-tree selection method imitates the smallest scale of disturbance—the mortality of one or two mature trees. This creates a small opening marginally sufficient for development of a very small cohort of regeneration, provided that the species being managed is sufficiently tolerant of shade to develop.

Thus, the entire gradient of natural disturbance events, from severe events that give rise to continuous regeneration cohorts across the stand to localized events that give rise to discontinuous regeneration cohorts within the stand, are reflected in the reproduction cutting methods used to naturally regenerate managed stands.

23.2. SILVICULTURE FOR SOUTHERN PINES

Silviculture is defined as the theory and practice of controlling forest composition and development (Smith and others 1997). The practice of silviculture is generally subdivided into three general areas: the regeneration of the desired species from germination through early development, the intermediate treatments or

Figure 23.5—Ice damage from a December 2000 ice storm in a recently thinned poletimber stand of shortleaf pine, Winona Ranger District, Ouachita National Forest. (USDA Forest Service photograph by James M. Guldin)

tending of established stands from immediately after the regeneration phase up to the point of maturity, and the reproduction cutting methods used to harvest a mature stand and concomitantly to establish the succeeding stand.

The individual treatments in the practice of silviculture can fit in several categories: treatment of the forest site, the forest floor, the woody vegetation in the main canopy, the woody and nonwoody vegetation in subordinate canopy positions, or the residues of vegetation. All have some degree of influence in stand development, stand structure, rates of growth, and yield. Different treatments also have different degrees of usefulness in reducing the hazard and the rate of change of hazard in relation to SPB.

A silvicultural system is the collection of individual silvicultural treatments conducted over time to transform a forest stand from its existing condition to a desired future condition. The system is identified by the reproduction cutting method that initiates the new stand, because of the inordinate ecological influence that the initial reproduction cutting creates, especially in the first decade or two after the new stand or age cohort is established (Smith and others 1997).

The silvicultural system encompasses the specific regeneration treatments designed to prepare the site and establish a new generation of seedlings either naturally or artificially, the intermediate treatments designed to promote stand development, and the subsequent reproduction cutting method at the end of the rotation to establish the succeeding stand. Systems can be amended or changed as needed if a given forest landowner decides on different objectives, or if ownership of the land changes hands.

Generally speaking, the silvicultural systems a landowner applies in southern pine stands depend on a host of objectives related to timber and fiber growth and yield, recreation, aesthetics, range, agroforestry, watershed, and other values that combine to satisfy the goals of ownership across the landowner's forest holdings. The kinds of treatments that are prescribed, the intensity with which they are applied, and the timing by which they are implemented can have profound differences in achieving the landowner's goals.

That spectrum of treatments also results in different levels of hazard in a given stand to SPB, and can result in different rates of change of SPB hazard as well. Further, that hazard might change depending not only on what the landowner chooses to do, but also on what adjacent landowners may choose to do in their pine stands.

There is no better set of forest types to practice diverse silvicultural prescriptions than those dominated by the four major southern pines: loblolly pine, shortleaf pine, slash pine, and longleaf pine. The greatest two silvicultural advances of the 20th century were, arguably, the development of genetically improved pine planting stock with which to reforest cutover stands or abandoned agricultural lands, and the development of chemical amendments such as fertilizers and herbicides with which to promote rapid pine growth and discourage the development of woody and herbaceous vegetation competing with the pines (Fox and others 2007).

Concurrently, though, many landowners seek ownership goals that are difficult to achieve using pine plantations. The four southern pine species, again with generally good success, also respond quite well to even-aged and in some cases to uneven-aged silvicultural systems that rely on maintaining some degree of continuous overstory cover, and that rely on natural regeneration rather than planting to reforest the site when a new age cohort is sought (Guldin 2004).

These different silvicultural systems and the tools used to manage them can create very different stand conditions that run the gamut from an age cohort of seedlings of genetically identical origin planted on the same day, to stands having many different ages and size classes on the same acre of land. Thus, the challenge and the fun of being a silviculturist for a landowner is to interpret the landowner's ownership goals using this spectrum of available silvicultural systems across the forested landscape that includes the owner's forest lands, as well as some consideration of what the owner's neighbors are doing.

The science of silviculture is knowing the technical details that underlie the individual practices prescribed in a given stand, in what part that specific prescription plays in the larger silvicultural system for the stand being managed, and in how the landowner's forest lands can be managed to be healthy, sustainable, and productive in the context of the forest landscape within which the owner's lands occur. The art of silviculture is in the details—the ways in which the orchestration of the combined benefits produced among the many individual stands concurrently achieve the landowner's goals.

Excellent summaries of the silviculture of southern pines have been developed over the past 4 decades and are still appropriate references for landowners and the foresters who advise them. Burns (1983) includes general discussions for most of the important forest types in North America, including the southern pines. Overviews of the general principles of plantation silviculture and silviculture of naturally regenerated stands were recently published (Fox and others 2007, Guldin 2004). State-of-the-art summaries of the selection method are also available, one for longleaf pine (Farrar 1996) and the other for loblolly and shortleaf pines (Baker and others 1996).

23.2.1. Reproduction Cutting Methods

Eventually there comes a point in the life of a forest stand where the forester decides to harvest all or part of the overstory, and to obtain a new age class or cohort of regeneration for the future. The success of this process is fundamental to the concept of forest sustainability. The first indicator of sustainability is whether, when a reproduction cutting is made, a new cohort of the desired species is successfully established in conditions that will allow it to grow and develop in an acceptable manner.

Overall, there are two broad categories of reproduction cutting methods: even-aged methods and uneven-aged methods. The even-aged methods (clearcutting, seed tree, and shelterwood methods) result in a new crop of seedlings of proper density distributed uniformly across the entire stand. That new age cohort is then managed through immature stages of development to maturity, and eventually to some predetermined final harvest age generally identified as the rotation age. In these even-aged methods, then, the forester is usually dealing with one age class, but some modifications of the even-aged methods allow for two age classes to be concurrently present either during the establishment of the new cohort or throughout the rotation (Smith and others 1997).

The even-aged silvicultural system applied to establish and manage the new stand is generally identified by the reproduction cutting method used to establish the stand, and calls for a successive series of age- or size-appropriate silvicultural treatments from the point of planning for the new stand through its maturity. Each prescription is applied more or less homogeneously across the entire stand of trees.

The second category of reproduction cutting methods is the uneven-aged methods (single-tree selection and group selection), which are managed under an indefinite time horizon rather than a specific rotation, mediated by use of a regularly occurring cutting cycle that guides the silvicultural treatments in the stand. Uneven-aged stands have three or more age cohorts of trees of the desired species intermingled to varying degrees throughout the stand, from identifiable groups of the same age class interspersed through the stand under the group selection method to a more intimate and unmappable mixture of trees of different ages occurring across the stand in the single-tree selection method. Cutting cycle harvests are used to concurrently satisfy the need for reproduction cutting, to create growing space of a new age cohort, for intermediate treatment of immature trees, and to prepare mature trees for their role as progenitors of new age cohorts in subsequent cutting cycle harvests.

The uneven-aged silvicultural system is usually identified by whether group or single-tree selection is prescribed. Under either method, the prescription is implemented using a repeated series of cutting cycle harvests of appropriate pattern for establishment of the new age cohort. These harvests also serve to conduct concurrent treatments in both immature and mature age cohorts, and to stimulate growth of seed-bearing mature trees.

Even-Aged Reproduction Cutting Methods

Even-aged reproduction cutting methods harvest all or nearly all of the mature trees in the overstory, with the intent of creating a new cohort across the entire stand. The three most common even-aged methods are the clearcutting method, the seed tree method, and the shelterwood method, with variations of each that allow for natural or artificial regeneration, and retention or removal of seed trees as appropriate.

The clearcutting method

In the last half of the 20th century, the predominant application of reproduction cutting methods in southern pine stands across the South focused on one silvicultural system—clearcutting and planting. This focus has been made possible by two great advances during that time—the development of genetically improved planting stock and the advent of herbicide technology for control of unwanted vegetation in planted stands.

The silvicultural system of clearcutting, planting, and associated intensive treating has come to define intensive forest management. Forest industry, nonindustrial private forest (NIPF) landowners, and government agencies have all employed variations of this prescription, and as a result the area in plantations in the South has gone from virtually none to roughly 31 million acres (12.5 million ha) in the last 50 years (Conner and Hartsell 2002).

It is unequivocally true that if one seeks to maximize fiber production, the clearcutting reproduction method followed by plantation establishment using genetically improved planting stock and properly timed herbicide and fertilizer treatments is far and away the best approach to use. In 1995, plantations occupied 15 percent of the forest land in the South but provided 35 percent of the harvested volume (Wear 2002). By 2040, pine plantations will occupy approximately 50 million acres (20 million ha), or 25 percent of the southern forest area. This will represent roughly half of the projected pine-dominated forest area at that time (Wear 2002).

Modern silvicultural practices using clearcutting and planting are extraordinarily efficient. Intensive practices prescribed with careful attention to month and year will produce pine stands that grow from two to three times as fast in early height growth, and up to four times as rapidly in total merchantable volume in the first several decades, as naturally regenerated pine stands in the region (Fox and others 2007).

The dominant application of the clearcutting method is in association with artificial regeneration using genetically improved planting stock, and the practice is the mainstay of forest industry and forestry investment land managers across the South. The typical silvicultural prescription is to clearcut the stand, utilizing as much biomass as can be removed, and then to conduct supplemental silvicultural treatments that dispose of logging slash, eliminate or reduce competing vegetation as needed, and treat the forest floor or mineral soil if necessary. This sets the stage for planting genetically improved pine seedlings selected for rapid growth and other favorable attributes such as stem straightness, small branches, and crowns that photosynthesize efficiently.

Clearcutting is also occasionally used on public lands in the region, with a somewhat less intensive set of site preparation treatments. On national forested lands, the practice has been applied with all of the four major southern pines, generally such that the planted species is native to the site.

It is on public lands where shortleaf pine and longleaf pine plantations are most commonly planted. With the reductions in clearcutting on public lands, most shortleaf plantations are generally older, but are commonly found in the southern Appalachians, the Piedmont, the Ouachitas, and to a lesser extent the Ozarks. On the other hand, there is keen interest in restoration of longleaf pine on the lower Gulf Coastal Plain from Florida to Texas, and one key element of that restoration will involve rehabilitation of understocked stands or clearcutting stands dominated by other species such as slash pine.

Slash pine is not native west of the Mississippi River. However, afforestation with slash pine by planting and direct seeding was important to rehabilitate cutover longleaf stands that had utterly failed to regenerate naturally to longleaf pine after the highgrading of virgin stands in the first half of the 20th century. Today on public lands especially, efforts are under way to convert those slash pine stands outside the native range of the species back to longleaf pine through clearcutting, and planting containerized longleaf pine planting stock is a key to the success of the prescription.

To a lesser extent, similar practice will be increasingly common on industry lands acquired by the Federal government in Arkansas and Oklahoma. Here, the native shortleaf pine stands were converted to loblolly pine by forest industry in the past 4 decades, despite the fact that the Ouachitas are just to the north of the natural range of loblolly pine. Some of those industry lands are now being brought into Federal ownership through purchase and land exchange. Where this occurs, plans are to grow the loblolly to appropriate maturity, then clearcut those stands and convert them back to shortleaf pine through planting. Prescribed burning will then be done a few years after planting to eliminate any naturally seeded loblolly pine regeneration from the sites.

Across both public and private lands, clearcutting has been a controversial practice, mostly because of cutover appearance of recently harvested stands. But there is no question that, silviculturally, clearcutting is a very effective reproduction method that quickly results in the establishment of a new fast-growing stand of species that are sought by land managers and landowners, especially those primarily interested in fiber production and return on investment, and increasingly by those who seek to restore species to sites where no seed source locally exists.

The seed tree method

In the seed tree method, a few mature pine trees of good form, evidence of fruitfulness, and an appearance of windfirmness are retained on the site after harvest to serve as a seed source for the cutover stand. Typically, seed trees are distributed more or less uniformly across the site in such a way that the entire area of the harvested stand is within an acceptable dispersal distance of one or more of the residual seed trees. However, the exact spacing of the residual trees is less important than the attributes of form, fruitfulness, and sturdy appearance.

A reasonable estimate for the number of seed trees depends on tree size, but it is not unusual to reserve 4-10 trees per acre (10-25 pine seed trees/ha), with a corresponding residual basal area (BA) from 5 to 15 square feet per acre (1-3 m^2/ha). The harvest that takes all but the seed trees is called the seed cut, and the subsequent harvest that removes the seed trees is called the removal cut (Smith and others 1997).

The modern application of the seed tree method has nothing in common with the retention of seed trees codified during the cutting of the virgin southern pine forest in the early 20th century. Those laws mandated retention of a few trees per acre after harvest, and led to nothing more than leaving the poorest trees of marginal size to reforest the site, which was largely ineffective.

Under modern prescriptions, proper application of the seed tree method includes the retention of trees with good form, acceptable branch characteristics, and evidence of past seed production. These attributes are easier to determine in some species than others. For example, in shortleaf pine, cones tend to persist for a number of years after seed are shed (Lawson 1990), whereas loblolly and longleaf pines tend to drop their cones after seedfall (Baker and Langdon 1990). In shortleaf pine stands, marking crews must inspect tree crowns to find evidence of past fruitfulness, whereas in loblolly or longleaf pines, marking crews must look on the forest floor beneath a tree to judge whether it is a good cone producer.

The biggest limitation in applying the seed tree method is ensuring that the residual trees can produce enough seed to adequately reforest the site. Of the four major southern pines, the seed tree method works best with loblolly pine in the West Gulf region, where adequate or better seed crops are produced, on average, 4 years in 5, and where bumper crops produce more than a million seed per acre (Cain and Shelton 2001). Slash pine, which also tends to produce abundant seed, can also be managed quite easily with the seed tree method.

Conversely, seed production in longleaf pine is highly periodic, and use of the seed tree method is rarely successful with this species. Empirical evidence suggests that the seed tree method can also be made to work in shortleaf pine, which falls between loblolly and longleaf in periodicity of seedfall (Guldin and Loewenstein 1999).

The archetypal example of the seed tree method in application to southern pines has been described for the mixed loblolly-shortleaf pine type in the upper West Gulf Coastal Plain (Zeide and Sharer 2000), and captures the silvicultural system widely used by a major forest industry landowner in the region during the last 4 decades of the 20th century. Prescriptions called for retaining 10-20 square feet per acre (2.3-4.5 m^2/ha) of BA of trees with good form and with dbh of 16-20 inches (40-50 cm). The seed trees were usually taken in a removal cut 3-5 years later, which produced an operable harvest of 500-1,500 basal feet per acre (2.9-8.8 m^3/ha) of sawlogs.

Removal of the seed trees also thinned the excessive pine regeneration that was common in this forest type. The first commercial thinning occurred between the ages of 17 and 20 years, leaving about 70 square feet per acre (16 m^2/ha). The next thinning, at age 25, included some small sawlogs. Subsequent thinnings on a 5-year cycle averaged 2,000 basal feet per acre (11.7 m^3/ha) in each thinning. The final seed cut produced between 5,000 and 7,000 basal feet per acre (29.2-40.8 m^3/ha). Thus, growth for the rotation averaged more than 300 basal feet per acre (1.75 m^3/ha) annually.

Late-rotation thinning also released the crowns of the future seed trees, which increased cone and seed production for subsequent reproduction cutting. Regularly scheduled prescribed fires on a 3-5 year cycle, coupled with hardwood control on a 5-10 year cycle, promoted visibility within the stand that enhanced subsequent thinning treatments, and if carried through the end of the rotation, reduced the need for intensive site preparation in the subsequent rotation.

The shelterwood method

The shelterwood method is similar to the seed tree method in that residual trees are retained to reforest the site after harvesting occurs, but more trees are retained. In their description of the shelterwood method, Smith and others (1997) include three specific elements: the preparatory cut, the seed cut, and the removal cut.

The preparatory cut is designed to enlarge the crowns and root systems of the future seed trees so as to optimize their ability to produce cones. Late-rotation thinning commonly conducted in pine sawtimber stands generally fulfills the intent of the preparatory cut. But if the stand has not been thinned for an extended period, a preparatory cut 5-10 years prior to the seed cut to a residual BA of 75-90 square feet per acre (17.2-20.7 m^2/ha) is warranted. During the seed cut, 15-30 trees per acre (35-75 trees/ha), having 20-40 square feet per acre (4.5-9 m^2/ha) of BA, are selected for retention (Figure 23.6). Favorable traits for residual pines include stem form, windfirmness, and evidence of past seed production. The removal cut harvests the seed trees after the new stand has developed past the point of risk from seedling-related mortality.

One operational advantage of the shelterwood over the seed tree method in southern pines is that the volume of the residual trees in the shelterwood is greater than that of the seed tree method, and thus is more likely to attract interest from loggers during the removal cut. Conversely, if carelessly done, logging during the removal cut can adversely affect stem density of the regeneration, especially at higher residual BAs

Depending on management objectives, the final harvest may be deferred for half or more of the rotation length, resulting in a two-aged

Figure 23.6—Several years after the seed cut in a shelterwood reproduction cutting method applied in a shortleaf pine stand, Wimble Ranger District, Ouachita National Forest. (USDA Forest Service photograph by James M. Guldin)

stand; this method is referred to as an irregular shelterwood (Helms 1998, Smith and others 1997).

Under traditional application of the shelterwood method, microclimatic ecological conditions are ameliorated relative to those found in fully open conditions (Valigura and Messina 1994). Thus, one reason to apply the shelterwood is to moderate conditions that might be too harsh for seedlings to survive under a clearcut or a seed tree prescription. But as a practical matter, the shelterwood method is popular for species in which seed production is erratic or unreliable; the added numbers of seed trees that remain in the shelterwood often make the difference between adequate stocking and less-than-adequate stocking.

Among the most prominent examples of the shelterwood method in southern pines is the experience with longleaf pine developed for the lower Atlantic and Gulf Coastal Plain (Figure 23.7). Longleaf pine has the deserved reputation of being the most difficult of the southern pines to regenerate naturally, but clever research has identified the practices needed to naturally regenerate the species using the shelterwood method (Boyer 1979, Croker and Boyer 1975). Seed production in longleaf is optimal when the seed cut retains 30-40 square feet per acre (6.9-9.2 m^2/ha) of BA (Maple 1977). Fewer trees result in fewer cones per unit area, and more trees do not enhance cone production.

Figure 23.7—Longleaf pine saplings established after the seed cut in the shelterwood method. Savannah River Forest Site, Aiken, South Carolina. (USDA Forest Service photograph)

Prescribed fires are essential to control brown spot needle blight, and thereby to release seedlings from the grass stage (Boyer 1979). However, seedling mortality is highest beneath the crowns of residual trees because the buildup of pine straw promotes prescribed fires sufficiently intense to kill them. All of these factors have led scientists to conclude that the need for available growing space, the need for frequent prescribed fire, the optimal development of cones in the canopy, and the ability to store seedlings in a seedling bank beneath the overstory of longleaf pine could be achieved using the shelterwood method.

Uneven-Aged Reproduction Cutting Methods

Uneven-aged methods harvest a small portion of the mature and immature trees in the stand, with the intent being to promote the growth of the trees that remain, as well as to encourage regeneration establishment and development in the openings that are created from the harvest of the mature trees. The two most common variants of uneven-aged reproduction cutting methods are single-tree selection and group selection, which vary largely based on the size of the opening created during the harvest and the manner in which subsequent harvests are made.

Applying uneven-aged reproduction cutting methods in species that are intolerant seems counterintuitive, but the earliest successful examples of the selection method were in pines. The Dauerwald in Germany (Troup 1952) was implemented to convert plantations of Scots pine (*P. sylvestris* L.) to a more naturalistic system, and the improvement selection method was developed in Arizona (Pearson 1950) to meet unique stand conditions in ponderosa pine (*P. ponderosa* Dougl. ex Laws.).

In the South, uneven-aged silviculture has been used in the region since the 1950s by family lumber companies and forest industry landowners. The longest record of success with the method has been in west Gulf Coastal Plain loblolly-shortleaf pine stands in southeastern Arkansas (Baker 1986; Baker and others 1996; Guldin 2002, 2004; Guldin and Baker 1998; Reynolds and others 1984), with other long-term demonstrations reported in Mississippi (Farrar and others 1989) and southwestern Arkansas (Farrar and others 1984). Uneven-aged methods have also been used in longleaf pine in Florida and Alabama (Brockway and Outcalt 1998, Farrar 1996, Mitchell and others 2006), and in shortleaf pine stands in the Ouachita Mountains (Guldin and Loewenstein 1999, Lawson 1990).

There has been virtually no research on uneven-aged reproduction cutting in slash pine, but the group selection method has been suggested (Langdon and Bennett 1976), and other methods suitable for longleaf pine should also work with slash pine. In short, the selection method can be used in southern pines if attention is paid to marking, regeneration, and stand structure (Guldin and Baker 1998).

By definition, uneven-aged reproduction cutting methods create discontinuous stand conditions. They provide a temporally and spatially transient distribution of logging slash and debris within the stand, resulting in a heterogeneous distribution of volatile fine fuels. This reduces the need to treat fuels, since there is less of a chance that the entire stand will have fine fuels throughout, but it also makes it difficult to treat those fuels if one should decide to do so. The added complication is that regeneration is being recruited in a discontinuous spatial pattern as well, and recruitment is repeated following every cutting-cycle harvest.

Stand-wide treatments such as prescribed burning are difficult to implement in uneven-aged stands. On the one hand, fuels are sufficiently heterogeneous to confound uniform fire effects and fuels treatment. On the other, the logging debris is concentrated in the openings where the desired regeneration is found, and the saplings won't survive the fire. More research is needed to better understand the degree to which uneven-aged stands can be managed with fewer age cohorts obtained every 2 decades rather than 1, which might provide a window during the second decade when prescribed burning would not kill the youngest age cohort.

The single-tree selection method

The single-tree selection method is still occasionally used to manage for large high-quality pine sawtimber. The standout experience over 7 decades with the Farm Forestry Forty demonstrations at the Crossett Experimental Forest in south Arkansas had its origins in the rehabilitation of understocked stands (Baker and Shelton 1998) and was imposed using a simple marking rule—cut the worst trees and leave the best, regardless of diameter or pattern of occurrence. Stands that had initially been understocked recovered to full stocking within 2 decades (Figure 23.8).

Figure 23.8—Classic uneven-aged stand structure after 69 years of implementation in west Gulf Coastal Plain loblolly-shortleaf pine stands, Crossett Experimental Forest, Ashley County Arkansas. (USDA Forest Service photograph by James M. Guldin)

Details of the implementation of the selection method in these mixed loblolly-shortleaf pine stands have been outlined elsewhere (Baker and others 1996, Guldin 2002, Guldin and Baker 1998), and serve as appropriate mensurational guidelines for any of the intolerant southern pines managed using either volume regulation with a guiding diameter limit or structural regulation using the BDq method. Similar guidelines have been developed explicitly for longleaf pine (Farrar 1996, Guldin 2006).

Expressed in the customary units of measure used in the United States and specifically in field forestry applications nationwide, stands are marked every 10 years to leave about 5,000 basal feet per acre (29.1 m^3/ha) of volume in 60 square feet per acre (13.8 m^2/ha) of BA of the best trees across all size classes with about 45 square feet per acre (10.3 m^2/ha) in sawtimber-sized trees and the balance in smaller size classes. The residual BA should include the best looking trees, and the poorer trees should be harvested.

It is feasible to operate on a 10-year cutting cycle if stands have annual growth rates of approximately 200 basal feet per acre (1.2 m^3/ha) and 2 square feet per acre (0.5 m^2/ha) of BA, which give operable cutting cycle harvest volumes of about 2,000 basal feet per acre (11.7 m^3/ha) every 10 years. Thus, the stands grow back to about 7,000 basal feet per acre (40.8 m^3/ha) of volume and 80 square feet per acre (18.4 m^2/ha) of BA prior to the subsequent cutting cycle harvest. All four of the major southern pines meet this rate of growth, and Coastal Plain loblolly and slash pine stands exceed it.

The scarification from logging is usually sufficient to expose a mineral soil seedbed for optimum germination and establishment of pine seedlings. However, site preparation treatments targeted to control competing vegetation are difficult to do; as a result, periodic herbicide treatment to control hardwoods is highly recommended (Baker and others 1996). One effective hardwood control treatment per decade, generally a year or two after a cutting cycle harvest, is usually sufficient to suppress fast-growing hardwood sprouts so that the slower growing pine seedlings are not overtopped and shaded out.

It is difficult to firmly conclude that the single tree selection method will be successful in converting even-aged pine and pine-oak stands to balanced uneven-aged structure because the process will require several cutting cycles to achieve. Uneven-aged stands are defined as supporting three or more age classes (Helms 1998, Smith and others 1997), and balanced stands probably have closer to six or eight different age cohorts separated in age by a decade or two from one to the next.

When converting an even-aged stand to uneven-aged structure, a major goal of the first entry is to obtain desired regeneration within some parts of the stand so as to begin the process of recruiting new age cohorts as soon as possible. That is best accomplished by marking the stand to leave a variable pattern of residual stem density and BA, which creates locally understocked conditions in parts of the stand within which regeneration might become established.

A common problem in the first cutting cycle harvest of an even-aged to uneven-aged conversion is marking the stand with insufficient attention to spatial heterogeneity. If marking crews have experience thinning even-aged stands, they are prone to mark the first cutting cycle harvest as a free thinning conducted with attention to a uniform distribution of trees across the stand, which fails to create an appropriate degree of spatial heterogeneity within the stand. This can delay the establishment of the first new age cohort in the stand, which adds a cutting cycle's worth of time to the period of conversion.

The biggest disadvantage of the selection method in intolerant southern pines is the management commitment required to maintain proper stand structure, especially with single-tree selection. The concept is to manage size classes rather than age classes, relying on the assumption that diameter approximates age in stands with three or more age classes. To maintain adequate sunlight in the understory for development of the seedling and sapling classes, the overstory and midstory diameter classes of the stand must be deliberately maintained in a slightly understocked condition.

Most uneven-aged stands of southern pines grow from 2 to 3 square feet per acre (0.5-0.7 m^2/ha) annually, and regeneration becomes suppressed beneath a stand carrying roughly 75 square feet per acre (17 m^2/ha) or more. Cutting cycle harvests usually leave between 45 and 60 square feet per acre (10.3-13.8 m^2/ha) immediately after harvest, which suggests that cutting cycle of 10 years or less will be needed to maintain acceptable understory development.

If timely cutting cycle harvests are not repeatedly maintained, the understory development needed to maintain stand structure will be lost. This will lead to a reversion of the midstory and overstory crown classes to a homogeneous canopy profile more typical of a late-rotation even-aged stand, rather than the heterogeneous canopy profile that characterizes a well-regulated uneven-aged stand.

The group selection method

In the group selection method, prescriptions call for the first cutting cycle harvest to create an initial set of group openings and to conduct the equivalent of a light low thinning in the matrix between the group openings. Operational implementation of group selection in this region usually results in the group openings being used as logging decks, with the result being that they are heavily scarified and become excellent seedbeds for establishment of pine reproduction.

If needed, release treatments using individual stem application of herbicide are prescribed to control the fast-growing hardwood sprouts competing with the slower growing pine seedlings. These treatments are usually conducted only within the group openings because the main effort to secure regeneration is within the openings rather than in the matrix between the openings.

Another reason some practitioners prefer group selection to single tree selection when converting even-aged stands to uneven-aged stands is the efficiency of administrative operations. Follow-up treatments such as individual-stem herbicide applications or regeneration surveys are easier to conduct under group selection where the only area to be treated is the group vs. single tree selection where the entire stand must be evaluated.

Finding the way to the group opening can be simplified using a good sketch map, or by locating the opening with a handheld geographic positioning system receiver. Administratively, follow-up treatments such as cleaning or precommercial thinning should be targeted specifically to the openings, an easy process to work into operational contracts using maps or geographic locations of the openings where treatments are to be conducted.

On the other hand, there has been virtually no experience in the South with long-term repeated application of group selection to determine whether the group identity can be retained in the long run so as to control stand operations indefinitely as in an area regulation context. If not, the group selection methods will probably gravitate more toward a single tree selection method as multiple age cohorts are established and stand structure becomes more balanced.

The group selection method offers ecological advantages in managing the intolerant southern pines as well (Figure 23.9). The relatively open conditions found in group openings resemble the early seral conditions that are best for regeneration establishment and development in the southern pines, and this would further suggest that larger group openings rather than smaller ones would be more favorable (Fischer 1980).

Figure 23.9—Longleaf pine seedling and sapling development in a group opening under the group selection method, Winn Ranger District, Kisatchie National Forest. (USDA Forest Service photograph by James M. Guldin)

The openings created using group selection can be made without residual trees, relying on existing advance growth or natural seedfall from adjacent trees or by supplemental planting within the group opening. Retaining some residual trees at shelterwood BAs within group openings is also an option for longleaf pine (Farrar 1996, Guldin 2006), and would probably work nicely in shortleaf pine as well.

The major disadvantage to group selection is that the methods works well early in the installation of group openings, but are difficult to maintain over repeated cutting cycles without strictly adhering to an area-based regulation system—which may fall more into the realm of an even-aged patch clearcutting system rather than an uneven-aged selection system. That is not important to the trees, but might be important to managers if commitments have been made about the proportions of even-aged vs. uneven-aged area being managed across an area, as is often the case in national forest management plans.

23.2.2. Regeneration Treatments

Both natural and artificial regeneration can be used to regenerate pine-dominated forests in the South. Natural regeneration refers to methods designed to take advantage of the natural seedfall produced by trees in the forest through treatments that promote seed production, prepare the site to be receptive to seedfall, and nurture the establishment and development of the new seedlings that occur. Artificial regeneration refers to the deliberate collection of seed, either from trees growing in the wild or, preferably, from a seed orchard established expressly for the purpose. Those seeds are then handled in one of two ways—scattered as-is on the site through a practice called direct seeding, or planted under controlled nursery conditions to produce seedlings for outplanting in the field.

Artificial Regeneration

The vast majority of silvicultural prescriptions in pine stands on forest industry land or intensively managed forestry investment ownerships in the South rely on clearcutting, followed by intensive mechanical site preparation, herbicide and/or fertilizer application, and planting genetically improved nursery-raised pine seedlings at predetermined spacing. Coastal Plain and Piedmont sites across the South are highly suited to this practice because of gently rolling terrain. This supports conditions suited to mechanized harvesting operations, efficient and effective site preparation treatments, and easy access either for hand planting or machine planting.

Genetically improved planting stock is the mainstay of the southern pine industry in the South. The high-grading of forests in the South at the turn of the 20th century had, among other effects, an extraordinary removal of genetic material in the harvested trees. High-grading involves removing the biggest and best trees and leaving the worst.

There is a strong association of genetic quality of trees with growth rates and size on a given site especially in even-aged stands, where if all trees start at the same time, the largest in diameter and volume after a period of time are likely to have favorable genetic attributes that promote growth and vigor on the particular site where they are found. The widespread high-grading of the biggest and best trees across the region unquestionably had deleterious effects on the prevailing genetic quality of all of the southern pines in the South.

However, southern pines have a broad genetic base (Dorman 1976), and the forests that recovered from that high-grading still retained a wealth of genetic potential. Growth of the new stands that accidentally followed high-grading, as well as the response of trees that escaped the high-grading harvests of the day, provided a biotic refugium of genetic material that scientists in the middle of the last century were able to tap using the principles and practices of forest genetics, a quantitative field of study that concurrently required a highly advanced understanding of pine tree biology and physiology.

Careful field selections of superior trees across the South and careful breeding trials using the many families represented by those trees have resulted in the identification and widespread application of a variety of improved families for each of the southern pines. These are maintained in seed orchards across the South where seeds are produced and collected. Seeds are then planted under controlled nursery conditions, and seedlings are carefully tended for one growing season in the nursery. In the dormant season, seedlings are lifted from the nursery beds, stored, and transported to the field sites under highly controlled conditions, and outplanted on recently harvested sites that have been site-prepared appropriately for planting.

Most harvested sites on the Piedmont and Coastal Plain are able to be planted with relative ease (Wakeley 1954). Effective planting requires a number of steps to prepare the site prior to planting, and the number of these steps varies according to site conditions and the judgment of the forester about the ability of seedlings to survive.

At the least, site preparation involves the reduction or removal of harvest residues and other debris from the harvest of the previous stand. Removal of varying levels of competing woody, perennial nonwoody, and herbaceous vegetation through mechanical treatment, burning, or herbicide application is commonly done depending on the degree of vegetation control that is sought. Supplemental treatment of the forest floor or mineral soil is often prescribed if needed to ameliorate compaction or to alter microtopographic relief on the site for some reason. Fertilization is also used if needed to ameliorate or restore nutrient content of a site, or to boost early height growth of seedlings (Allen 1987).

If site preparation is sufficiently complete to allow machine access to a site, or if abandoned agricultural fields are being reforested, planting can be done by machine, typically a small crawler tractor or skidder that pulls a planting machine with a plow that creates a furrow, a cab for the field worker to sit and insert the seedling into the furrow, and a set of coulter wheels to close the furrow.

Hand-planting using a dibble is far more commonly used across the South, for the simple reason that sites are typically not clean enough to allow access to the equipment for machine planting. Planting crews can better negotiate the typical harvested site than the machine.

Direct seeding is occasionally used to reforest cutover sites. The heyday of direct seeding was the middle of the last century, when vast areas of the South, especially in the lower west Gulf Coastal Plain, remained unforested after harvest of virgin stands of longleaf pine (Derr and Man 1971).

In some of the mountainous terrain in the South, planting after clearcutting is not a trivial matter because of the high stoniness of the soils. The Ouachita Mountains of west-central Arkansas and eastern Oklahoma are arguably the most difficult planting environment in the South because of the stoniness of the thin soils that only marginally cover the underlying jumbled geological substrate throughout this rugged region. Hand-planting is tiresome, inefficient, and impractical because of the difficulty workers have working around the surface and subsurface rocks using a dibble or other tool.

It's virtually impossible to make a hole large enough for a seedling with only a hand tool.

In addition, late summer on a south-facing ridgetop in the Ouachitas presents such hot and dry microclimatic conditions for newly planted seedlings that plantation survival rates without supplemental site preparation averaged roughly 50 percent (Walker 1992), and some plantations simply did not survive the drier growing seasons with acceptable stocking.

Two changes were made in reforestation prescriptions to enhance seedling survival in the Ouachita Mountains. The first was to grow a larger seedling in the nursery that had previously been used (Brissette and Carlson 1992), which alters root-shoot biomass relationships favorably to enhance survival. This has been an increasingly common practice in the past 15 years for both pines and hardwood species in the South.

The second was to enhance the planting environment for the seedling using a site preparation treatment called ripping or subsoiling. This consists of using a bulldozer with a vertical steel bar attached to it to essentially plow a furrow 12-18 inches deep in the rocky hillside soil during the late summer of the year prior to planting, a practice that alone increased seedling survival by 10-30 percent (Walker 1992).

Ripping works in several ways. First, it breaks through surface rocks and provides roots with access to subsurface soils that retain moisture longer than surface soil layers. Second, rainfall dislodges soil particles from the sides of the furrow to the bottom, filling the ripped furrow with several inches of soil fines, into which the seedlings are planted in the dormant season. That small amount of microcolluvium provides an enhanced rooting medium for the seedling, allowing its roots to grow more quickly into the subsoil, and thus reduces the risk of mortality during the summer months.

Natural Regeneration

Given the interest and effectiveness of planting as a means of reforestation in the Southern United States, one might think that planting is required to properly manage southern pines. But this is not the case. All four of the major southern pines can be managed using natural regeneration methods.

Natural regeneration has particular advantages for the private forest landowner because it is far less costly to establish a new stand using natural regeneration than planting, especially using the modern planting prescriptions that include mechanical treatment followed by herbicide application and fertilization. A new stand can be established using natural regeneration for 10-25 percent of the cost of establishing a new plantation. Many landowners find this an attractive alternative.

The added benefit of natural regeneration is that residual seed trees are retained on the site after harvest, especially when using the shelterwood or selection methods. The ability to obtain timber revenues from a stand and yet have the stand retain continuous forested cover is highly sought by many landowners.

Natural regeneration can be obtained in any number of ways. The most common are through direct deposition of seed from trees on a recently harvested site, germination of seed stored in the forest floor, response of seedlings that have become established in advance of harvest, or stems that sprout after being cut or damaged in logging. The pattern followed by a given species varies, and depends upon the frequency of adequate or better seed crops.

Loblolly and slash pine, with their frequent seed crops, are the most easily regenerated of the southern pines, using the simple tactic of having residual seed trees cast seed in the autumn in recently harvested stands that have been properly site-prepared so as to expose mineral soil, which is the best seedbed upon which seed can germinate and become established.

The tactic for longleaf pine involves more attention to monitoring seed trees in late spring so foresters can get advance warning of an impending good seed year (Boyer 1979), which is relatively rare in longleaf pine. That triggers extra effort in site preparation, especially prescribed burning in units where regeneration is sought, to prepare a suitable seedbed. But with the grass stage of longleaf, one must plan for several years of nurturing seedlings to the point where they escape the grass stage and initiate height growth. All in all, the regeneration dynamics in longleaf pine are far more complicated than in loblolly and slash pine—which may help explain the dreadful decline in the natural range of the species in the early part of the 20th century.

Fully stocked shortleaf pine stands are not reliable seed producers. In the Ouachita Mountains, studies show 3-5 adequate or better seed-crops per decade, with an average of 100,000 seed per acre (247,000 seed/ha) annually (Shelton and Wittwer 1996, Wittwer and others 2003). These studies also report considerable geographic variation in seedfall, with higher amounts in the eastern Ouachitas and lower amounts in the western Ouachitas.

The sprouting habit of shortleaf pine might be useful in silvicultural applications in the context of pine regeneration accumulation, where foresters might rely upon both new seedlings and sprouts from established sapling rootstocks to regenerate a stand (Guldin 2007). A properly timed surface fire in a stand with some existing shortleaf pine saplings will result in topkilled seedlings that subsequently resprout, and will also create exposed seedbed conditions favorable to germination of new seedlings. Repeated fires of proper intensity should result in a bioaccumulation of pine seedlings and sprouts that serves essentially as a stored seedling bank ready to be released as a new age cohort after a natural disturbance event affecting the overstory—or after a properly timed reproduction cutting.

Site Preparation Treatments

Site preparation consists of the different kinds of treatments used to prepare the understory of the stand or the forest floor so as to promote the germination, establishment, and growth of the desired species. The intent of site preparation is to create microclimatic, edaphic, or physiographic conditions on the site that benefit establishment and development of seedlings and saplings of the desired species.

Site preparation typically falls into three classes of treatments: treatment of the slash remaining after reproduction cutting, control of competing vegetation, and treatment of the forest floor (Smith and others 1997). The goal of site preparation treatments is to reduce logging slash and competing vegetation, and to prepare the seedbed. Usually, the intensity of treatments prescribed depends on whether natural regeneration or planting is to be used, with more intensive site preparation activities usually being conducted for plantation establishment. In even-aged reproduction cutting, harvest activity removes all of the commercial timber, and the noncommercial residual biomass is removed by mechanical felling (shearing, chopping, or chainsaw felling), sometimes concentrated by piling, and then either broadcast burning or burning of piles is conducted to eliminate slash from the site. If needed, ripping usually follows again in late summer, with planting feasible in the following spring.

Bedding is an increasingly common practice as a tool for site preparation to rehabilitate soils from compaction during logging, and to provide a more stable soil structure for establishment of new plantations. The process involves the use of specialized equipment to create the bed, which then lies fallow for several months prior to planting (Figure 23.10).

Figure 23.10—Bedding as a final step in site preparation prior to planting on an upper west Gulf Coastal Plain site in Bradley County, Arkansas. (USDA Forest Service photograph by James M. Guldin)

Treatments of the woody and nonwoody vegetation are often species-specific. Some are intended to promote the development of the best trees of the desired species by removing more poorly formed trees of the same species, or to better regulate stem spacing so that tree crowns of the best trees are free of intraspecific competition. Others seek to remove different species with aggressive growth patterns or foliar canopy distribution, such as sprouting species when seedlings of a different species are sought.

In southern pines, two kinds of control of competing vegetation are typically practiced, and they commonly depend upon whether artificial or natural regeneration is used. The intensive site preparation applied in plantations prior to planting generally eliminates any residual woody vegetation, but herbaceous vegetation can impede seedling development if not controlled with herbicides.

With natural regeneration in southern pines, control of competing vegetation typically means controlling hardwoods, especially sprouting hardwoods that aggressively compete with seedling or sapling pines. This can be done with mechanical means, such as by cutting, with herbicides applied directly to competing vegetation, or with a broadcast herbicide timed to affect hardwoods that are still actively growing late in the growing season after pines have become dormant (Figure 23.11).

Soil displacement as a result of site preparation is a concern for cumulative watershed effects of silvicultural activity. Prescriptions which require raking, pushing, or dragging logging debris into rows or piles cannot be accomplished without some degree of soil movement. The less of this activity that is prescribed, the less of a problem there will be with soil movement. Ripping is designed to deliberately promote soil movement so rainfall can wash soil particles from the sides of the rip into the furrow, thereby creating an ideal planting medium and increasing the survival of planted seedlings. Cumulative watershed effects can be minimized by ripping along the contour, by creating periodic discontinuities of the rip along the contour so flow of water within the rip is interrupted, and by stopping the ripping before sensitive watershed areas such as stream zones are encountered.

Foresters see advantages in using prescribed fire as a site preparation tool both before and after harvest. Prior to harvest, burning is best conducted in spring or fall as a tool to prepare the seedbed for natural seedfall and, in shortleaf, to promote resprouting. If used after harvest, burning is used in late summer to dispose of slash often after it has been raked into piles. It

Figure 23.11—Effects of an August herbicide application for hardwood control in uneven-aged loblolly-shortleaf pine stands on the Crossett Experimental Forest, Ashley County, Arkansas; the stand to the left of the fireline was treated, the stand to the right was not treated. (USDA Forest Service photograph by James M. Guldin)

is not wise to use prescribed burning for site preparation before harvest during summer months or after harvest if a residual stand is in place because the heat of the fire might kill the residual stand.

When using uneven-aged silvicultural systems, site preparation is easier to impose under group selection rather than single tree selection. The reason is that regeneration in group selection is only expected in the groups, so site preparation can be concentrated in the groups to achieve the desired effect. Moreover, the groups are often located on a map, which makes it easy for field crews to work efficiently. In single tree selection, regeneration is often scattered across the stand, and there is no way to advise field crews where to go to apply the proper site preparation method. As a result, the entire stand must be examined, which results in inefficient fieldwork.

23.2.3. Intermediate Treatments

Intermediate treatments are intended for application in immature pole-sized or sawtimber stands. The goal of these treatments is to optimize the development of trees in the existing stand rather than to promote new regeneration (Smith and others 1997). Three basic practices comprise the bulk of intermediate silvicultural treatments for the southern pines: release, thinning, and prescribed burning. All have effects to be considered in silviculture because some of the byproducts of intermediate treatments are often of marginal commercial value.

Release Treatments

Release treatments are intended to promote development of the desired species by removing competing species that threaten to suppress individuals of the desired species (Smith and others 1997). In the southern pines, this usually means removing small hardwoods or herbaceous plants competing with small pines that are less than 10 years old. Release can be done using either chemical, mechanical, or ecological methods. Herbicides offer the most permanent solution to the elimination of competing vegetation because both shoots and roots of the hardwoods are killed and there is no resulting resprouting.

When one seeks a more permanent approach to sprout control through cleaning, weeding, or release treatments, the best is the use of herbicides designed to kill both the tops and the roots of the sprouts. Aerial application of herbicides is effective when the goal is to control hardwoods competing with pines; a number of chemicals and application methods exist that allow for control of hardwoods with minimal effect on pines. For example, late-summer herbicide application targets the seasonal window when hardwoods are still photosynthetically active but pines are dormant. This concentrates the herbicidal effect on the hardwoods rather than the pines in a way that allows stands to be treated with a single treatment that is easy to apply over large areas either by helicopter or skidder.

Individual-stem treatment methods are more labor-intensive but have several advantages in specificity of target application and minimized nontarget effects. These treatments are usually done in one of two ways: through mechanical felling of a tree with hand tools followed by applying herbicide directly to the cut stump or by using a backpack sprayer to apply herbicide directly on the foliage of the tree targeted for removal. Although these methods are labor-intensive, they minimize the volume of herbicide applied across a stand, and are specific to a target tree rather than a target species—meaning that they can be used in pine-hardwood, hardwood-pine, or hardwood stands to release a desired tree from competitors that will impede its development. These differences in application often reflect ownership differences as well; the broadcast methods are more typically conducted on private lands, and the individual-stem applications are more common on public lands.

The cumulative effects of herbicide applications are considerably lower than decades ago. Modern herbicides are developed to act specifically on plant metabolism by inhibiting photosynthesis or inhibiting the synthesis of amino acids that are limited to plants. Thus, they have much lower nonplant effects than herbicides used in the past. A short half-life in the environment is also a desirable attribute. Watershed effects are generally limited to the movement of soil solution containing the herbicide prior to its degradation in the environment, and by the general chemical activity of the inactive ingredients of herbicide formulations such as carriers and surfactants. The common safety precautions used in applying herbicides should be applied to limit cumulative watershed effects, such as application setbacks from sensitive areas, no direct application to streams, and attention to environmentally safe loading and cleanup procedures

But achieving the silvicultural objective of releasing pines from overtopping hardwoods may not necessarily require killing the entire hardwood; topkilling alone (in which the plant subsequently resprouts) may provide a sufficient elimination of competition, allowing the pine to gain the upper hand competitively. Both mechanical and prescribed burning treatments fit this pattern. They have been increasingly used on national forest lands in the region as a substitute for herbicides (Guldin and Loewenstein 1999), which are often unpopular with the public. Mechanical treatments include cutting or felling the tree, either with a sharp-edged hand-held tool such as a machete or axe, or a power tool such as a small circular saw or a chainsaw. The treatment is usually done by contract crews who specialize in this work and are efficient in conducting it.

Prescribed burning in young stands for release requires an experienced burning crew and a cool fire because of the risk of excessive heat killing the pines. Backing fires ignited using hand tools in the coldest months of the dormant season is a good combination of intensity and timing to apply in these stands. If properly done, there is an added benefit—the stand will not carry a fire later in the growing season. Thus, conducting a series of prescribed burns in all of the regeneration areas within a large watershed in January of a given dormant season is a good way to protect them when that watershed is burned several months later using aerial ignition (Figure 23.12).

Thinning

Thinning is a treatment conducted in immature and mature stands to reduce stem density of trees primarily by removing trees of poor quality, form, or vigor, or that are otherwise at risk of density-dependent mortality. These activities are intended to promote the vigor of the trees that remain and thereby improve stand growth and forest health (Helms 1998). Thinning can be conducted using one of several methods, which are outlined in Helms (1998) and explained in considerable detail in Smith and others (1997).

Low thinning or thinning from below removes trees in the lower part of the canopy to favor those in the upper canopy. Crown thinning or thinning from above removes dominants and codominants of comparatively poor form or quality to favor better dominants and codominants. Selection thinning (not to be confused with the selection method of reproduction cutting) removes trees of poor form in the dominant crown classes to favor better-formed trees in the subordinate crown classes. Mechanical or geometric thinning removes

Figure 23.12—Landscape-scale prescribed burning for pine-bluestem woodland restoration on the Big Piney Ranger District, Ozark-St. Francis National Forest. (USDA Forest Service photograph)

trees according to a geometric pattern, such as rows or strips, simply to reduce stem density in a predetermined pattern. Finally, free thinning, which is that most commonly done, combines elements of several of the above methods, such as when a mechanical thinning removes every fourth row in a plantation followed by a low thinning between the rows.

In the past, thinning (especially when stands are pulpwood-sized) has been far more common in pine stands than in hardwood stands for a number of reasons. First, small pines had value as pulpwood that exceeded that of small hardwoods, although this has changed in the past decade or two. Second, there is little need to be selective about species in southern pine stands, where the trees thinned and retained are usually the same. However, there are important reasons to retain one species rather than another when thinning hardwood stands. This effect leads to a far easier mechanization of operations in pine stands than in hardwood stands.

Almost by definition, thinning is the major tool foresters have to reduce the volume of fuels in a forest stand. At the stand level, thinning reduces biomass in rough proportion to BA; retaining 75 percent of BA after thinning will result in about the same proportion of biomass being retained. The pattern of thinning might affect the size class and distribution of the biomass being removed, which may result in some treatments being more effective than others for purposes of reducing fuels. A key consideration is whether the thinning can be conducted using a commercial timber sale. Payments made to the landowner from timber sales can then be reinvested in treatments to further reduce fuels, especially fine fuels such as branches and tops that might not have been hauled from the stand during logging.

Thinning that is prescribed in stands too small to sell commercially is called precommercial thinning, and is the biggest single challenge in managing sapling-sized pine stands. Stands that are candidates for precommercial thinning in southern pines are usually of natural origin because the initial spacing in planted stands is often selected so as to render the first thinning a commercially feasible operation (Figures 23.13A and B). But if plantations are planted at too dense a spacing, precommercial thinning will also be needed.

Stands in need of precommercial thinning are overstocked with small trees of marginal to no commercial value, with foliage in the canopy close to the ground. Dead needles shed during needlefall in autumn often drape over the lower dead branches of the trees. The number of stems and the volume and distribution of fine fuels create conditions that put these stands at high hazard with respect to wildfire, and the forester responsible for the stand has no easy decision.

In southern pine stands that require precommercial thinning, the best decision is almost always to do it—even if that requires out-of-pocket investment. Research in southern pines in the West Gulf region shows that precommercial thinning is more than offset by

Figure 23.13—A 22-year-old naturally regenerated loblolly-shortleaf pine stand, Crossett Experimental Forest. Ashley County, Arkansas; (A) unthinned, (B) thinned at age 20 to 100 trees per acre (247 trees/ha). (USDA Forest Service photograph by James M. Guldin)

faster growth in diameter and volume, with a favorable return on investment (Cain 1996). The earlier the precommercial thinning is conducted, the better. Stands treated earlier will respond more quickly, and the costs of conducting the operation in trees of small size are lower. The alternative—waiting until the stand grows to commercial size and then conduct a commercial thinning—requires no out-of-pocket cost by the landowner, but at the cost of delayed stand development and a longer period of time before financial returns can be obtained in thinning (Cain and Shelton 2003).

Prescribed Burning

Prescribed fire is generally applied as an intermediate treatment, with a goal of removing midstory vegetation in even-aged naturally regenerated pine, pine-hardwood, and hardwood stands, as well as in pine plantations (Van Lear and Waldrop 1989, Waldrop and others 1992). It also has excellent benefits for wildlife habitat (Komarek 1974). The prescription is usually applied on Federal lands, where burns in the dormant season through the early part of the growing season typically are conducted from January through April. Forest industry avoids using prescribed fire on their lands because of concerns about unwanted reductions in growth and yield in the loblolly pine plantations that they manage. Private nonindustrial landowners similarly tend to avoid the method, partly because they do not have access to the personnel required to efficiently burn large areas, and partly for reasons related to liability in the event that the fire should escape to neighboring property.

When prescribed fire is used, the ignition source depends on the condition of the landscape being burned, the possibility of young stands within the landscape that need special attention to withstand prescribed fire, and the proximity to private land. Burn units near or interspersed with private land are usually burned with drip torch ignition earlier in the burning season to better control the intensity of burning and the area covered by the fire. Young stands are often burned very early in the growing season, again using drip torches, to consume fine flashy fuels that might create too hot a fire if burned later in the growing season. Otherwise, especially in large well-burned landscapes where sensitive stands have been preburned, aerial ignition is preferred because of the efficiencies gained in cost and labor that result from burning large areas.

The watershed effects of prescribed fire are usually minimal. Vegetation recovers quickly after prescribed burning, and the risk of direct erosion through overland flow is minimal. Smaller fires ignited directly with drip torches are often imposed at a stand level, and in these cases permanent and intermittent stream channels usually provide an opportunity to establish one of the boundaries of the burn unit. The intensity of larger fires ignited by aerial ignition can be adjusted by the spacing of the incendiary spheres dropped from the helicopter, and stream channels are likely to burn with lower intensity if no spheres are dropped within them or if soil conditions in the stream zone are wet, as they usually are in the spring. The greatest likelihood of unwanted watershed effects is if firelines directly cross the perennial or intermittent stream, and this can be avoided as conditions warrant.

23.3. SILVICULTURE IN THE CONTEXT OF SPB

From a forest management perspective, the use of silviculture to control the SPB is a subset of the larger field of silviculture generally, and specifically for those practices appropriate for southern pines. Outbreaks of the SPB occur as spots of dead and living infested trees in southern pine stands having a high hazard for infestation based on tree and stand attributes. SPB spots expand quickly, usually in a discrete direction and at a rapid rate. When this occurs, there is an immediate and urgent need to conduct some kind of silvicultural treatment to suppress the outbreak, which emphasizes cutting of infested and uninfested trees at the active margin of the spot. This reactive silviculture is critically important to limit the spread of the infestation within and between stands, and is explored in detail elsewhere in the Southern Pine Beetle II.

The long-term view is that southern pine stands can be managed in a proactive manner using appropriate silvicultural systems that not only satisfy the goals of a landowner, but also maintain forest health and minimize losses from any of the biotic and abiotic natural disturbance agents and events that occur in the region. Few landowners would be comfortable with an explicit ownership objective that promotes the loss of standing timber from SPB, but landowners can and do differ about the degree of risk of SPB infestation they are willing to assume to achieve their goals of forest ownership. More and more foresters are coming to the realization that damaging agencies of regional scope such as the SPB are important to evaluate not only within a given landowner's ownership but across ownerships as well.

Natural disturbance events such as an infestation of the SPB complicate the job of the land manager. When outbreaks of the SPB are active within a forested landscape, silvicultural control of damaging agencies is triggered by exposure, which turns trees with high hazard into trees at risk. Emergency silvicultural treatments are used to quickly stop a given beetle spot, and these are discussed elsewhere in great detail in the Southern Pine Beetle II. Generally, those measures fall in the discussion of silvicultural control of damaging agencies (Smith and others 1997).

23.3.1. Immediate Silvicultural Treatments to Control SPB Outbreaks

When an active SPB spot is detected, the best silvicultural plans of the forester to meet the long-term objectives of the landowner are quickly dismissed, and the stand faces a natural disturbance event of destructive potential similar to that created by a tornado, hurricane, wildfire, or ice storm. The only advantage to the landowner is the length of time required for the insect epidemic to run its course. Windstorms and other severe weather events act within a very short period of time; in some cases, a stand is destroyed in a matter of minutes. In an SPB infestation, the landowner will have a few weeks or months to limit the spread of the infestation, and quick emergency action can be the difference between saving and losing a stand.

The fact that an outbreak of the SPB takes several weeks to develop gives a landowner a chance to respond with emergency silvicultural treatments to limit the spread of the infestation. These treatments are typically labeled as direct control treatments. They have been discussed thoroughly in the literature (Billings 1980b, Swain and Remion 1981, Wood and others 1985), and are a major topic elsewhere in the Southern Pine Beetle II.

Silviculturally, the emergency treatments to control an active or imminent threat to forest health are a subset of silvicultural treatments called improvement cutting (Smith and others 1997), a general category of silvicultural treatments intended to improve the species composition or health of immature or mature forest stands. The specific improvement cuttings imposed as direct control for the SPB fall into three categories: sanitation cutting, salvage cutting, and presalvage cutting (Smith and others 1997). Each is important and an element of the direct control tactics used to suppress SPB spots.

Sanitation cutting is defined as treatments to remove trees being attacked by the damaging agency but still alive (Helms 1998, Smith and others 1997). The theory behind sanitation cutting is that cutting these trees might alter the underlying epidemiology of the damaging agency. The archetypal example of sanitation cutting is cutting the green infested trees in an SPB spot; removing these still-living infested trees is highly effective in eliminating the brood of beetles that cause spots to continue to expand.

Salvage cutting is defined as treatments to harvest trees killed by the damaging agency, primarily for fuel reduction or economic reasons (Helms 1998, Smith and others 1997). With the SPB, salvage cutting is mostly an effort to capture and utilize volume already dead but still usable for timber or fiber production. There is usually little reason epidemiologically to cut the dead trees at the center of an SPB spot because the beetles no longer infest dead trees. However, there may be operational value for loggers engaged in salvage and sanitation cutting to cut and haul not only the green infested trees to the mill, but also the usable recently killed trees.

Presalvage cuttings are designed to remove trees in stands that are not yet affected by the damaging agency, but that are at high risk and lie in the expected path of the disturbance (Smith and others 1997). Presalvage cutting is triggered by the interaction of hazard, risk, and exposure; trees and stands that are high-hazard become at high risk of loss only when the SPB is active within a landscape. Presalvage is a low priority in the context of SPB direct control methods. Operationally, if the SPB becomes active, most of the emergency response will be directed at sanitation and salvage cutting; presalvage in stands not yet attacked is a lower priority. However, in the absence of SPB, any treatments intended to reduce hazard fall outside of the scope of presalvage treatments.

23.3.2. The Influence of Silvicultural Systems on SPB Hazard

The larger question in this chapter is to explore the silvicultural systems and the prescriptions that implement them over time to meet a landowner's goals and that, while being applied, concurrently reduce the hazard of infestation by the SPB. The necessary direct control treatments to control the SPB specifically such as sanitation and salvage cutting are, paradoxically, very disruptive in the context of long-term management plans and efficient conduct of silvicultural operations during the period between outbreaks.

Some landowners deliberately choose to manage stands in ways that meet their specific goals but that concurrently maintain a high SPB hazard. In some cases, these landowners understand the loss that they might face should the SPB become active and have factored that potential loss into their management planning. In other cases, landowners do not realize the hazard they face. For landowners who seek to manage their forest lands to be resistant to SPB, the better approach might be to practice forestry using silvicultural systems that maintain stands in a low-hazard condition.

Foresters have a relatively good understanding of stand-level silvicultural treatments that can reduce SPB hazard in the short term, to alter the behavior of the SPB should they occur. But the more profound impact created through forest management in stands and landscapes is not through short-term stopgap solutions to the SPB when the insect is active, but in long-term programmatic management practices that integrate treatments to reduce SPB hazard with the larger long-term ownership objectives of the landowner. Hazard reduction treatments are therefore more robust if they are examined within the context of the silvicultural system (Smith and others 1997).

Because of the rapid growth rates found in southern pine stands, ecological conditions can change rapidly. It is not unusual for southern pine stands on good sites to grow 3 square feet per acre (0.7 m^2/ha) in BA annually. This means that immature poletimber pine stands thinned to a residual BA of 80 square feet per acre (18.4 m^2/ha), for example, will grow to 110 square feet per acre (25.3 m^2/ha) in 10 years, and change from low SPB hazard to high SPB hazard. A forester should not only pay attention to a given estimate of hazard at a given point in time, but should also pay attention to the hazard trajectory of a given stand—that is, the rate of change in hazard over time.

Some silvicultural systems will result in steep hazard trajectories that change rapidly in a short period of time. Other silvicultural systems are characterized by relatively flat hazard trajectories. An understanding of the rate of the elements that condition whether stands are high-hazard or low-hazard, and the rate of change in hazard, is important to make good management decisions.

A number of elements are key indicators of susceptibility to the SPB. These include excessively dense stocking, growing conditions that result in the reduced vigor of individual trees relative to their potential, and stands combining these traits with a high degree of uniformity. The three silvicultural practices most useful in reducing the probability of beetle attack and spot growth are thinning, regenerating mature and overmature pine stands, and favoring resistant species (Belanger and others 1993).

Overstocking

High-hazard stands are often overstocked, and this feature is an important consideration in any discussion of hazard ratings. SPB infestations are frequently reported in overstocked stands (Bennett 1965, Lorio 1980a). Dense stocking and slower radial growth are common characteristics of high-hazard stands across the South (Coster and Searcy 1981), and thinning these stands is consistently noted as a tool to reduce their susceptibility to the SPB (Brown and others 1987, Burkhart and others 1986, Nebeker and Hodges 1983). A number of residual BA targets have been suggested.

The lower limit of residual BA generally mentioned in SPB studies reported in the literature is 70 square feet per acre (16.1 m^2/ha). Belanger and others (1993) reported that at or below a residual BA of 70 square feet per acre (16.1 m^2/ha), there is a very low probability of spot expansion spread. Brown and others (1987) used 70 square feet per acre (16.1 m^2/ha) as their lowest residual BA in a plantation thinning study, concluding that all three levels of thinning showed less induced SPB activity than the control stands. This residual BA is also appropriate as a lower limit in typical even-aged intermediate treatments in both poletimber and sawtimber stands (Figure 23.14).

The upper limit of residual BA appropriate to consider in the context of SPB hazard reduction probably falls at about 100 square feet per acre

(23.0 m^2/ha). For example, Belanger and others (1993) note that thinning to a residual BA of 80-100 square feet per acre (18.4-23.0 m^2/ha) is useful to reduce SPB hazard. Others report that plantations should be thinned periodically to BA <100 square feet per acre (23.0 m^2/ha), which reduces susceptibility (Burkhart and others 1986, Hedden 1978).

Hazard-rating systems are used to identify high-hazard stands (Lorio 1980b, Mason and others 1985, Stephen and Lih 1985), and nearly all of them rely upon stand or pine BA in one form or another as part of the hazard calculation. In some models total BA is used (Ku and others 1981); others use pine BA as the key variable (Hicks and others 1980, Kushmaul and others 1979), and still others use both pine BA and total BA (Daniels and others 1979). In all instances, higher total BA and higher pine BA contributed to increased susceptibility to the SPB.

The higher the residual BA target after thinning, the greater the need for frequent thinning to maintain acceptable low-hazard conditions. A pole-sized stand of loblolly pine in the west Gulf Coastal Plain thinned to a residual BA of 100 square feet per acre (23.0 m^2/ha) will reach 120-130 square feet per acre (27.5-29.8 m^2/ha) of BA in 10 years, and will quickly need another thinning to reduce SPB hazard. For example, Zeide and Sharer (2000) captured the prescription for typical industry practice in mixed naturally regenerated loblolly-shortleaf pine stands on the upper West Gulf Coastal Plain in the late 20th century. This prescription called for repeated thinning on roughly a 5-year cycle to residual BA less than 100 square feet per acre (23.0 m^2/ha) from age 15 through age 45, which met a number of resource needs including reduced SPB hazard.

All other things being equal, plantations established with lower planting densities will be less susceptible than plantations established with higher planting densities (Clarke 2001). The decision to use a given plantation spacing is informed by a number of silvicultural considerations including individual tree characteristics (shape of the crown, branchiness, size of the stem, and individual tree growth rate). However, a key consideration is often whether a stand can develop rapidly enough so that the first thinning will produce commercially viable sale of pulpwood for which the landowner would be paid, rather than require a precommercial thinning to avert stagnation of the new stand, but that would require the landowner to pay for the treatment. Because of this, the general trend in plantation establishment, at least up to the end of the 20th century, was to strive for lower planting densities.

Figure 23.14—Thinned loblolly pine plantation on the left, and the same plantation but unthinned on the right, on the Cold Springs Ranger District, Ouachita National Forest. (USDA Forest Service photograph by James M. Guldin)

Tree Vigor

Tree vigor is related to stocking. A tree growing in the open without competition from other trees is able to obtain a maximum amount of sunlight, atmospheric carbon dioxide, soil moisture, and soil nutrients; it will grow at its maximum rate, and is at its optimum vigor. But a given site only has a certain amount of sunlight, soil, and water resources. Competition with other trees of the same species, or trees of different species, will determine the degree of vigor a tree has at any point in its life. The ability of the tree to survive and dominate its surroundings depends on its genetics, its ability to adapt to the local environment, and the competitive environment in which the tree exists.

Generally speaking, there is a wide range of stem density within which a given forest site will grow roughly the same amount of biomass (Assmann 1970). It follows that if the overall level of stand biomass is constant, one can distribute that biomass in a stand of a given age in several ways—either in a large number of trees that have a small average diameter or in a small number of trees that have a large average diameter. But even though the stand volume growth will be similar across a wide range of stem density, individual tree vigor and volume growth will be different, with more vigorous trees being the larger ones with fast radial growth and the less vigorous trees being the smaller ones with slow radial growth. It is this latter situation—many trees with reduced vigor and slow radial growth—that finds a southern pine stand susceptible to the SPB.

Among the advantages in managed forest stands is that foresters can manipulate the number of trees and the BA within a stand to achieve goals of individual tree diameter growth and stand volume. Thinning removes some trees so the trees that remain have ample sunlight and soil resources to grow vigorously. Foresters cannot see root systems below the soil competing with one another, but the crowns of trees are readily visible, and foresters base relative decisions about the comparative attributes of trees almost entirely on two elements—spatial relationship of the crowns of the trees with one another and the rate at which the tree is growing, based on a quick examination of the tree's growth rings, with wider rings associated with healthy tree vigor (Figure 23.15).

Reduced radial growth in southern pines is a common factor in increased host susceptibility to the SPB (Coulson and others 1974). Slow radial growth is an indicator of reduced tree vigor. Physiologically, reduced vigor is manifest by an inability of the tree to produce pine resin, an important defense mechanism that when produced in abundance can kill or repel the

Figure 23.15—Wide spacing after commercial thinning and midstory removal in a mature shortleaf pine stand being managed as part of the shortleaf pine-bluestem management area, Poteau Ranger District, Ouachita National Forest. (USDA Forest Service photograph by James M. Guldin)

attacking beetle (Coulson 1980, Hodges and others 1979). It follows that a regular program of thinning in southern pine stands is important to maintain rapid radial growth and to promote individual tree vigor, and by implication to have trees capable of copious resin production as a primary defense against SPB attack.

For example, Cameron and Billings (1988) conducted a study examining 5- to 15-year-old loblolly and slash pine plantations in Texas, and observed that spots were more frequent in older plantations, in loblolly pine plantations, and in plantations that had recently been treated with prescribed burning. The association with prescribed burning, the authors suggest, is related to crown scorch commonly resulting from burning, and the associated slight reduction in individual tree growth and vigor while recovering from the crown scorch.

The pattern of earlywood to latewood growth may also be important. Lorio (1986) proposed a growth-differentiation process that may be important in understanding the reaction of trees to thinning. The oleoresin canals important in resin production upon wounding are more directly related to latewood formation than earlywood formation. If cultural practices are designed to optimize earlywood growth or to produce wide earlywood rings relative to latewood rings, the oleoresion production even of trees with rapid radial growth may be less than a tree of similar diameter and radial growth with a more equal distribution of earlywood to latewood. Thus, conditions that enhance earlywood formation and extend its duration may increase pine susceptibility to SPB attack (Lorio and others 1990). This could include natural weather events such as abundant rainfall in late spring and early summer, but it could also include cultural treatments designed to accelerate earlywood growth in spring, such as fertilizer application.

Susceptible Species and Sites

Managers have known for some time that some species of the southern pines tend to be more resistant to the SPB than others. A description of species susceptibility by region is shown in Table 23.1 (Kelley and others 1986a). Relatively speaking, slash and longleaf pine are more resinous species than loblolly or shortleaf, which may partially explain this general indication of resistance. In light of that, the transformation of the southern forest, especially in the lower Gulf Coastal Plain from a longleaf-dominated forest to a loblolly and slash dominated forest, may help explain the general increase in SPB outbreaks over time. Clarke (2001) speculates that one cause of the increased activity of SPB over the last century was the inability to regenerate cutover longleaf pine stands back to longleaf; the loblolly and slash pine stands that were established in place of longleaf are generally more susceptible to the SPB.

Stand, site, and tree characteristics associated with SPB attacks differ considerably among the Piedmont, the Coastal Plain, and the Southern Appalachian Mountains (Coster and Searcy 1981). Belanger (1980) provides an excellent summary of the general conditions associated with SPB in these different regions of the South. One way to quickly understand these issues is to examine the significant variables included in different hazard rating models (Lorio 1980b).

In the Piedmont, agricultural activity led to exhaustion and erosion of soils, and the forests that reclaimed or were established on abandoned agricultural land have been adversely affected as a result. Hazard rating models in the Piedmont include several soil variables—percent of clay in surface 15 cm of soil, depth in cm of the A horizon, and percent of clay per cm in the A horizon (Belanger and others 1980)—and suggest that higher hazard exists with thinner soils and higher levels of clay in the surface soil. This is most likely due

Table 23.1—The relative resistance and susceptibility of the major southern pines, by geographic region (Kelley and others)

Susceptibility	Geographic region		
	Coastal plain	Piedmont	Southern Appalachians
Most resistant	Slash, longleaf	Virginia, loblolly	Virginia, eastern white
Most susceptible	Loblolly, shortleaf	Shortleaf	Shortleaf, pitch

to the slow radial growth and lack of vigor in pines on these depauperate sites.

On Piedmont sites such as this, the best approach to minimize hazard is to shift from shortleaf pine to loblolly, especially on poorer sites. This will allow the forester to maintain low residual BA in the stands, to manage for live crown ration greater than 33 percent to ensure high individual tree vigor, and to regenerate overstocked stagnant stands because they have little hope of responding with improved individual tree vigor if thinned (Belanger 1980).

Southern Appalachian pine stands have also had SPB problems throughout the latter part of the 20th century. In this region, stands attacked by the SPB feature dense stocking, slow radial growth, and a high proportion of pine sawtimber. Recommendations include managing species composition toward resistant species of pines and including some hardwoods, and using intermediate treatments (thinning, improvement cutting, and salvage cutting) to lower stocking and increase individual tree vigor (Belanger 1980).

In the Coastal Plain, variables significant in several hazard models for mixed loblolly-shortleaf pine stands tend to be related to overstocking more than soils, and unlike Piedmont conditions, higher hazard tends to be associated with better sites (Ku and others 1981, Kushmaul and others 1979). These better sites are found in mesic or wet poorly drained sites where the abundance of soil moisture contributes to higher site indices but that have also been reported as more susceptible to the SPB (Belanger 1980).

Generally, mature Southern Coastal Plain pine stands of natural origin, especially on lands outside forest industry ownership, have been characterized by high density, a high proportion of sawtimber, and declining radial growth. In such stands, infestations are more common on poorly drained sites, the potential for problems is related to site quality (being worse on moist high-quality sites), and damage from windstorms and ice promote beetle attack and spot proliferation (Belanger 1980).

Mature Stands

Through the last half of the 20th century, forestry was a booming business in the Southern United States. Modern forest management is built upon a firm foundation of science and gives landowners and foresters excellent tools to manage forest stands to meet the needs of landowners. The inherently favorable humid temperature climate is ideal for growing southern pines across much of the South. At the end of the 20th century, virtually all of the metrics used to quantify forest timberland volume were at their highest level since the 1930s (Conner and Hartsell 2002).

Changes in management intent and philosophy, especially on government and nonindustrial private forest lands, have led to a maturing of the forest across the South. In some cases on Federal lands, stands are being deliberately managed with longer rotations to provide habitat in mature forest for species underrepresented on the landscape. In other cases on private lands, stands are simply getting older through reduced intensity of management. In both circumstances, inattention to stocking can allow dense stands of overmature pines to develop that are highly susceptible to SPB (Billings 1998, Clarke 1995). As growing stock increases, and as stand age increases, stand volume also increases, leading to more timber, more pine sawtimber, and older sawtimber (Belanger and others 1993), all indications of greater susceptibility to the SPB (Hedden 1978, Lorio and Branham 1988).

Over the past 2 decades, management of mature pine stands to provide habitat for the endangered red-cockaded woodpecker has encountered unique problems with SPB, which is a primary mortality agent of the large mature trees, especially loblolly pines, that serve as cavity trees (Belanger and others 1988, Conner and others 1991). Pine BA in cavity tree clusters, recruitment stands, and replacement stands should be kept at 60-80 square feet per acre (13.8-18.4 m^2/ha) (Figure 23.16), a stocking that is not conducive for expanding SPB infestations (Clarke 2001).

The challenge in the future will be to develop and sustain markets on Federal lands and lands in the nonindustrial private sector for large sawtimber pine products. Increasingly, the forest industry is turning to smaller diameter products that are available from plantations on the industrial land base, where trees are harvested before they reach large sawtimber size. As harvesting operations in the South become increasingly mechanized, equipment is designed for smaller tree sizes rather than large tree sizes; cutting and hauling large pine sawtimber is becoming somewhat specialized. In addition, modern mills are increasingly designed to operate using small diameter logs.

Figure 23.16—A mature shortleaf pine stand suitable for nesting and foraging habitat for the red-cockaded woodpecker as part of the shortleaf pine-bluestem management area, Poteau Ranger District, Ouachita National Forest. (Missouri Department of Conservation photograph by David Gwaze)

A challenge will be to maintain some forest manufacturing capability designed for large pine sawlogs and the dimension products they provide. This is especially critical because of the need to maintain proper stocking in mature stands, and because of the high potential for spot expansion that is found in mature pine stands containing trees of large size (Lorio 1984).

Attributes of Low-Hazard Stands

Throughout the literature describing the susceptibility of stands to the SPB, corresponding suggestions abound as to ways in which hazard and susceptibility can be reduced, and these tie in to many of the factors that have previously been discussed. Belanger (1980) summarizes three key elements in reducing hazard: manage to promote stand resistance, manage to promote individual tree resistance, and protect the site.

Individual tree resistance is promoted by favoring resistant species on appropriate sites, removing high-risk trees, and practicing cultural treatments that maintain good radial growth and vigor of individual trees in the stand (Figure 23.17).

Stand-level resistance is promoted by maintaining proper density and by getting that work on the ground in effective ways (Nowak and others 2008). Other silvicultural treatments that reduce competing vegetation and ultimately increase individual tree and stand vigor, such as prescribed burning, may decrease the impacts of SPB when applied judiciously (Clarke 2001). The SPB prefers susceptible stands that are uniform and continuous; managing stands in ways that increase within-stand and between-stand heterogeneity might act to limit spot expansion in the early part of an infestation (Figure 23.18).

Managing species composition includes not only managing for resistant pines as appropriate but also managing mixed pine-hardwood stands (Figure 23.19). Management practices such as planting less susceptible species, maintaining a mix of pine and hardwoods, and matching the pine species with the site also can reduce losses to the SPB (Belanger and Malac 1980). A mixture of pines and hardwoods is thought to promote resistance to attack and to deter the spread of endemic beetle populations (Belanger and others 1979, Kelley and others 1986a, Zhang and Zeide 1999). However, pine-hardwood mixtures provide little resistance to epidemic populations of the SPB; observations in Texas, Louisiana, and Georgia indicate that bark beetles can attack and kill pines widely distributed throughout such mixtures (Kelley and others 1986b).

Figure 23.17—Regular cutting cycle harvests allow foresters to maintain excellent radial growth of sawtimber-sized trees in uneven-aged loblolly-shortleaf pine stands, as illustrated from this recently cut stump in the Poor Farm Forestry Forty demonstration area on the Crossett Experimental Forest in Ashley County, Arkansas. (USDA Forest Service photograph by James M. Guldin)

Figure 23.18—A thinned and burned mature longleaf pine stand treated with additional midstory removal to maintain radial growth and vigor of sawtimber-sized longleaf pines on the Sam Houston National Forest, National Forests and grasslands of Texas. (USDA Forest Service photograph by James M. Guldin)

23.4. STAND MANAGEMENT DECISIONMAKING IN THE CONTEXT OF SPB

The general conditions prevailing across the southern forested landscape have changed over the past 50 years. Old stagnant mature and overmature sawtimber stands were once a primary concern for managers wrestling with SPB, and such stands still merit careful management where they still exist. But in the 21st century, harvesting, species conversion, fire prevention and suppression, and short rotation plantation forestry have promoted the establishment and maintenance of forest structures that are highly susceptible to the SPB (Clarke and others 2000, Schowalter and others 1981).

23.4.1. Clearcutting and Planting

Clearcutting and planting have become the standard practice for management of forest industry and timber investment forest lands in the South. In 1993, Belanger and others reported that the increasing regional occurrence of the SPB was related to the fact that the South had 25 million acres (10.1 million ha) of plantations at that time, of which more than half were greater than 10 years old. As of 1999, data show that the 30 million acres (12.1 million ha) of planted pine stands across the South are nearly the equal of the 34 million acres (13.8 million ha) of naturally regenerated pine dominated stands (Conner and Hartsell 2002). Projections are that by 2050, 50 million acres (23.9 million ha) or 25 percent of the South's timberland will be in pine plantations (Wear 2002). The challenge that Belanger reported in 1993 is becoming more prominent, not less.

Figure 23.19—The retention of overstory hardwoods as part of the shortleaf pine-bluestem woodland restoration prescription may reduce hazard of SPB spot expansion. Poteau Ranger District, Ouachita National Forest. (USDA Forest Service photograph by Brian R. Lockhart)

Modern plantations are generally established following intensive site preparation that often includes use of bedding, use of herbicides to control herbaceous competition, use of fertilizers to boost early stand volume growth, and use of thinning early in the rotation to regulate stem density. The goal of these cultural practices is to optimize early growth and promote within-stand uniformity of tree size for efficiency in mechanized thinning and harvesting operations.

The advantage of pine plantations in the southern landscape is that they are not managed to old age. In 1999, forest survey data showed that of the 30.1 million acres (12.2 million ha) in pine plantations in the South, more than 99 percent were younger than 48 years of age. Thus, the likelihood that overmature pine stands containing trees of large diameter will develop in the planted forests of the South is low.

The disadvantage facing pine plantations relates to the possibility of delay in the timely application of silvicultural treatments, especially thinning. The rapid rates of individual tree and stand growth in plantations will be associated with rapidly changing hazard trajectories over relatively short periods of time. The question is the degree to which foresters can manage the steep hazard trajectories in these fast-growing stands continually below the threshold of high hazard.

An aggressive program of frequent thinning beginning early on (ideally before age 10) in these stands is essential to maintaining radial growth at an acceptable level and to keeping stand BA at or below 100 square feet per acre (23.0 m^2/ha). If pulpwood and small sawtimber markets remain strong, the ability to thin stands economically and in a timely way will be feasible. Questions remain whether the BA and volume in an increasing area of plantations in the region can all be thinned in a way to keep hazard trajectories low if markets weaken.

The organization of operations in the world of intensive southern forestry has also changed in the past decade, with forest industry lands changing hands to timber investment management organizations. A byproduct of this shift is a reduction in staffing because the investment organizations believe that efficient forest management can be done with fewer field staff. Part of this decision is based on reliance on State forestry organizations to provide support for fire suppression and pest management on private lands. This loss of ready labor to engage in suppression activities has been a gradual change, and State agencies have responded with the acquisition of additional firefighting assets. But the thin line of available State personnel to participate in future rounds of SPB control on a broader sector of private lands will be tested in future outbreaks that are certain to occur.

23.4.2. Even-Aged Methods Using Natural Regeneration

Management of even-aged stands through rehabilitation of naturally regenerated even-aged or two-aged cohorts on cutover lands and use of even-aged seed-tree and shelterwood methods of management in naturally regenerated stands have been quite effective as a tool to meet objectives for management of large sawtimber products. This is especially true on public lands, some industry lands (though fewer than supported these methods several decades ago), and also in the nonindustrial private forest land ownership sector. Even-aged methods have been especially useful in Coastal Plain longleaf pine, west Gulf Coastal Plain mixed loblolly-shortleaf pine, and Ouachita Mountains shortleaf pine.

The advantages in using even-aged methods revolve around tradeoffs between minimizing out-of-pocket costs in capital intensive stand management and rehabilitation, and maintaining structural conditions such as continuous overstory cover in mature forest stands that meet more than simply a financial return on investment. The tradeoff is slower growth rates of regeneration and reliance on the prevailing genetic expression of open-pollenated parent trees rather than the robust genetics associated with improved seedlings grown for planting. The stands are not necessarily optimal short-term investment portfolios, but often provide owners with values such as wildlife, recreation, and aesthetics that outweigh the bottom line on an investment calculation.

From the perspective of the SPB, the challenge in naturally regenerated stands is managing them to reduce stocking and maintain or develop acceptable rates of radial growth and individual tree vigor. Generally speaking, if one inherits an overstocked stand greater than 48 years in age, it will be difficult to apply thinning treatments that cause a similar response to release as one would see in younger stands. This is important in the context of managing the SPB hazard in mature and overmature stands. As a frame of reference, 1999 forest survey data showed that of the 33.1 million acres (13.4 million ha) of natural pine stands remaining in the South, slightly more than 20 percent are 48 years old or older.

When regenerating even-aged stands naturally, the forester has much less control over stem density and stocking than in a plantation. This increases the importance of timely precommercial thinning by age 10 if not before, in order to avoid stagnation and to develop vigorous dominant and codominant trees that have acceptable diameter growth rates in stands within acceptable limits of BA, to reduce hazard to SPB. The slower growth rates of naturally regenerated stands compared to plantations will result in slow to moderate rates of increase in hazard, especially after the initial precommercial thinning. However, as these stands grow into poletimber and small sawtimber sizes, the SPB hazard trajectory will change more rapidly, and attention to a timely program of thinning to appropriate residual stem density and BA is just as important in naturally regenerated stands as it is in planted stands.

A key in managing naturally regenerated pine stands in the South is to forego the opportunity for rapid pulpwood production and concentrate instead on development of sawtimber products. It would be a mistake, both for future development of the trees in the stand and in the evaluation of SPB hazard, to allow naturally regenerated stands to develop without precommercial thinning in order to eventually obtain a first commercial thinning. The precommercial thinning will forego some initial pulpwood return, but in truth the first commercial thinning in naturally regenerated stands often is designed simply to cover the costs of the harvesting, with future benefits from the added growth on the residual stand.

Landowners who seek guidance in the timely application of thinning during the life of the stand have a model in the prescriptions that codified the practice of forest industry in the naturally regenerated mixed loblolly-shortleaf pine stands of the upper west Gulf Coastal Plain. These prescriptions were used to grow sawtimber products on 45-year rotations in southern Arkansas and northern Louisiana (Zeide and Sharer 2000), and provided that the thinning schedules were maintained, SPB problems remained minimal.

23.4.3. Uneven-Aged Methods Using Natural Regeneration

The quiet alternative for landowners interested in continuously forested southern pine stands that produce high quality sawtimber on a regular basis is the application of uneven-aged silviculture. The refinement of the method for southern pines occurred on the Hitchiti Experimental Forest in Georgia with Ernst Brender (1973), and on the Crossett Experimental Forest in south Arkansas with

Russ Reynolds and his successors (Guldin and Baker 1988, Reynolds and others 1984). The fact that uneven-aged systems work is a tribute to the ecological flexibility of loblolly pine, which despite its reputation as the primary planted species in the South, is also uniquely suited for survival and growth in the unique ecological conditions created in uneven-aged stands.

Stem density and age are far less important in uneven-aged stands than working within the recommended BA constraints of from 60 to 75 square feet per acre (13.8-17.2 m^2/ha) during the cutting cycle, with 67 percent of that BA in the sawtimber size classes (Baker and others 1996). These stands are deliberately managed in a relatively understocked condition, which optimizes individual tree growth and vigor of sawtimber-sized trees and creates available growing space in varying locations within the stand for regeneration establishment and development.

The goal of uneven-aged silviculture is to optimize stand volume growth in the sawtimber component and to maintain acceptable periodic rates of sawtimber volume growth over time. As a result, radial growth even in the large diameter classes 18 inches in diameter and up remains relatively rapid. A key reason is the low BA in the sawtimber component of these stands, which results in healthy and vigorous crowns that retain a high live crown ratio. This condition produces rapid volume growth on big trees and is responsible for the reputation the method enjoys for producing high quality sawtimber.

That is also why the method is notoriously inefficient in the production of pulpwood (Guldin and Baker 1988), because a relatively small percentage of the stocking in the stand is devoted to the pulpwood-size classes. The trick in properly managing uneven-aged stands is to retain enough ingrowth from seedlings and saplings into the submerchantable classes, and then into the merchantable poletimber and sawtimber classes, in order to maintain the long-term sustainability of the system.

All other things being equal, group selection stand will have slightly greater hazard to SPB than single tree selection stands. The reason lies in the greater stand-level discontinuity represented by the gaps vs. the matrix between the gaps. The matrix is often managed essentially as an even-aged stand, and often carries a higher BA especially early in the process if the method is being used to convert stands from even-aged to uneven-aged condition. Managers should pay attention to residual BA in the matrix between the groups, and the same guidance to reduce SPB hazard in even-aged stands—BA less than 100 square feet per acre (23.0 m^2/ha), and preferably closer to 80 square feet per acre (18.3 m^2/ha)—should be applied in the matrix. In addition, it may be necessary to follow the establishment of pine regeneration within the group openings with timely thinning, including precommercial thinning if longer cutting cycles are being used.

These low residual BA levels in the sawtimber component are a key reason to suggest that the hazard trajectory of uneven-aged stands generally, and especially stands managed using single tree selection, will be relatively flat. At the end of a cutting cycle prior to harvest, the maximum BA in the stand will still be in the lower range of acceptable BA to minimize hazard. In addition, trees in the sawtimber-size classes are managed to maintain acceptable radial growth, and marking rules generally dictate cutting the worst trees and leaving the best. All these indications lead to the conclusion that well-managed uneven-aged southern pine stands will maintain an unusually low hazard of SPB outbreak over the long term.

23.5. CONCLUSIONS

SPB outbreaks are a natural event in southern pines. They are important insofar as their occurrence contributes to the risk of loss of the forest in the event of uncontrolled outbreak. Management of forest stands using proper silvicultural techniques can alter the natural population dynamics of this destructive insect. But it is more holistic not to think of silviculture for control of the SPB separately from the larger question of silvicultural practices applied within prescriptions designed to maintain forest health, productivity, and sustainability in the context of the goals of ownership of the landowner.

Silvicultural tools to prevent SPB outbreaks are most effectively implemented if they fall within the context of the larger silvicultural systems being imposed within stands and landscapes, rather than as stand-alone treatments applied at a given point in time. Active management under the guidance of professional foresters is the most effective way to integrate considerations for SPB in operational management programs, and to minimize the hazard to southern pine stands and landscapes as elements of a larger program of active forest management.

Managers have many silvicultural options for managing forests to provide the mix of commodities and amenities desired by society because of the diversity of tree species in the Southern United States, the large ecological amplitude and geographic distribution that most species exhibit, and the variety of uneven- and even-aged silvicultural systems available.

Silvicultural systems are designed to achieve multiple resource objectives often simultaneously within ecological, social, and economic constraints. Silvicultural systems are dynamic and can be adapted as better knowledge is gained, management goals change, and stochastic events occur that alter forest condition and succession from the desired pathways. Silvicultural stand prescriptions integrate resource objectives, apply ecological principles, and identify the system of treatments that are effective and efficient in attainment of forest goals with a degree of certainty.

The best long-term strategy to combat the certain future attack by any of the many threats to forest health, and especially threats of SPB outbreaks, is the proper application of silviculture within the framework of sound forest and regional planning. Silvicultural prescriptions can be developed to treat current stand conditions, to manage composition, and to promote tree vigor and forest health. Healthy forests are less susceptible to attack by insects and pathogens, are less vulnerable when attacked, and are more resilient to survive and recover from the biotic attack or stress from environmental extreme. Forest plans should seek to diversify composition and structure of forests, woodlands, and savannas across the landscape to buffer these effects.

24

Forest Restoration following Southern Pine Beetle

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Abstract

Forest restoration is the process of transforming a damaged or unhealthy forest into a healthy one. After the southern pine beetle (SPB) has damaged a forest, it is sometimes, if not most times, necessary to restore that forest. It is important to know the restoration goals, conditions prior to SPB, current conditions, and potential future conditions of the forest before beginning a restoration project. Restoration projects have political and social implications that also cannot be overlooked. The practical methods and concerns in conducting restoration will vary by location. Only within the proper conceptual framework can restoration following southern pine beetle outbreaks be successful.

24.1. WHY RESTORE?

The question regarding "why restore?" is intricately woven and intermingled with (a) how we define forest restoration, (b) where we are restoring forests, (c) how we are restoring forests, and (d) our world view of ecological systems and the concept of nature. If one is willing to accept that a forest has been damaged by human intervention and that the best recourse to fix that damage is through further human intervention, then the question has been answered. However, the answer to the question becomes fuzzier or clearer as more specific questions are asked and answered. Is the forest on public, private, or commercial land? Is the forest actively managed or is it wildlands? How much will it cost to restore the forest; is it worth it? What are the potential negative residuals from the restoration process? These questions and more are essential to ask before engaging in any restoration effort. Thus, a sound understanding of the ecological, political, economic, and social implications of the proposed restoration project is essential. Here, I will present these concepts in the context of restoration following damage by southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB).

24.1.1. Ecological Implications

In the wake of growing human populations and subsequent land use changes, forests have become natural remnants in a human-dominated landscape. Because many of our existing forests were once fully or nearly clearcut, it is potentially difficult to maintain that even those are "natural." Aside from the previous assertion, forests are natural systems that provide a variety of ecological services. Forest stands that have been killed or damaged by SPB provide the potential to alter important ecological functions. This fact is particularly true in areas beyond the normal home range or in outbreaks of unprecedented size, where beetles act as invasive agents. One place where this is occurring is in the Southern Appalachian Mountains. In the Southern Appalachians, SPB threatens to eliminate Table Mountain pine (an Appalachian endemic). SPB also endangers habitats for other ecologically important species. Red-cockaded woodpeckers, for example, left the Daniel Boone National Forest because suitable pine habitat was no longer available (USDA 2005). Moreover, SPB outbreaks may increase the risk of severe wildfires. Fuel loading from wood debris has been found up to three times higher in infested stands (110.3 m^3) vs. uninfected stands (30.6 m^3) (Nicholas and White 1984).

However, there can also be negative implications from restoration activities. When damaged areas are replanted with dense monoculture pine stands, previous habitat could be altered and the potential for more future SPB outbreaks could even increase. Forest managers, therefore, should aim to conduct restoration activities in a sustainable context. The best way to mitigate potential negative residuals from restoration is to involve extensive preplanning research. Having positive/successful restoration outcomes is essential as the outcomes will have implications on policy regarding future restoration activities.

24.1.2. Policy Implications

The Healthy Forest Restoration Act of 2003 is the broadest piece of legislation governing forest restoration. Title IV of this act refers specifically to Insect Infestations and Related Diseases. More specifically Section 403(a)(1) states: "…the Forest Service and United States Geological Survey, as appropriate, shall establish an accelerated program to plan, conduct, and promote comprehensive and systematic information gathering on forest-damaging insects and associated diseases, including an evaluation of -

1. infestation prevention and suppression methods;
2. effects of infestations and associated disease interactions on forest ecosystems;
3. restoration of forest ecosystem efforts;
4. utilization options regarding infested trees; and
5. models to predict the occurrence, distribution, and impact of outbreaks of forest-damaging insects and associated diseases."

While this act does not provide support for restoration of SPB-damaged areas per se, it does highlight the need for gathering information regarding the extent of damage and an assessment of restoration efforts.

Below the Executive level, the Forest Service, particularly Forest Health Protection (FHP) and the Southern Research Station (SRS), provides funding through SPB initiative funds to focus resources on SPB restoration efforts. SRS-4552: Insects, Diseases, and Invasive Plants unit of the SRS funds millions of dollars in cooperative research to aid in SPB research. In 2003, the USDA Forest Service supported a meeting that identified SPB research, development, and applications, and has provided a framework for action (Coulson and others 2003). Also in 2003, the SPB Prevention and Restoration Program (SPBPRP) was established. The goal of SPBPRP is to encourage eligible nonindustrial forest landowners to improve forest health and reduce SPB damage through technical assistance and cost-sharing of recommended prevention practices. Approximately $60 million have been allocated to State and national forestry agencies since 2003, making it one of the larger Federal bark beetle prevention programs in the U.S. history of forest health management.

In addition, the National Association of State Foresters issued the statement "Southern Pine Beetle: A Time for Action to Protect the South's Forests." The statement emphasizes actions to reduce immediate and long-term threats to forest resources and associated impacts to forests that include:

1. Continued suppression of pine beetle epidemics using time-tested and effective control strategies
2. Reduction of future epidemics by making existing forests more beetle resistant
3. Prevention of loss of the southern yellow pine ecosystem through restoration of forests destroyed by the beetle, but in a form less susceptible to future beetle attack, including removal of beetle-killed trees that pose imminent hazards to people in high public use areas
4. Assistance to communities affected by beetle epidemics to protect jobs and to develop the infrastructure necessary to employ effective beetle control and prevention techniques
5. Funds necessary for full compliance with all laws, planning, implementation, monitoring, accountability, and coordination among Federal and State agencies
6. Funds for educating the public and landowners about the SPB and the need for suppression and prevention activities
7. Research to support suppression, prevention, and restoration activities

The relationship between SPB outbreaks, restoration activities, and policy is one of ongoing feedback. There are, of course, ecological consequences to this relationship in terms of forest management activities. In addition, there are also many potential economic and social implications as a result.

24.1.3. Economic and Social Implications

SPB is the most destructive forest insect pest in the Southeastern United States. The USDA Forest Service SRS-4802: Forest Economics and Policy working unit reports that the total value of damage caused by SPB from 1973 through 2004 was $3.57 billion. From 1991 through 2004 alone SPB has been responsible for over $1 billion in damage (Pye and others 2004).

While regional estimates vary, significant outbreaks can severely impact local economies. During the 1999-2001 outbreak, SPB affected more than 1.5 million acres of pine in North Carolina and destroyed timber valued at more than $12.4 million in 1 year. During the same outbreak period, Tennessee experienced the destruction of approximately 390,000 acres of pine timber valued at $358 million. The Bankhead National Forest in Alabama alone experienced more than $20 million in damage between 1986 and 2001 (Tchakerian and others unpublished data).

Restoration is a costly business whether conducted on public or private land. Many private landowners cannot restore their forests without financial assistance. The SPB cost-share program is one approach to restoring forests after SPB. In this program, eligible landowners receive funds at the cost-share rate of 70 percent. Landowners who accept funding are required to maintain those acres in forest land for a period of 10 years and to comply with provisions set forth in the approved forest management plan. Several States have issued policies and detailed guides on this program. Cost-share assistance is limited to $8,000/ownership/State/fiscal year. However, funding may be limited to costs associated with approved precommercial thinning practices. Many landowners are unaware that SPB is a source of timber loss or have little interest in limiting SPB impact. This lack of awareness creates an opportunity to educate landowners about the benefits of healthy management and ways to restore forests so that they are no longer conducive to massive beetle outbreaks.

24.2. BACKGROUND

24.2.1. Defining Forest Restoration

Forest restoration involves some transition from a damaged state, where damage can come in the form of an unnatural or unwanted change in forest pattern, process, and/or composition, to some desired condition. From an ecological perspective, forest restoration involves the reestablishment of natural ecological processes that produce dynamic ecosystem structure, function, and processes (Stanturf and others 1998). Stanturf and Madsen (2002) identify three restoration descriptors: afforestation, reclamation, and rehabilitation. Afforestation and reclamation involve some sort of change in landcover. Generally, afforestation refers to the reforesting of agricultural land, and reclamation is more extensive and can involve reforestation of urban areas or other areas where soil productivity has been altered (e.g., strip mines).

However, what makes restoration following SPB damage different from restoration following other forest disturbances? SPB-damaged forests fall under the rubric of forest rehabilitation. Rehabilitation does not involve a change in landcover. Rehabilitation is an action to correct instances where structure or species composition has been altered (Stanturf and Madsen 2002). In the case of SPB, specific restoration questions must be answered. Most important, forests should be restored in a way that will prevent or reduce damage from future outbreaks while maintaining the forest purpose (e.g., timber stock, biodiversity enhancement, game habitat, ecosystem preservation). Other questions regarding forest restoration can be further subdivided according to the specific restoration goals, namely the restoration of species, the restoration of ecosystem/landscape function, and the restoration of ecosystem service.

24.2.2. Restoration Goals

Before beginning to even plan forest restoration following SPB, it is first necessary to answer the question: What is the goal of restoration? There is no simple answer to this question, and not necessarily one answer to the question. The answer may depend on forest ownership (private, public, commercial) as well as the site location and forest use, among other issues. The goals of restoration, while varied, can fit under two general categories: restoring forest processes and restoring forest services. This section addresses each of these in detail.

Restoring Forest Processes

Forest processes refer to the workings of the natural forest system as unaffected by human intervention. Largely, in this context, the process that is most important for forest restoration is the reintroduction of fire. Fires play a key role in pine systems by providing the dual role of thinning forests, which helps prevent SPB outbreaks, and by promoting regeneration of serotinous pine species. Because allowing wildfires to burn unmanaged is impractical due to the potential threats to human habitations, prescribed burning is a reasonable alternative.

Prescribed burning (Figure 24.1) has been shown to be an effective tool at restoring pine and pine-hardwood mix stands in the Southeast (Vose and others 1999, Waldrop and Brose 1999, Stanturf and others 2002). Restoring fire into forest ecosystems requires knowledge of both how often to burn a site (fire rotation interval) and what severity of fire to burn (fire intensity). Depending on the ecosystem type, rotation intervals can vary from a few years to hundreds of years, and intensities can range from low-intensity surface fires to stand-replacing crown fires.

Recent modeling research (Waldron and others 2007, Lafon and others 2007) has verified the existing hypothesis (Williams 1998) that in natural systems, SPB and fire work in combination to maintain yellow pine woodlands on xeric slopes, ridges, and peaks in the Southern Appalachian Mountains (Figure 24.2). This same research also demonstrated that different ecological regions, defined by moisture and elevation gradients, require differences in both species and fire regimes to maintain ecological integrity. Further research by Cairns and others (2008b) demonstrates that as pine aggregation increases, so does the probability of SPB outbreaks. Because fire reduces pine aggregation, it is an ideal tool for structuring naturally fire-prone areas to be more SPB-resistant while promoting the growth of yellow pine species.

Restoring Ecosystem Services

Ecosystems provide valuable recreational, economic, and ecological services. Services can include providing scenery and habitat for passive recreation activities such as hiking, camping, and bird/wildlife watching; providing habitat for game species; increasing biodiversity; and acting as carbon sinks. Although these services can be very different from one another, they all involve the restoration of certain species at set densities.

Figure 24.1—Prescribed burning for restoration: (A) prescribed crown fire, (B) one day after burn, (C) six months after burn, and (D) six years after burn. (photographs provided courtesy of USDA Forest Service, Southern Research Station)

Ecologically, species restoration is important to consider when dealing with endemic and/or endangered tree species. It can also be important to restore species to repair biodiversity. Economically, species restoration is important to those people engaged in the timber industry. Commercial forests are of particular concern for restoration. While many factors such as global warming (Ungerer and others 1999, Tran and others 2007) and drought have been suggested as triggers for recent SPB outbreaks, silvicultural practices (particularly by industry) have by far held the most blame (Perkins and Matlack 2002). The goal of commercial forestry, as any industry, is the maximization of profit. Historically, this

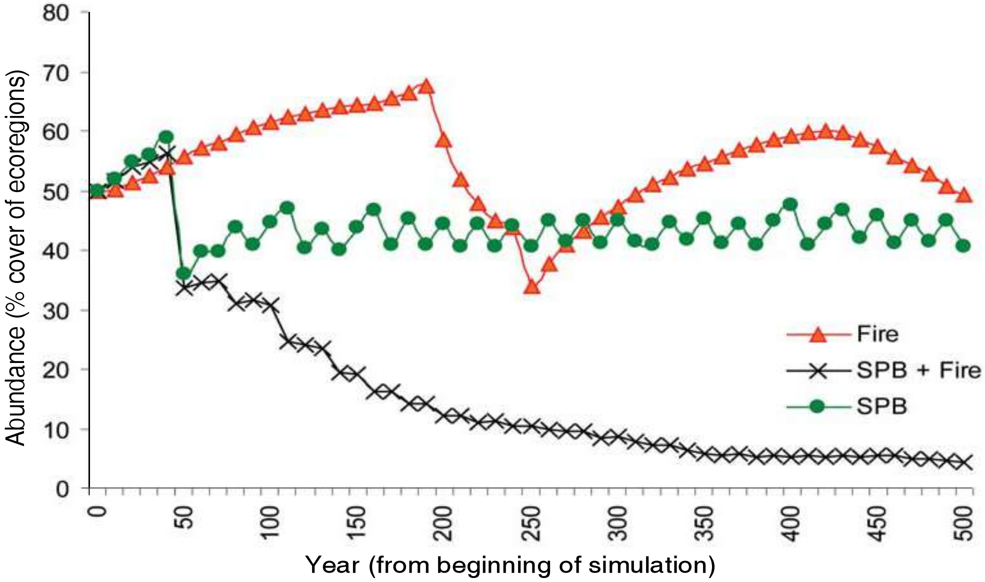

Figure 24.2—Table Mountain pine persistence on mid-elevation (~3,000-4,500 feet) ridges and peaks in the Southern Appalachian Mountains. Simulated using LANDIS 4.0.

has meant planting large, even-age, densely spaced, monoculture plantations of high-yield pines (usually loblolly). Of course, this creates prime SPB habitat, and hence, high outbreak potential. Finding a restoration scenario that will allow companies to maintain profit while reducing SPB hazard is not an easy task.

In general, industry should guide replant activities with SPB outbreak potential in mind. This means experimenting with alterative planting strategies such as spacing trees at greater than 20 feet apart, planting less-susceptible pines (e.g., longleaf pine), planting uneven-age stands, and intermingling non-hosts (hardwoods) with pine species. While there has been some research that suggests lesser density stands will result in higher biomass and yield (Baldwin and others 2000), the feasibility of convincing industry to follow one or a combination of these scenarios will require more research to find the scenario that can best balance SPB prevention and profit maximization.

24.3. PRERESTORATION PLANNING

Restoration, as with any activity, must begin with proper planning to ensure a successful outcome. Planning for restoration is usually a longer and more complex activity than the actual act of restoration. Prerestoration planning involves an understanding of pre-outbreak conditions, an assessment of current conditions, and predictions of post-restoration conditions to adequately understand how to direct restoration activities. In this section, these components are discussed in detail.

24.3.1. Understanding Preoutbreak Conditions

Before beginning any restoration effort, it is first necessary to have an understanding of the composition, structure, and dynamics of natural forests (Landres and others 1999, Bergeron and others 2002, Kuuluvainen 2002). The pre-outbreak conditions should guide restoration. That is not to say that forests should be restored to how they were immediately preceding an infestation. It is important to understand the forest conditions prior to outbreak so that we can be better prepared to not recreate a forest that will be susceptible to SPB outbreaks.

It is equally important to understand the ecological setting of the forest to be restored. Factors such as slope, aspect, soils, climate, surficial geology, precipitation, and proximity to different ecological zones/developed areas are all important in determining how to restore a particular piece of land. These factors will not only affect the establishment and growth of certain plant species, they will also have an impact on the probability of future SPB outbreaks.

In addition, it is important to have clear understanding of the ecological history of that forest, or at least have an ecological analog using a site in similar condition. In recent years, dendroecologists have made significant steps in reconstructing forest disturbance histories in terms of fire and beetle outbreaks (Lafon and Kutac 2003). As more of this data is collected and disseminated, a more accurate understanding of preoutbreak conditions can be gleaned. Also it is important to note the SPB outbreak history of a particular site. If a site has been the subject of multiple past outbreaks, a structural reconfiguration such as thinning may be required for areas adjacent to the restoration area in addition to the actual restoration activity.

24.3.2. Assessing Current Conditions

For a restoration project, a considerable amount of reconnaissance and assessment is needed to set goals for restoration and to evaluate the success of particular restoration actions (Lake 2001). In restoration plans, working towards desired future conditions (natural appearing forests and natural processes, species diversity, eliminating exotics, recreating native understory vegetation, structural components based on the restoration costs and benefits analysis) helps to prioritize activities (Holmes 2004).

Current forest conditions can be assessed through some combination of field visits and remotely sensed imagery. Important factors to assess include species of dead and damaged trees, composition and structure of undamaged areas nearby, spatial extent of the damage, condition and composition of the understory, and presence of invasive exotics. Without a complete and comprehensive understanding of both the conditions on the site to be restored and the conditions in the surrounding landscape, it would be nearly impossible to develop a successful restoration outcome.

24.3.3. Predicting Future Conditions

Restoration, while well intended, is still another form of human alteration of the natural processes. The only means available to determine if restoration efforts are going to achieve desired consequences is through computer modeling. When restoration goals are known and defined *a priori*, models can help determine management strategies to fit those goals. When restoration goals are not defined *a priori*, iterative modeling can be employed to investigate the potential consequences of a variety of single and multiple management strategies. Through this process, more defined restoration goals can be developed.

Models can be used at different spatial and temporal scales of inquiry, as well as to answer different sorts of questions. Four basic model types of interest to forest practitioners are: Forestry Growth and Yield, Stand Regeneration, Gap, and Landscape Models. A description of the first two of these types can be found at http://www.forestencyclopedia.net/p/p1609. The latter two are described below.

Gap models simulate changes in forest gaps or stands that are less than 1 ha in size. These models project the establishment, annual growth, death, and regeneration of individual trees within a defined area. Gap models continue to be important in developing and testing theories about the overall functioning of forests, and are also used in reconstructing past and future forest composition (Shugart 2002). These models are appropriate when restoration is limited to a small area, such as a confined SPB outbreak spot. One limitation of these models is that they preclude study over an extensive geographic range. However, the output from gap models can be, and has been, used to inform landscape models (He and others 1999).

In the wake of large beetle outbreaks that have damaged forest systems, a landscape modeling approach is recommended. Landscape models simulate temporal change using spatially referenced data across a course spatial scale (ca. 1~1,000s km^2). These models are used to investigate the reciprocal interactions between landscape composition and structure and a host of natural (e.g., insect outbreaks, fires, wind storms) and anthropogenic disturbances (e.g., land use change, harvesting) across and between multiple ecosystems. The limitation to these models is that they do not include the physiological detail of gap models. This approach has been tested successfully on SPB in the southern Appalachians using the LANDIS model (Waldron and others 2007, Xi and others 2007, Cairns and others 2008b).

24.4. CONDUCTING RESTORATION

When restoring SPB-damaged forests, one of the main objectives of the restoration initiative should be to create healthy forests by developing stands that are less susceptible to future SPB outbreaks. While there are several practical concerns (e.g., site access, organization of labor, cost) that must be addressed before any restoration effort, these concerns are so variable with time and location. Generally speaking, it costs landowners about $200-$250 per acre to restore an area damaged by SPB, including the costs of removing dead timber, site prep, and replanting (Nowak Personal Communication).

There are two distinct phases to the restoration process: site preparation and site restoration. Each of these phases involves its own set of activities and outcomes and will be described in detail in the following sections.

24.4.1. Site Preparation

After SPB outbreaks it is necessary to prepare the site for restoration. The goal of site preparation is to provide conditions that will enhance the growth and survivability of desired plant species. The removal of offsite and invasive species and dead or severely damaged trees is of paramount importance. Invasive exotic plant species have become an extremely detrimental problem in American forests. Because these species tend to thrive in disturbed areas, it is necessary to remove them immediately from the site of disturbance as well as from the immediate area due to the potential to seed-in during restoration. Dead and damaged trees also must be removed from the site. Leaving large amounts of dead or damaged trees on or near the restoration site will leave the stands vulnerable to future insect outbreaks and wildfires.

In addition to removal of damaged and/or undesirable species, there are a variety of soil preparation techniques that can be employed to improve tree vigor and productivity. Subsoiling (also known as ripping or deep-tilling) is one technique that has shown to be beneficial in promoting root growth (Gwaze and others 2007). However, many sites, particularly in mountainous areas, might not be easily accessible to tilling equipment. Other techniques can involve bedding (McKee and Wilhite 1986) or mounding (Knapp and others 2006). Bedding forms a linear mound of soil with a narrow two-axled disk or bedding plow (University of Florida 2006). Bedding is usually done on sites with poor drainage. On upland sites, bedding perpendicular to slopes can minimize soil erosion. Again, because bedding involves the use of heavy machinery, some sites may be inaccessible. Mounding has been used more commonly in Scandinavian and Canadian uplands as well as in the Great Lakes States (Sutton 1993, Londo 2001, Cohen and Walker 2006). Mounding also involves heavy machinery, but rather than using the plowing technique of bedding, it involves scooping soil into buckets and depositing it bottom-side up (Londo 2001).

One of the most economical site preparation techniques is prescribed burning (McKee 1982, Abercrombie and Sims 1986). Whether restoring process through continued burning or using it as a site preparation technique for planting, fire is a useful tool in restoring pine ecosystems (Knoepp and Swank 1993, Swift and others 1993, Waldrop 1997). Because fire is easily transportable compared to heavy machinery, it is an ideal choice for forest preparation in deep forest interiors and mountainous areas. More information on prescribed burning as a management tool can be found at http://www.forestencyclopedia.net/p/p139.

24.4.2. Site Restoration

Site restoration can occur through the restoration of some combination of species replant and/or prescribed burning as dictated by the environment at hand. For true ecological restoration, replanting efforts on SPB-damaged areas should concentrate on restoring those species that make ecological sense on the area undergoing restoration.

In some cases, restoration will entail restoring the species that existed during the outbreak; in other cases this could involve planting other species. Selection of species for planting should be dictated by determining which species should exist in the restoration area based on site factors. In addition to proper species, proper density must also be considered. In particular, when replanting monospecific pine stands, care must be taken to plant in low densities to impede future outbreaks (Figure 24.3). SPB spots are unlikely to appear in stands that have an inter-tree distance greater than 20 feet (Gara and Coster 1968).

Prescribed burning is currently used in southern pine forests to reduce understory competition and to establish and propagate fire-dependent species (Nowak and others 2008). Recent modeling efforts (Lafon and others 2007,

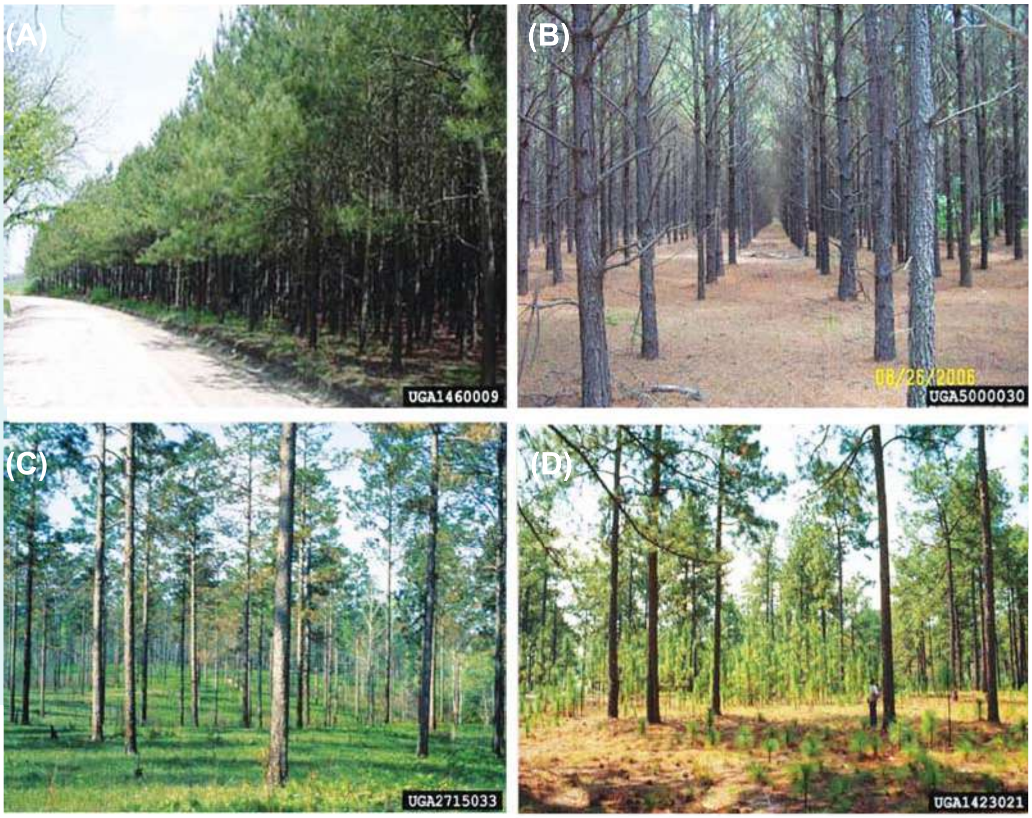

Figure 24.3—Comparisons of options for commercial pine stand types in relation to probability of SPB outbreaks. (A) poor option: very dense loblolly pines, (B) poor option: dense even-aged loblolly pine, (C) better option: less dese even aged longleaf pine, and (D) better option: less dense uneven aged longleaf pine. (photographs (A) by Chuck Bargeron, (B) by David Stephens, (C) by USDA Forest Service Archive, and (D) William D. Boyer, www.forestryimages.org)

Waldron and others 2007) have demonstrated the utility of using fire as a tool in ecological restoration of SPB-damaged areas in the Southern Appalachian Mountains. A more indepth examination of the use of fire as a management tool in the Southern Appalachians can be found at http://www.forestencyclopedia.net/p/p139.

24.4.3. Current SPB Restoration Activities

On January 21-22, 2004, a meeting, "After the Southern Pine Beetle—A Workshop to Discuss Options for Public Lands in the Southern Appalachians and the Cumberland Plateau," was held in Murphy, NC. The goal of this workshop was to have researchers, practitioners, and policymakers share information and discuss strategies on what to do with the hundreds of thousands, if not millions, of acres killed or severely damaged by SPB. The outcomes of this meeting were 3 fold. First, it was determined something has to be done. It was determined that in the modern context of danger from threats such as wildfires and invasive species, as well as the needs of multiple varied forest users, the hands-off scenario of natural regeneration was not a viable alternative. The second outcome of the meeting was that we do not know enough about how to restore these systems. The final outcome was that there is a disjunction in the flow of information between researchers and practitioners. While each of these groups possesses expert knowledge that can better inform restoration, practitioners and researchers more often work apart rather than together to develop viable restoration scenarios.

Current SPB restoration activities include both research efforts and silvicultural activities. The leader in SPB restoration research has been the USDA Forest Service SRS Insects, Diseases, and Invasive Plants Work Unit. Funded research has focused on a wide variety of studies, including silvicultural treatments, ecological modeling, and natural regeneration (Table 24.1). Each of these existing and former research projects has greatly contributed to our knowledge of how to restore SPB-damaged forests. However, much more research is needed to adequately address restoration solutions in the cornucopia of landscapes and forest use types that SPB affect.

The best available data on silvicultural activities are found through the USDA Forest Service Southern Pine Beetle Prevention and Restoration Program (Table 24.2). While I have included data on prescribed burns in this table, it is important to note that prescribed burning has usually been considered a prevention technique in this context rather than a restoration technique. Therefore, the amount of dollars actually spent on restoration, rather than prevention, is substantially lower. In some cases, it is also difficult to discern whether an activity would be classified as restoration or prevention. In fact, restoration should be performed in a way to prevent future outbreaks. Restoration is prevention.

24.5. SUMMARY

Restoration following the southern pine beetle is an intricate and complicated task. A sound understanding of the ecological, political, economic, and social implications of the proposed restoration project is essential. Restoring SPB-damaged areas, as with all restoration planning, involves following a series of steps. The first step in restoration is to determine the goal. Specific goals will vary depending on whether you are restoring ecosystem process or ecosystem service, or some combination of the two. The second step is prerestoration planning, which incorporates knowledge of preoutbreak conditions, current conditions, and potential future conditions. In the context of restoration following SPB, these first two steps are essential. Without proper planning the third and fourth steps have little chance for success at a large cost.

The third and forth steps in this process are the on-the-ground activities associated with restoring a site. The third step is site preparation. Before a damaged area can be restored, the site must be cleared of undesirable conditions to help ensure successful restoration. The final step is restoration itself. The specifics of restoration will vary depending upon the goals, extent of damage, and site location. It is important to keep in mind throughout the process that any action has with it resultant ecological, economic, social, and policy implications that should be addressed in the prerestoration planning phase.

Table 24.1—Restoration research funded by USDA Forest Service, Southern Research Station, Insects, Diseases, and Invasive Plants Unit

Project Title	Lead PI	Institution	Year
Direct Restoration Research			
Development of silvicultural treatments to restore southern pine beetle affected forests in the Francis Marion National Forest	G. Wang	Clemson University	2007
Forest restoration planning and assessment for the southern pine beetle and other invasive pest species	R. Coulson	Texas A&M University	2006-2007
Restoration planning and evaluation following damage by the southern pine beetle in southern Appalachian forests	R. Coulson	Texas A&M University	2003-2006
Restoration planning and evaluation following damage by the southern pine beetle in a sustainable forest management context	R. Coulson	Texas A&M University	2004
Revegetation and forest succession of southern pine beetle-killed shortleaf stands in the southern Appalachian/Cumberland Plateau region	L. Rieske Kenney	University of Kentucky	2004-2005
Guidelines for regenerating small patches of forest killed by southern pine beetle	J. Goelz	SRS-4158	2004
Research that Supports or Informs Restoration			
Determination of stand susceptibility to southern pine beetle during periods of endemic population levels	S. Roberts	Mississippi State University	2007
Southern pine beetle: The causes of transitions between endemic and epidemic conditions	M. Ayres	Dartmouth College	2005-2007
Simulation of dynamics of SPB hazard rating with respect to silvicultural treatment and stand development	J. Goelz	SRS-4158	2005
Landscape evaluation of establishment probability and outbreak potential for southern pine beetle in non-traditional host forests	F. Hain	North Carolina State University	2006
Developing and validating a methodology for monitoring and tracking changes in southern pine beetle hazard at the landscape level	R. Billings	Texas Forest Service	2004

Table 24.2—Outbreak Damage and Restoration Activity by State

	1999 - 2003 SPB Outbreak			2003 - 2007 Restoration Activity		
	Sawtimber killed (*Millions BF*)	Pulpwood killed (*1000s Cords*)	Dollars damaged	Funding given	Prescribed burn (*acres*)	Planting (*acres*)
AL	61	466	$30,144,329	$3,750,000	0	0
AR	0	0	$0	$2,700,000	1113	5120
FL	190	515	$64,080,257	$2,900,000	19563	0
GA	340	319	$82,493,736	$5,550,000	21283	7300
LA	0	0	$0	$950,000	20293	0
NC	191	218	$47,433,306	$9,825,000	0	0
SC	1,176	1,855	$374,601,351	$5,275,000	0	15848
TN	2,081	3,241	$477,904,932	$4,200,000	0	23269
TX	0	0	$0	$4,750,000	0	0
VA	7	31	$1,691,855	$2,025,000	0	171

Restoration activity refers only to funds distributed through the SPB Prevention and Restoration Program.

Funding dollar amounts include allocations for prevention activities which are not presented here. Data sources: http://www.srs.fs.usda.gov/econ/data/spb/, and John Nowak (Unpublished Data)

24.6. ACKNOWLEDGMENTS

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Section IV

IV. Treatment Tactics and Strategies

Section IV addresses treatment tactics and strategies that can be applied to regulate or suppress populations of the southern pine beetle. The unit contains four chapters: the first deals with chemical (pesticide) control procedures, the second deals with use of semiochemicals to manipulate southern pine beetle behavior, the third deals with mechanical control tactics, and the fourth deals with biological control. The chapter dealing with chemical controls examines the various approaches used to apply pesticides, the appropriate forest condition for the approach, and the insecticides approved for this purpose. The chapter dealing with use of semiochemicals addresses the various chemical compounds that have been identified to be involved in host- and mate-finding for the southern pine beetle. Deployment of behavior-modifying chemicals offers an environmentally sensitive approach to suppression of the southern pine beetle. The third chapter deals with mechanical control procedures and addresses specifically how habitat management can be used in suppression of populations and prevention of enlargement of southern pine beetle infestations. The fourth chapter deals with the potential for biological control of the southern pine beetle.

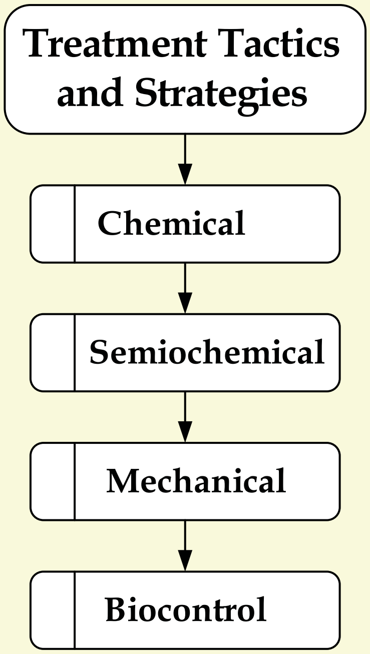

Figure IV.1. Diagrammatic representation of the organization of Section IV of *The Southern Pine Beetle II* dealing with treatment tactics and strategies. This section contains three chapters that deal with tactics involving chemical treatments, semiochemical applications, and mechanical control.

25

Use of Chemicals for Prevention and Control of Southern Pine Beetle Infestations

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Abstract

The southern pine beetle (SPB) is a major threat to pine forests in the Southeastern United States, Mexico, and Central America. In concert with one or more species of southern pine engraver beetles, SPB also may attack and kill pines in residential, recreational, or urban settings. Different control strategies and tactics have been used over the years to try to eliminate beetle problems or reduce resource losses during periodic outbreaks. Insecticides, once the principal means for treating southern pine beetle infestations in forest situations, are now used almost exclusively to protect individual high-value pines in urban settings. Reasons for discontinuation of large-scale insecticide use in forests in the early 1970s included the high cost of chemicals, questionable effectiveness on a landscape scale, and adverse impacts on the beetle's natural enemies. Although mechanical control methods (cut-and-remove and cut-and-leave) have since replaced chemical control in forest situations, there is still a need and demand for insecticides to prevent bark beetle attacks in residential or recreational areas. Currently, only insecticides containing the active ingredients bifenthrin and permethrin are registered and proven effective for prevention of bark beetles in the Southern United States, and application of these chemicals is limited to uninfested pines in residential or ornamental settings. Methods for applying these chemicals to standing trees for prevention of attacks by the southern pine bark beetle guild are discussed herein, together with safety precautions. Various systemic insecticides have recently been evaluated and found effective for preventing bark beetle attack in standing trees. Those containing the active ingredient emamectin benzoate or fipronil show the most promise, and EPA registration of these chemicals is expected. The advantages and disadvantages associated with the use of topical sprays and systemically injected insecticides to treat SPB populations or prevent the colonization of high-value trees also are discussed in this chapter.

Keywords

bark beetles
Dendroctonus frontalis
insecticides
suppression
tree protection

25.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), is a major bark beetle pest of pine forests throughout its range in the Southeastern United States, Mexico, and Central America (Thatcher and others 1980). In turn, this native pest has been the target of more sustained and aggressive direct control programs than any other bark beetle in the world (Billings 1980b). These control programs have been justified due to the economic, social, and ecological impact that periodic outbreaks of this insect are capable of causing to both commercial forests (Clark and Billings 2003, Redmond and Nettleton 1990) and high value pines in residential settings (Hayes and others 1996). A variety of strategies and tactics have been used over the years to address SPB outbreaks (Billings 1980b, Price and others 1998). This chapter describes the use of chemical insecticides in forest and urban situations for prevention and suppression of SPB.

25.2. EARLY DIRECT CONTROL STRATEGY AND TACTICS FOR SPB SUPPRESSION

Before the 1960s, foresters and pest managers knew little about the underlying causes of periodic SPB outbreaks and relationships between beetle attacks and host condition (Dixon and Osgood 1961, Thatcher 1960). In these early days, SPB was considered a beetle problem rather than a tree problem. With a limited knowledge of the insect, early attempts were aimed at eliminating the beetle when outbreaks were detected. At that time, direct control was the first and only line of defense for protecting valuable timber resources (Price and others 1998).

Early methods for killing bark beetles were varied and imaginative—rapid utilization of infested trees (i.e., salvage) and burning infested slabs, tops, and unmerchantable trees (St. George and Beal 1929); immersing infested logs in water (Hetrick 1949); exposing infested trees to solar heating (St. George and Beal 1929); and injecting poisonous chemicals into the sap stream of recently infested trees (Craighead and St. George 1938). Several of these methods proved inefficient, and most were impractical on an operational basis.

The search for more efficient means to kill beetle broods within trees led to the use of toxic chemical sprays. Orthodichlorobenzene in kerosene or fuel oil was successfully used on SPB-infested trees during outbreaks in the 1940s (Thatcher 1960). Following World War II, a new chlorinated hydrocarbon insecticide —benzene hexachloride (BHC)—became available and was first used in 1950 to address a SPB outbreak in East Texas (Billings 1980b). For the next 20 years throughout the South, the standard formulation for SPB control was 0.5 percent BHC in diesel or fuel oil; during summer months, an emulsion of 1 percent benzene hexachloride in water proved equally effective and reduced costs for operational applications (Bennett and Pickard 1966).

With BHC and its gamma isomer lindane as lethal weapons, pest control specialists at that time firmly believed that outbreaks could be suppressed and SPB problems solved by treating a sufficient number of infested trees to eliminate the beetle's pest status, if not the insect itself (Billings 1980b, Thatcher 1960).

The strategy in the 1950s and 1960s throughout the South was to eliminate the beetle population by applying insecticides to all infested trees in as many SPB infestations (called "spots") as possible during periodic outbreaks. Infested trees were identified during aerial surveys and subsequent ground evaluations. All trees with SPB brood or fresh attacks were felled, bucked into logs, and sprayed with BHC using hand-operated sprayers (Figure 25.1A). Prior to 1970, this was the most recommended method for suppression of SPB throughout the South (Dixon and Osgood 1961, Thatcher 1960).

State and Federal agencies, forest industries, and private landowners pursued this brute force strategy aggressively and with dedication. Chemical control had priority over salvage because of the belief at the time that "salvage contributes little or nothing to the control of the beetle population" (Texas Forest Service 1950). No SPB spot was too small to escape treatment if crews equipped with chainsaws and hand sprayers could locate it.

25.3. LIMITATIONS OF CHEMICAL CONTROLS IN FOREST SITUATIONS

Pest managers eventually recognized the limitations of the "kill the beetle" strategy and use of toxic chemicals as the primary tactic for SPB suppression in forest situations. Insecticide applications in commercial forests were expensive and time-consuming. Costs for 0.5 percent solution of BHC in fuel oil ranged from $1 to $10 per tree (Billings 1980b). Keep in mind that fuel oil sold for $0.10-$0.15 per gallon in the 1960s, a fraction of the costs at today's prices. Also, to be effective, chemical controls required careful, thorough treatment to ensure high beetle mortality (Anderson 1967). Infested trees had to be felled and bucked into logs, and each log rolled over so that all bark surfaces could be sprayed.

Perhaps more important, research findings from East Texas suggested that intensive use of chemical control was prolonging, rather than alleviating, the SPB outbreak by selectively

Figure 25.1—(A) Application of the insecticide benzene hexachloride in fuel oil for suppression of southern pine beetle infestations in the 1960s in East Texas (photograph by Max Ollieu, Texas Forest Service). (B) Application of Dursban® to SPB-infested tree in the 1990s, Sam Houston National Forest, Texas (photograph by Ron Billings, Texas Forest Service). Note differences in spray equipment and applicator protection in Figure (A), compared to that shown in Figure (B).

eliminating the principal predator of SPB, the clerid beetle *Thanasimus dubius* (Williamson and Vité 1971). These research findings, coupled with the increasing costs of application, resulted in the voluntary discontinuation of wide-scale chemical control for SPB in the South. By 1970, the BHC era had ended as abruptly as it had begun 2 decades earlier, and the search for new and more environmentally acceptable alternatives had begun (Billings 1980b).

In the late 1970s and early 1980s, two additional insecticides were tested and approved by the Environmental Protection Agency (EPA) for use against SPB: fenitrothion (Sumithion® or Pestroy®) (Billings 1987, Mizell and others 1981) and chlorpyrifos (Dursban®) (Brady and others 1980, Hastings and Coster 1981, Hastings and Jones 1976). These insecticides were used to protect high-value pines in residential areas and, to a limited extent, in forest situations (see Figure 25.1B). The high cost and logistical problems associated with forest applications limited their use for this purpose. More important, about that time, forest pest managers changed their tactics for direct control of SPB in favor of less costly and more environmentally friendly mechanical control methods. Due to environmental constraints, EPA eventually cancelled registration of these insecticides, and they are no longer available for bark beetle control. The registration for lindane was cancelled in the 1990s, despite support for its continued use for bark beetle prevention and control (Swain 1976).

25.4. CURRENT DIRECT CONTROL STRATEGY AND AVAILABLE TACTICS

The strategy for suppression of SPB in forest situations since 1970 has been to reduce resource losses by identifying and treating those SPB spots most likely to expand (Figure 25.2). These expanding infestations typically represent only about 30 percent of all SPB spots detected but account for 70 percent or more of the resource losses (Billings 1980b, Leuschner and others 1976). As a result, they are the primary targets of current direct control programs while cut-and-remove (salvage) (Texas Forest Service 1976) and cut-and-leave (Texas Forest Service 1975) have become the preferred control tactics in forest situations (Swain and Remion 1981).

Recommendation for use of these mechanical control tactics is based on a more comprehensive understanding of SPB biology, host relationships, and seasonal limitations in attack behavior (Billings 1980b, Payne 1980). Because of the proven effectiveness of mechanical control methods under operational conditions (Billings 1995, Clarke and Billings 2003, Redmond and Nettleton 1990), combined with their relatively low cost of application, these tactics have almost entirely replaced chemicals for direct control of multiple-tree SPB infestations (Billings 1980b, Price and others 1998). The rationale for this spot disruption strategy and how to apply the recommended mechanical control tactics are explained in detail in chapter 27.

Figure 25.2—Example of an expanding infestation of the southern pine beetle in East Texas, exhibiting the characteristic pattern of infested trees in various stages of foliage fade. (photograph by Ron Billings, Texas Forest Service)

25.5. SPB AND OTHER PINE BARK BEETLES IN URBAN SETTINGS

Chemical insecticides are still in demand to protect high-value pines from bark beetle attack. Pines in residential settings within the Southeastern United States may be infested by up to five bark beetle species. These include three species of pine engraver beetles (*Ips calligraphus*, *I. grandicollis*, and *I. avulsus*), the black turpentine beetle (BTB) (*Dendroctonus terebrans*), and SPB (Cameron 1987, Conner and Wilkinson 1983). Although the SPB has deservedly received more notoriety as a forest pest, the three species of engraver beetles and the BTB are more ubiquitous than SPB and typically are a more common cause of tree mortality in urban settings. A notable exception is the severe outbreak of SPB in Gainesville, Florida, in 1994-1995 (Hayes and others 1996). Losses of trees in residential or recreational sites (e.g., campgrounds) generally result in reduced shade, screening, and aesthetics; reductions in home property values, and costs associated with hazardous tree inspections and removal (Fettig and others 2009).

25.5.1. Beetle Interactions and Infestation Patterns in Individual Trees

A pine tree may be attacked and killed by a single bark beetle species, but more commonly, two or more species are involved. Each of the five bark beetles typically are found in certain portions of pine trees in the South (Figure 25.3). The black turpentine beetle, the largest of the five species, seldom attacks higher than 10 feet above the ground (Godbee and Franklin 1976). Its attacks can be recognized by the large, reddish masses of resin (pitch tubes) produced along the trunk of the tree. Each pitch tube is about the size of a 50-cent piece and marks the location where an adult BTB has attacked the tree (Figure 25.4). Low-density attacks by BTB may not kill the tree if no other bark beetle species are involved (Cameron 1987).

Of the three species of engraver beetles, the small southern pine engraver (*I. avulsus*) often limits its attacks to the tops and larger branches of stressed pine trees, creating I-shaped parent galleries between the bark and wood (Figure 25.3). If this is the only bark beetle present, the end result may be a topkill in which the lower limbs remain green and the tree survives (Figure 25.5).

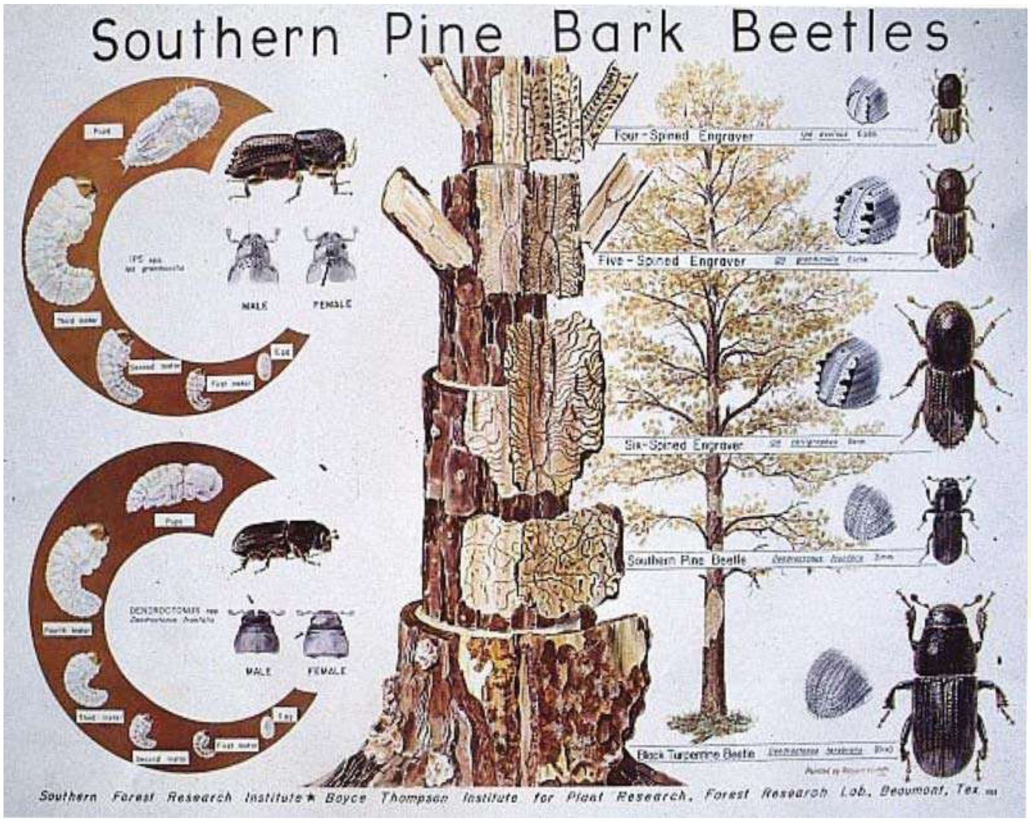

Figure 25.3—Illustration of the five species of southern pine bark beetles, typical position on an infested tree, and their characteristic gallery patterns. (painting by R. Kliefoth, Southern Forest Research Institute, Boyce Thompson Institute for Plant Research, Beaumont, Texas)

The six-spined engraver (*I. calligraphus*) and the eastern five-spined engraver (*I. grandicollis*) are common in the mid-bole region of bark beetle-infested pines, and they may share the tree with SPB, BTB, and the small southern pine engraver (Cameron 1987, Thatcher and others 1978). The parent galleries of engraver beetles are distinct from those made by adult SPB. Indeed, for the nonentomologist, it is easier and more reliable to distinguish SPB attacks from those of engraver beetles by examining the gallery patterns beneath the bark of infested trees rather than trying to identify the adult beetles themselves. Galleries of *I. grandicollis* and *I. calligraphus* are Y- or H-shaped, whereas those made by attacking SPB adults are S-shaped (Figure 25.3). Also, parent galleries of *Ips* beetles are usually maintained free of boring dust; in contrast, SPB parent galleries are packed with this sawdust-like material (Payne 1980).

Figure 25.4—Large pitch tubes characteristic of attacks of the black turpentine beetle on the lower trunk of a loblolly pine; also note coarse resin granules at base of tree. (photograph by Ron Billings, Texas Forest Service)

25.5.2. Symptoms of Bark Beetle Attack

Successful treatment of bark beetles with insecticides, whether for preventive or remedial control, depends on recognizing infested trees during early stages of bark beetle attack. The SPB and three species of engraver beetles have rapid life cycles, and the entire process of attack, colonization, brood development, and emergence may be as short as 25-35 days under favorable temperatures (Conner and Wilkinson 1983, Payne 1980). Thus, beetles may have completed their development and emerged from the infested tree by the time the crown begins to change color and beetle attack is noticeable from a distance. Often the bark beetle population may be found nearby in green-crowned pines.

The first symptoms of SPB or engraver beetle attacks to look for are pitch tubes on the surface of the bark and/or reddish boring dust at the base of the tree or in spider webs and on understory plants (Billings and Pase 1979a; Figure 25.6). These so-called Stage 1 trees will have green crowns, an inner bark-wood interface that is white similar to an uninfested tree, and no bark beetle galleries visible beneath the bark. If sufficient numbers of bark beetles attack, the tree dies rapidly due to the girdling effects of parent galleries and the blue stain fungi—carried by the attacking beetles—that invade and plug the water-conducting tissues of the tree. Once the tree is dead, adult beetles mate and the female lays eggs along the galleries constructed beneath the bark. The eggs soon develop into larvae, then pupae, and eventually into callow adults. Infested (Stage 2) trees supporting SPB broods are typically characterized by a green or fading crown (red crown in winter months), a bark-wood interface that is brown in color, and well-developed S-shaped galleries in the bark/wood interface (Figure 25.3, 25.6C).

Upon completing their development, bark beetles emerge by boring a circular hole through the bark, then fly in search of other trees to attack. The adults often infest adjacent pines in response to aggregation-inducing odors (pheromones) produced by other attacking bark beetles. The life cycle is then complete and immediately begins anew. Stage 3 trees, defined as those vacated by bark beetles, typically have red or bare crowns (although some may still be yellow), will have no bark beetle stages in or beneath the bark, and will have numerous round exit holes about the size of a pencil lead indicating where the beetles have emerged through the bark (Billings and Pase 1979a). Insecticide applications applied to Stage 3 trees will have no effect on bark beetle populations because the trees have been abandoned by the beetles.

25.6. INSECTICIDES FOR BARK BEETLE PREVENTION IN URBAN SETTINGS

The Federal government regulates pesticide use under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA). FIFRA regulations require that all pesticide products be registered by the EPA prior to sale and/or use. Researchers have developed rigorous methods for evaluating the efficacy of insecticides for preventing SPB attacks (Berisford and others 1980) and used these methods to support EPA registration of several new chemicals in the 1980s, including chlorpyrifos (Dursban®) (Berisford and others 1982, Brady and others 1980, Hall and others 1982) and fenitrothion (Hastings and Coster

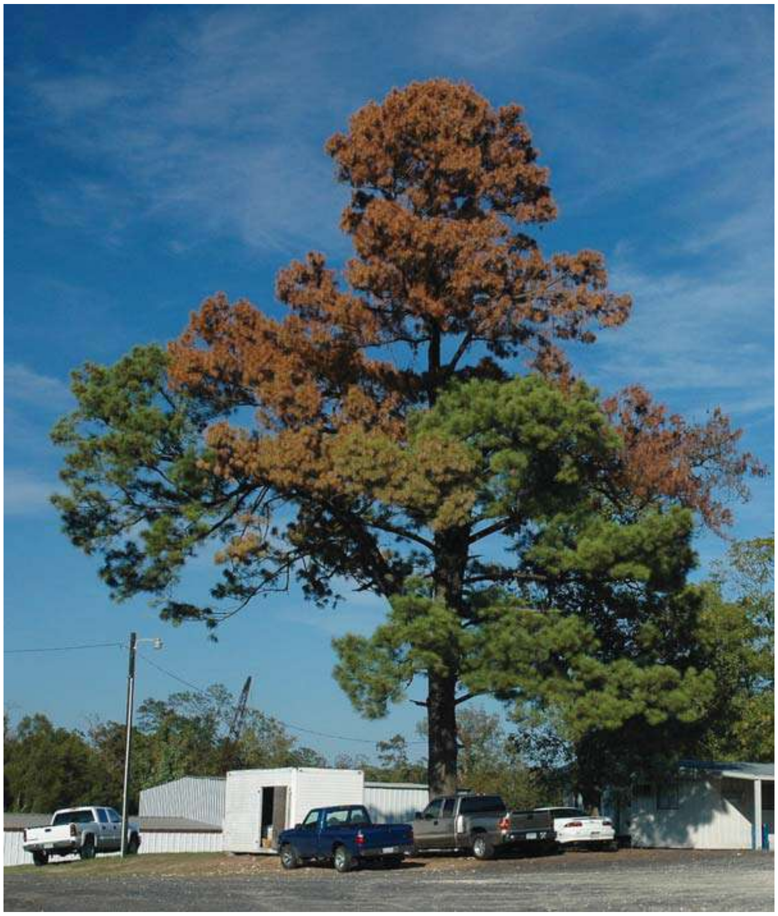

Figure 25.5—Top kill of loblolly pine, indicative of attacks by the small southern pine engraver, *Ips avulsus*. (photograph by Ron Billings, Texas Forest Service)

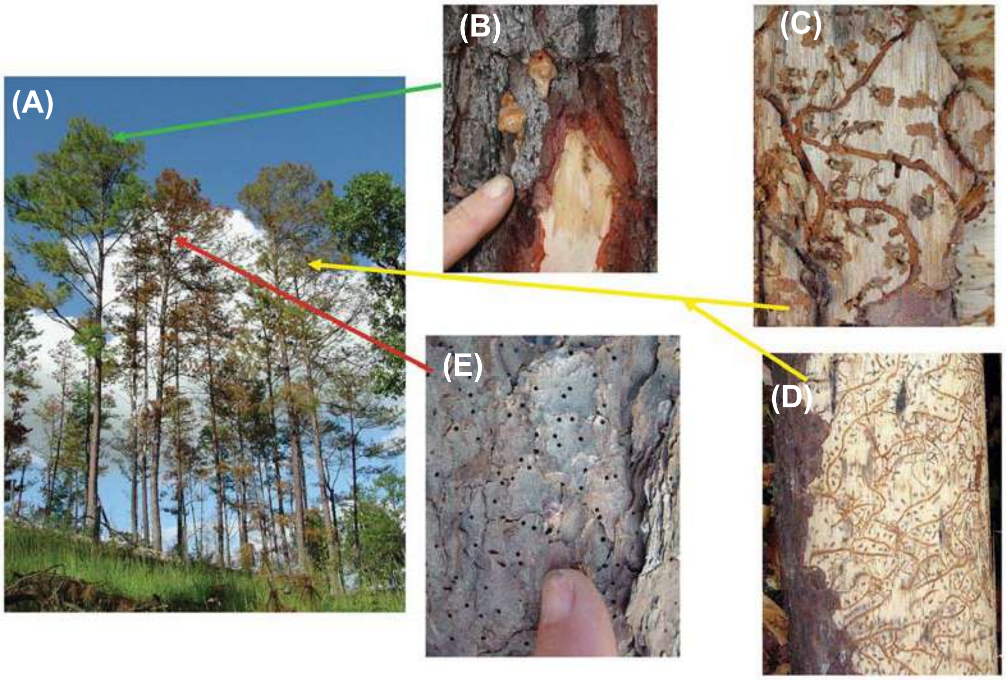

Figure 25.6—Crown color (A) and attack symptoms of a pine freshly attacked by the southern pine beetle (Stage 1) (B), an infested pine containing SPB brood (Stage 2) (C, D), and a tree vacated by SPB (Stage 3) (E) (photographs by Ron Billings, Texas Forest Service)

1981, Hastings and Jones 1976). Unfortunately, the number of insecticides registered for preventive use against bark beetles by the Environmental Protection Agency (EPA) has dwindled in recent years.

Lindane (BHC), chlorpyriphos, and fenitrothion (Hall and others 1982, Hastings and Coster 1981, Swain 1976), chemicals once used for bark beetle prevention and direct control, are no longer available. Carbaryl (Sevin®) is currently registered for bark beetle prevention and control, and frequently used to treat western conifers against bark beetle attack (DeGomez and others 2006; Fettig and others 2006a, 2006b; Gibson and Bennett 1985; Hastings and others 2001; Haverty and others 1985, 1998), but is not effective against SPB (Ragenovich and Coster 1974, Zhong and others 1994). Currently, ornamental pines in residential areas in the Southern United States may be sprayed with insecticides having the active ingredient bifenthrin or permethrin to prevent attack by SPB and related bark beetles. Chemicals containing 23 percent bifenthrin (sold under the trade name of Onyx®) and permethrin (Astro®, Dragnet®, Permethrin Pro®, or Permethrin Plus C® [Masterline®]) are currently registered and commercially available for bark beetle prevention.

For protection of high-value pines in residential areas from possible SPB infestation, a certified pesticide applicator should apply a spray mixture containing 1.0-2.0 pints of Onyx® insecticide (containing 23.4 percent bifenthrin) per 100 gallons (0.25-0.5 pounds active ingredient/100 gallons) of water to the trunk of the tree with a hydraulic sprayer in the spring of the year. Spray as high up the tree as possible, to at least halfway into the live crown, preferably prior to SPB attack. Do not apply more than 0.2 pounds active ingredient (12.8 fluid ounces) of this product to trees per acre. Repeat application may be necessary after 3-6 months or if probability of infestation is high. If Onyx® is unavailable, a registered insecticide containing permethrin (Astro®, Dragnet®, Permethrin Plus-C®, among others) may be substituted using application rates listed on the label. Consult your local State Extension or pest specialist or other qualified expert for more specific recommendations.

Permethrin Plus-C (Masterline) has proven effective for prevention of western pine beetle (*D. brevicomis*) attacking ponderosa pine (*Pinus ponderosa*) in California and mountain pine beetle (*D. ponderosae*) attacking lodgepole pine (*P. contorta*) in Montana for one field season (Fettig and others 2006a). This formulation of permethrin is rather novel because it contains methyl cellulose (i.e., plus–C). The process is thought to increase efficacy and stability by reducing drift, evaporation, and photochemical and biological degradation of the permethrin molecule (Fettig and others 2006a). This product has yet to be thoroughly tested for SPB prevention.

Note that Onyx®, manufactured by FMC Corporation, and the various permethrin products are not registered for use in forestry settings. Also, to prevent bark beetle attack on ornamental or other high-value pines, spray applications must be applied to point of runoff over the entire bole of standing trees (Cameron 1987) or, in the case of SPB, to just the upper half of the bole (Berisford and others 1982). This is difficult to do for trees much larger than about 40 feet tall. Nor are insecticides containing bifenthrin or permethrin registered for use as a cut-and-spray treatment for SPB suppression, as were lindane and chlorpyriphos (Dursban®). Rather, these chemicals are to be applied to standing, uninfested pines to prevent bark beetle attacks. Bifenthrin, the active ingredient in Onyx®, and permethrin, the active ingredient in Astro®, Dragnet®, and other brands, are broad-spectrum insecticides that will kill fish and a wide variety of insects, including bees and other beneficial species. Both chemicals may cause skin irritation and moderate eye irritation, and may be fatal if swallowed. Accordingly, homeowners should follow instructions on the label and take required safety precautions, described in section 25.8.

The safest approach is to hire a registered pesticide applicator or pest control operator (PCO) to make the application. Consult your local State Extension specialist, State Forest Service entomologist, or other qualified expert for specific recommendations.

25.7. INSECTICIDES FOR BARK BEETLE CONTROL IN URBAN SETTINGS

Insecticides are not recommended for application to bark beetle-infested trees in residential settings. Few insecticides are available for this purpose and none are permissible for use in forestry settings. Bark beetles in the South have rapid life cycles, and in most cases, the beetles will have emerged from infested trees before homeowners realize that the trees have been attacked. The best approach is to fell and remove all pines showing signs of bark beetle infestation (boring dust and pitch tubes in bark crevices, fading crowns). A registered insecticide should then be sprayed on uninfested, high-value pines nearby to prevent additional infestations (Cameron 1987, Thatcher and others 1978).

To be effective for remedial control, insecticides must be applied to pines in Stage 1 (fresh attacks) or Stage 2 (with brood). Unfortunately, as of early 2009, no insecticide is registered for this purpose in forest situations. Insecticides containing permethrin (Astro®, Dragnet®, Permethrin Pro®, and others) are available for use on ornamental pines but are of marginal effectiveness for control of SPBs. One botanical insecticide, sold under the trade name of Ornazin® 3 percent EC (AMVAC Chemical Corporation, Newport Beach, CA), is registered for pine bark beetle control on landscape trees. This insecticide contains the active ingredient azadirachtin, derived from the oil found in seeds of the neem tree (*Azadirachta indica*). It is an insect growth regulator that controls various insects in the larval, pupal, and nymphal stages by interrupting the molting process. Although pine bark beetles are listed on the Orazin® label, the efficacy of azadirachtin for SPB control remains to be demonstrated. Accordingly, until proven effective against bark beetles in general and SPB in particular, the author does not recommend this botanical insecticide for SPB control.

In most cases, trees already under attack by bark beetles other than BTB cannot be saved by use of chemical insecticides due to infection by blue stain fungi. If the goal is to reduce survival of beetles infesting ornamental pines, trees infested with SPB and/or *Ips* engraver beetles should be felled and cut into log sections, and the entire infested bole sprayed to the point of runoff (Cameron 1987). Such an approach to direct control, although needed during bark beetle outbreaks, is no longer available in forest situations. This discouraging status of chemical control for bark beetles will remain unchanged until an effective insecticide is developed and registered for this application.

25.8. SAFE APPLICATION OF PESTICIDES

If a homeowner must use pesticides to protect high-value pines from bark beetle attack, he/she should become acquainted with some general precautions to use them wisely and safely (http://ohioline.osu.edu/b504/b504_10.html).

1. Read the label. This is the first rule of safety in using any pesticide—read the label and follow the directions and precautions printed on it.
2. Store pesticides in closed, well-labeled containers out of the reach of children and pets. Do not store them under the sink, in the pantry, or in the medicine cabinet. Do not store them near food of any kind.
3. Store application equipment as you do pesticides—out of the reach of children or pets.
4. Do not save or reuse empty pesticide containers. Dispose of containers promptly as directed on the label.
5. Do not apply more pesticide than the label recommends. Overdosage is wasteful and may be dangerous.
6. Mix or prepare dusts or sprays outdoors or in a well-ventilated room.
7. In handling any pesticide, avoid contact with the skin. Do not get pesticide near your mouth, eyes, or nose.
8. If pesticide gets in your eyes, flush the eyes with water for five minutes; get medical attention.
9. Never smoke, eat, or drink while handling a pesticide. After finishing the work, wash exposed skin surfaces with soap and water.
10. If you spill pesticide on your clothing, launder the clothing before wearing it again.
11. If you become ill during or shortly after using a pesticide, call a physician immediately. From the container label, read to the physician the names of the active chemical ingredients; follow the instructions given for first-aid treatment.
12. Poison information centers are located throughout each state and are on call 24 hours a day. In an emergency, you could call the center closest to you but it

is preferable to let your doctor consult the center. Most telephone 911 systems can contact poison information centers directly.

25.9. POTENTIAL OF SYSTEMIC INSECTICIDES FOR SPB PREVENTION

Protection of individual trees from conifer bark beetles historically has involved topical applications of chemical insecticides to the entire bole of the tree using hydraulic sprayers. Even when available, insecticide spray applications have limitations. They are expensive, difficult to apply, effective for short periods (3-6 months), present a high risk for worker exposure and drift (Fettig and others 2008), and may be detrimental to natural enemies (Billings 1980b, Grosman and others 2002).

Accordingly, researchers have long been intrigued with systemic insecticides as an alternative. These largely water-soluble chemicals can be applied to the soil for absorption through the roots or by direct injection into the trunk. The chemicals are absorbed and transported throughout the sapwood and phloem tissues, and act to repel or kill insects that attempt to feed on or colonize the tree. One of the earliest approaches was to inject systemic chemicals into pines recently infested by SPB as a means to prevent brood development (Craighead and St. George 1938). In most cases, the treated trees died too rapidly to effectively take up the chemical, and this treatment was never used operationally.

In the late 1970s, Crisp, Richmond, and Shea (1979, unpublished data, in Billings 1980b) applied acephate (Orthene®) to foliage of loblolly pines prior to SPB attack at two different rates. The treatments were reported to reduce SPB larval survival but had no effect on eggs, pupae, callow, or parent adults. The investigators concluded that systemic insecticides will need to be more phloem-mobile, more toxic to all bark beetle life stages, and more persistent than acephate if this approach is to succeed.

Applications of fenitrothion (Pestroy®) to basal frills of SPB-infested trees showed promise for reducing SPB brood survival (Billings 1987), but never saw widespread use. Field trials using Mauget® injectors to deliver the insecticide metasystox-R (oxdydementon methyl) have been conducted and determined to be ineffective for bark beetle prevention (Haverty and others 1996). A more recent study evaluated fenitrothion (Pestroy®) and a combination treatment of sodium N-methyldithiocarbamate (SMDC, Vapam®) plus dimethyl sulfoxide (DMSO) applied to bark hacks and dicrotophos (Bidrin®) applied by Mauget® injectors (Inject-a-cide - B®) to trees at the leading edge of SPB infestations (Dalusky and others 1990). Although none of the treatments prevented tree mortality, dicrotophos significantly reduced both egg gallery length and subsequent brood production. Because dicrotophos has a relatively high mammalian toxicity, it is not available to the general public.

Recently two different systemic chemicals—emamectin benzoate and fipronil—have been identified that show substantial promise for preventing bark beetle attacks. Emamectin benzoate (Syngenta Crop Protection), an avermectin derivative, has shown systemic activity in pine and is highly effective against pine wood nematode, *Bursaphelenchus xylophilis* (Takai and others 2000, 2003), and coneworm, *Dioryctria* spp. (Grosman and others 2002). Protection from a single injection has been demonstrated to last more than 3 years. Preliminary trials also suggest that this chemical has insecticidal activity against coleopteran pests, including the Asian longhorned beetle, *Anoplophora glabripennis* (Poland and others 2006). Fipronil (BASF Corporation), a new pheny pyrazole insecticide, also has systemic activity in pine and is highly effective in reducing damage from Nantucket pine tip moth, *Rhyacionia frustrana*, on young seedlings for greater than 12 months (D.M. Grosman, unpublished data).

In 2004 an injection trial was conducted in East Texas to evaluate the potential efficacy of several systemic insecticides for protection of loblolly pine against *Ips* engraver beetles, since no SPB infestations were present in Texas that year. The results with *Ips* bark beetles have shown that both emamectin benzoate and fipronil were highly effective in preventing both the successful colonization of treated bolts 3 and 5 months after tree injection and the mortality of standing trees (Grosman and Upton 2006). However, the difusion of fipronil throughout the tree appeared to be slower than that of emamectin benzoate and provided incomplete protection 4 weeks after injection. Three months following injection, however, the chemical had dispersed enough in the tree to provide full protection from bark beetle attack.

With these positive results, field trials with these systemic insecticides were extended to more aggressive *Dendroctonus* bark beetles to determine efficacy and duration of treatment effects. Data from 2006 and 2007 from Mississippi and Alabama conclusively showed that emamectin benzoate was effective in preventing successful attack by SPB. Fipronil also significantly reduced mortality of trees compared to check trees (Figure 25.7). Emamectin benzoate successfully prevented parent gallery construction, brood development, and emergence of both *Ips* engraver beetles and SPB from treated loblolly pines, whereas

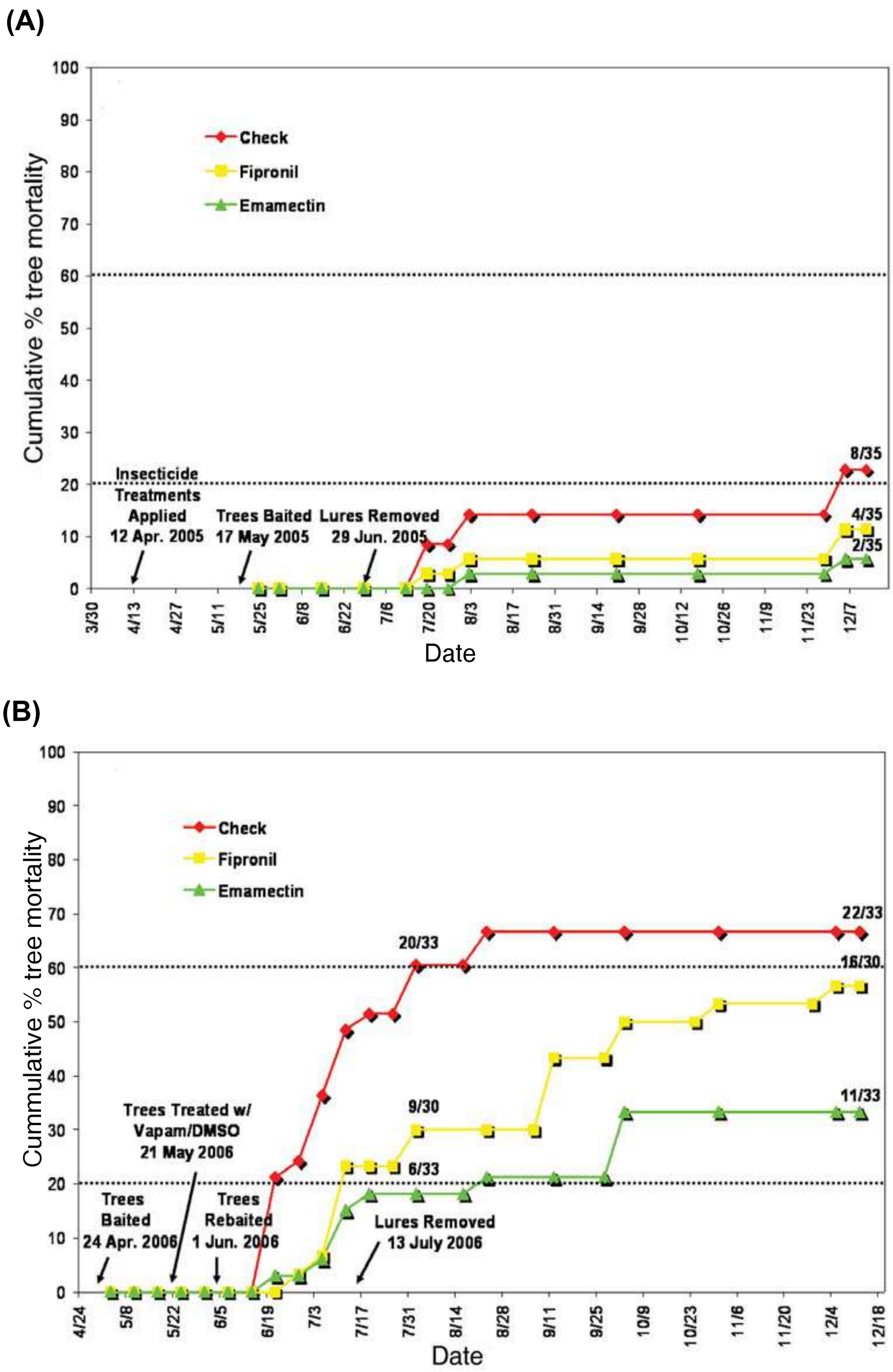

Figure 25.7—Cumulative first- (A) and second-year (B) mortality of emamectin benzoate- and fipronil-treated and untreated loblolly pine, *Pinus taeda* L., after attack by southern pine beetle, *Dendroctonus frontalis*, (2005) and *Ips* engraver beetles (2006), Chickasawhay Ranger District, DeSoto National Forest, Mississippi. The dashed line at 60 percent cumulative mortality is the level of tree mortality considered necessary for a valid test (Shea and others 1984); the dashed line at 20 percent cumulative mortality is the maximum allowable mortality for treatments to be considered efficacious.

Table 25.1—Effects of emamectin benzoate (EB) and fipronil (FIP) injection treatments on mean (± SEM) success of bark beetle adult attack, brood development and emergence, presence of blue stain fungi, and success of cerambycid larvae in logs taken from faded study trees in Mississippi and Alabama – 2006 (Grosman and others 2009)

				Ranking (Percent with:)					
Site	Treatment	N	No. of bark beetle *attacks per 1000 cm2*	Bark beetle galleries (Length > 2.5 cm) present	Bark beetle brood present	Bark beetle emergence holes present	Blue stain fungi present	No. of cerambycid *egg Niches per 1000 cm2*	No. of cerambycid *larval galleries per 1000 cm2*
			Ips Engraver Beetles						
MS	EB	11	9.3 + 1.5a[†]	0 + 0a	0 + 0a	0 + 0a	100 + 0a	22.8 + 4.5a	0.5 + 0.5a
	FIP	16	9.8 + 1.0a	22 + 4b	6 + 4a	6 + 4a	100 + 0a	20.3 + 1.9a	1.9 + 0.9a
	Check	22	9.5 + 0.7a	100 + 0c	100 + 0b	100 + 0b	100 + 0a	16.9 + 2.3a	11.3 + 0.7b
			Southern Pine Beetle						
AL	EB	7	11.0 + 1.8a	0 + 0a	0 + 0a	0 + 0a	100 + 0a	17.8 + 5.1b	0.4 + 0.4a
	FIP	12	11.8 + 1.8a	45 + 11b	46 + 11b	36 + 12b	100 + 0a	11.5 + 1.5a	4.8 + 1.3b
	Check	24	12.3 + 1.0a	100 + 0c	100 + 0c	100 + 0c	100 + 0a	8.9 + 0.8a	10.6 + 5.2c

[†] Means followed by the same letter in each column of the same site are not significantly different at the 5% level based on Fisher's Protected LSD (counts) or Kruskal-Wallis (ranked).

fipronil reduced brood success to a lesser extent (Table 25.1) (Grosman and others 2009). Although several emamectin benzoate and fipronil trees died, the primary cause was most likely the result of numerous inoculations of blue stain fungi by the numerous bark beetle adults that were induced with synthetic pheromones to attack the trees in these trials.

Imidacloprid and dinotefuran, both neonicotinoid compounds that were tested in the same trial, did not appear to have any marked effect against bark beetles (D.G. Grosman, Texas Forest Service, unpublished data). Additional trials to confirm the effectiveness of emamectin benzoate and fipronil against other species of destructive bark beetles and wood borers are currently under way.

It is conceivable that single injections of emamectin benzoate and fipronil may protect trees against bark beetles and wood borers for more than 1 year, as documented for these same chemicals used against other forest and seed orchard pests (Grosman and others 2002, Takai and others 2003). Duration trials using these chemicals for prevention of attacks by *Dendroctonus* or *Ips* bark beetles are needed to validate this hypothesis. Registration of emamectin benzoate and fipronil is currently being pursued with EPA.

25.10. CONCLUSIONS

The reduction or elimination of SPB populations using chemical insecticides was once the principal strategy for addressing periodic outbreaks of this pest throughout its range in the United States, Mexico, and Central America. During the 1950s and 1960s, benzene hexachloride mixed in fuel oil was used extensively to achieve this goal. The increasing cost of applying these chemicals in forest situations, adverse effects on the beetle's natural enemies, and the fact that SPB outbreaks persisted regardless of the level of suppression led to the discontinuation of this brute force approach by the early 1970s. Reducing resource losses by recognizing and treating expanding SPB infestations while they are still small has been the strategy used in recent decades. The primary tactics have been mechanical (cut-and-remove and cut-and-leave) rather than chemical.

There is still a need for chemical insecticides to prevent bark beetle attacks on high-value pines in residential areas, parks, and recreational sites. Unfortunately, most insecticides that have been tested and proven effective for this purpose in the past (e.g., lindane, chlorpyrifos, fenitrothion) are no longer registered for bark beetles. Only insecticides containing bifenthrin or permethrin are available for SPB prevention, and then only to protect trees in urban settings. But these chemicals must be applied as a topical spray, and their use is limited by all the disadvantages associated with such an application (need to cover entire bole of standing trees, possibility of spray drift and applicator exposure, short duration and need for repeated applications every 3-6 months, high cost, mortality of nontarget organisms). Also, bifenthrin, sold under the tradename Onyx®, is a restricted use pesticide that is to be applied only by certified pesticide applicators. Although bifenthrin has been shown to be efficacious for SPB prevention, whether insecticides containing permethrin are equally effective remains in question.

A promising alternative currently under development is use of systemic chemicals. Two active ingredients—emamectin benzoate and fipronil—have shown good efficacy for protecting standing trees from attacks by SPB, engraver beetles, and wood borers. Field trials have demonstrated that a single injection of either systemic insecticide may provide tree protection for 2 or more years. Use of systemic insecticides eliminates concerns with spray drift, threats to nontarget organisms, and for the most part, applicator exposure to the active ingredient. Hopefully, one or both of these chemicals will be registered for use for bark beetle prevention in the near future. It is anticipated that high costs will limit use of high-value pines in residential and recreational areas.

26

Use of Semiochemicals for Southern Pine Beetle Infestation Management and Resource Protection

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Abstract

Since their discovery in the late 1960s, a number of semiochemicals have been identified and deployed for management of the southern pine beetle (SPB). Attractant semiochemicals are used routinely in the Southeast to survey and monitor SPB. Disruptant semiochemicals, primarily verbenone, have shown some promise for spot disruption, but they are not used operationally. Changes in releasers, uncertain demand, uncertain efficacy, and perhaps uncertainty about enantiochemistry have contributed to the current situation in which there is no semiochemical product with an adequate registration and demonstrated efficacy for SPB. Research interest remains, however, largely because there is a paucity of alternatives, semiochemicals offer great flexibility for treating forest resources at a range of spatial scales and resource values, they are generally less toxic than insecticides, and they are believed to be environmentally unobtrusive. Semiochemicals also offer easily observed and sometimes dramatic effects during initial testing. However, when applied for direct control or resource protection, disruptant and/or attractant semiochemicals have been plagued by inconsistent results. Difficulties associated with behavioral complexities, chemistry, performance of release devices, and a lack of knowledge about interactions with the environment have been identified as some of the factors responsible for poor performance. Improving on the research methods used to evaluate and predict semiochemical effects, along with determining the environmental factors that affect when and where semiochemicals can be efficiently and effectively deployed, are keys to their future utility as tools for bark beetle management.

Keywords

direct control
semiochemical application
spot disruption
verbenone

26.1. INTRODUCTION

Direct control tactics against pine bark beetles are deployed when tree resources are imminently threatened. Semiochemicals have been used in this capacity for several decades, producing mixed results over many different types of applications. Some of the primary determinants in choosing a control tactic include the size, location (access), and value of the resource being targeted for protection. Suppression and protection efforts may target individual trees, a stand or smaller group of trees, or area-wide forests. Other considerations include host availability, time of year, costs, expected treatment efficacy, density of pest populations (observed as pest pressure), and the desired future forest condition. While tactics involving tree felling and insecticides traditionally have been employed to suppress southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) infestations, newer techniques utilizing semiochemical attractants and disruptants continue to be developed. In this chapter we discuss the current and potential use of semiochemicals for SPB suppression and resource protection across multiple scales of forest management.

The natural biological and ecological effects of semiochemicals are complex or unknown, making their successful application difficult. Compared to synthetic insecticides, semiochemicals are more flexible across a range of management unit sizes, but less so across bark beetle population densities (pressure levels). Semiochemical applications have been most effective when pest pressures were low or moderate (Bentz and others 2005, Borden 1996, Clarke and others 1999, Payne and others 1985, Progar 2005). Published results are skewed toward successful applications, and semiochemicals have frequently performed poorly when pest pressures or densities were high. In addition, real-world applications often produce results unlike those implied by trapping studies. In field tests, disruptant semiochemicals consistently have affected beetle behavior but have provided inconsistent protection of resources. A major challenge in improving their effective deployment for bark beetle management is the determination of conditions under which resources are sufficiently threatened to warrant semiochemical application but beetle pressures are not so severe that their use has a low probability of success.

Given the challenges and concerns associated with conventional methods of SPB control (e.g., synthetic insecticides and tree felling), the use of semiochemicals is likely to increase. In this chapter, we discuss why disruptant[1] semiochemicals have produced mixed, often unacceptable, results when deployed for managing bark beetles, even after more than 30 years of research and development. We detail the semiochemicals and elution devices used for SPB suppression and resource protection. We outline methods used to evaluate and develop semiochemical products and suggest why they may not accurately predict field efficacy or management utility. We also review the semiochemical tactics that have been developed for SPB and discuss advantages and concerns associated with their use. Finally, we discuss our vision of the future use of semiochemicals for protecting resources against losses to the southern pine beetle.

26.2. SEMIOCHEMICALS IN SPB MANAGEMENT

A number of semiochemicals have been identified that may have applicability in SPB management (Payne 1980, Vité 1970) (Table 26.1). In 1967, *trans*-verbenol and verbenone were identified from SPB (Renwick 1967), making them the first volatile chemicals identified from SPB that were believed important for influencing attack behavior. In the succeeding years, behavioral effects of these and other volatiles were reported for various *Dendroctonus* and *Ips* beetles (Pitman and others 1968, Renwick and Vité 1969). The identification of frontalin and its description as a primary cause of aggregation was reported (Kinzer and others 1969), and the activity of some major host volatiles was also described, including the primary role of α-pinene as a synergist to the attractant frontalin (Renwick and Vité 1969).

It has proven difficult to assign simple behavioral roles to other volatile compounds identified from SPB or its pine hosts. The behavioral effects of the semiochemicals listed in Table 26.1 represent our current understanding of their function. Response of SPB may also be influenced by dosage, purity,

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[1] We use disruptant to indicate a semiochemical treatment that acts to disrupt the host selection process of beetles. We consider antiattractant, antiaggregant, inhibitor, interruptant, masking pheromone, and repellent as synonyms of disruptant. We hope this usage will promote consistency in terminology among stimuli that affect any of a range of behavioral modalities (e.g., vision) while causing similar measured effects; e.g., reduction in numbers caught.

Table 26.1—Semiochemicals that have been used in direct control efforts against the southern pine beetle

Chemical	Putative behavioral effect	Management application	Reference
α-pinene	Attraction synergist	Monitoring/ push-pull (when applied with frontalin)	Renwick and Vité 1969
Frontalin	Aggregation	Monitoring/ push-pull (when applied with host volatiles)	Kinzer and others 1969
Verbenone	Disruption	Resource protection	Renwick and Vité 1969
4-allylanisole	Disruption	Tree protection	Hayes and others 1994
(+)-*endo*-brevicomin	Attraction Synergist/ inhibition?	Uncertain	Sullivan and others 2007b
Trans-verbenol	Attraction synergist	Redundant with α-pinene; not used in direct control	Renwick and Vité 1969
Green leaf volatiles	Disruption	Resource protection	Dickens and others 1992

and stereochemistry, among other things. Verbenone is the most frequently applied disruptant semiochemical, but the behavioral effects of its enantiomers on the SPB have not been fully elucidated. Rudinsky (1973) suggested that high concentrations of racemic verbenone inhibited the response of SPB, while low concentrations synergized attraction. A similar pattern was indicated for myrtenol (Rudinsky and others 1974). The brevicomins, *endo*- and *exo*-, were first identified from *D. brevicomis* in 1968 (Silverstein and others 1968). It is still uncertain whether *exo*-brevicomin is a semiochemical for SPB (Payne and others 1978, Pureswaran and others 2008a); *endo*-brevicomin, however, has long been considered important in SPB communication (Payne and others 1978, Vité and Renwick 1971). *Endo*-brevicomin was first found in small quantities in SPB by Vité and Renwick (1971) and was regarded as a disruptant (Payne and others 1978, Vité and Renwick 1971). Its effects are proving complex, as it is now recognized as a potent aggregation pheromone when placed near, but not with, frontalin and host volatiles (Sullivan and others 2007b). This reversal illustrates how ideas for effective applications can change with increased knowledge. It is now apparent that the concentration and sequence of detection of semiochemicals encountered during host habitat-finding and host selection can affect beetle behavior. Beetle quality and time of year may also alter SPB response to semiochemicals (Berisford and others 1990, Salom and others 1995). These factors complicate the assignation of behavioral labels to semiochemicals. The inability to develop consistently effective semiochemical-based management tactics thus may be influenced by the inherently complex nature of bark beetle communication and behavior. Modalities in addition to olfaction are in play, and the semiochemical environment is a rich and dynamic bouquet of many chemicals and concentrations. These factors may weaken the ability of exogenous and predictable governance of beetle behavior by semiochemicals alone. In the past, the availability of any new semiochemical was often rapidly followed by quick and easy trapping studies and/or field applications. This semiochemical treadmill (testing one semiochemical after another *ad infinitum*) often resulted in conflicting or errant conclusions. Numerous chemicals satisfy the research desire for significant effects in trapping studies; precious few affect bark beetle dynamics in the field or impact forest management. A more careful and thorough approach with improved chemical detection technology and an increased understanding of the role of each semiochemical in host selection and colonization should result in more carefully designed field tests and potentially improved applications of semiochemicals.

26.3. SEMIOCHEMICAL DELIVERY SYSTEMS

Delivery systems are an integral component of semiochemical applications. Releaser designs for forest entomology have four primary goals: release a stable or at least predictable quantity of semiochemical over a useful duration; be inexpensive and rugged; protect the semiochemical from degradation; and provide for safe handling, storage, application and disposal (modified from Holsten and others 2003, Jutsum and Gordon 1989). It is also helpful if a design is appropriate for a variety of chemicals. Devices can be generally categorized using two schemes: the mechanism by which release is controlled (passive vs. active) and their deployment pattern in space (point-source vs. nonpoint-source).

Passive systems are by far the most commonly used for managing insects with semiochemicals. Passive devices are typically first-order emitters, providing a decreasing rate of release over time (Holsten and others 2003, Jutsum and Gordon 1989). They have no power source, and their release rates depend on a variety of extrinsic factors, including the vapor pressure and load of the semiochemical, climatic conditions, exposure, and construction materials. They are relatively inexpensive and qualitatively reliable, but may be prone to leaking and generally are not reusable. Passive devices can also cause storage difficulties (see below). Active devices contain a power source that helps control the release of the semiochemical. These devices often can be programmed to release controlled doses at specified intervals and may achieve zero-order emission; i.e., not dependent on diffusion (Holsten and others 2003). They can be expensive initially (although commercial costs for active semiochemical devices have not been determined), but may be refillable and reusable. Point-source systems are self-contained, discrete devices designed to be applied at specific spatial intervals; e.g., on a grid or on individual trees. Nonpoint-source semiochemical systems are designed to be sprayed or spread across a target area, including by air, for resource protection.

Figure 26.1—A frontalin pouch (left) and *endo*-brevicomin bubblecap. (right). Scale is inches. (photograph by Erich G. Vallery and S. Walters)

26.3.1. Passive Systems

Passive systems are the only device type offered commercially for use in forestry. For SPB, frontalin lures consist of two Eppendorf capsules containing frontalin, sealed in a brown polyethylene pouch (Figure 26.1). Currently, *endo*-brevicomin is released from bubblecaps (Figure 26.1).

In the past, host-based attraction synergists, such as turpentine or α-pinene, were usually released from glass bottles with cotton wicks. At present, these semiochemicals are emitted by diffusion from polyethylene pouches (Figure 26.2).

Commercially available verbenone release devices also consist of a pouch. A specified dose of verbenone is loaded onto a carrier material (e.g., sponge or cardboard tablet backing) and sealed within polyethylene sheeting to make a pouch (Figure 26.3).

26.3.2. Active Systems

The active systems that have been developed are all point-source systems. These devices have most frequently evolved from technologies developed for related purposes with larger markets (e.g., air fresheners). An exception is piezoelectric devices (El-Sayed and Byers 2000), which are specialty devices used primarily for research where quantitative control of release is paramount. They are the most precise and the most expensive (about $2,500). So-called “puffers” were initially designed for delivering air freshener in lavatories. They are not yet commercialized for use in forestry, and must be modified for use outdoors and

Figure 26.2— Commercially available polyethylene sleeves used to enclose host monoterpenes (e.g., α-pinene). Synergy Semiochemicals, Corp. (Burnaby, BC, Canada) ultra-high release a-pinene (upper); Contech/Phero Tech, Inc. (Victoria, BC, Canada) ultra-high release a-pinene (lower). Scale from 0 to 6 is inches. (photograph by B. Strom)

Figure 26.3— Commercially available verbenone devices for deployment against bark beetles. Contech/Phero Tech pouch (far left) and Synergy Semiochemicals pouch (BeetleBlock™ center and right). Scale is inches. (photograph by B. Strom)

with harsher chemicals (Figure 26.4). They hold promise for excellent controlled release at an intermediate cost (estimated at $30-$150 per device), but are unlikely to supplant passive devices in forestry applications unless the necessity for increased control of semiochemical release and semiochemical and device costs changes significantly.

The Med-e-Cell device (Med-e-Cell, Inc., San Diego, CA; Figure 26.5) is less expensive (estimated at <$10) and reportedly is close to being commercialized. It was designed as a general releaser for diverse products, including semiochemicals and air fresheners. Semiochemicals are moved from a reservoir by a controlled pumping process. Chemical release takes place from an emanation pad that is subject to environmental conditions, so properties of the pad (e.g., size and material) must be considered if effective semiochemical release patterns are to be achieved. Though the Med-e-Cell devices may offer improved control over semiochemical release, their performance in forest settings is uncertain as field tests are incomplete.

Active systems may also be programmable, offering the option of turning off the release of semiochemical when its effects are unnecessary (e.g., at night for daytime fliers). This feature can reduce semiochemical costs and waste. The future availability of active devices for use in bark beetle management depends on their

Figure 26.4—Puffer devices adapted for use with bark beetle semiochemicals from Air Delights (Air Delights, Inc., Beaverton, Oregon) lavatory air fresheners. Adaptations include a timer to vary the period between puffs, thereby determining the daily rate of semiochemical released from the reservoir. (Adaptations made by USDA Forest Service personnel at the Missoula Technology Development Center, Missoula, Montana). (photograph by B. Strom)

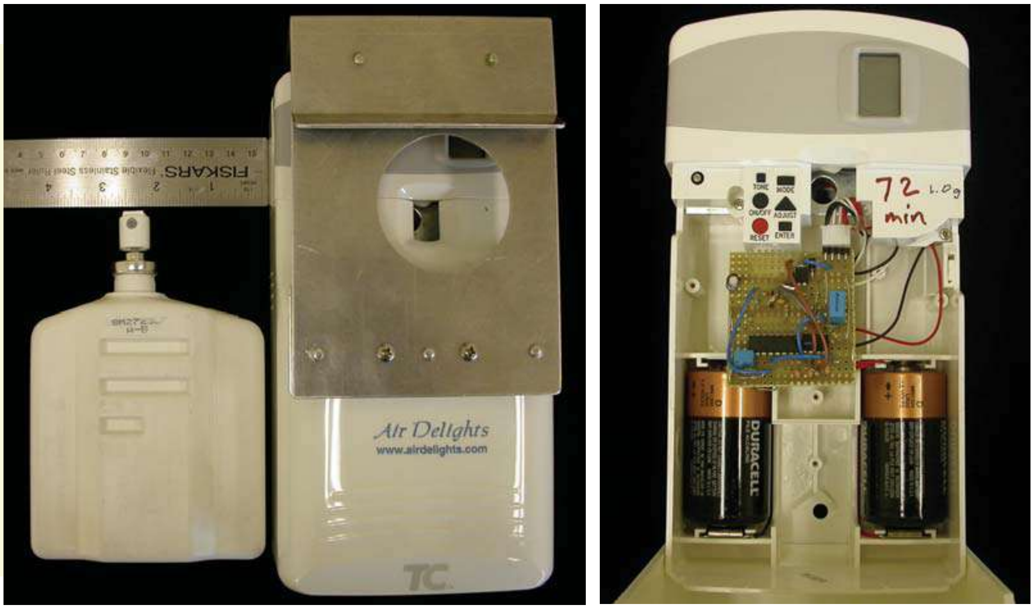

Figure 26.5—Prototype active, point-source releasers (pumps) developed by Med-e-Cell, Inc. (San Diego, California) to release bark beetle semiochemicals. Southern pine beetle verbenone releaser (left) was designed to release about 300 mg per day for 45 days. Western bark beetle version (right) was designed to release about 100 mg of verbenone per day for 3-4 months. Testing of performance in field applications has not been completed. (photograph by B. Strom)

ability to compete with simpler, potentially less expensive (but also less predictable) passive devices. Currently no active devices are registered for use in forest management.

26.3.3. Nonpoint-source Systems

Two types of nonpoint-source systems have been developed for bark beetles: those based on polymer microencapsulation (Payne and Billings 1989, Strom and others 2004) and those based on impregnated flakes or beads (Gillette and others 2009, Shea and others 1992). Registrations were granted in 2008 by the U.S. Environmental Protection Agency (EPA) for use of flakes (Hercon Environmental, Emigsville, PA) against bark beetles. Flake products are available for application against the Douglas-fir beetle, *D. pseudotsugae* (Disrupt Micro-Flake® MCH), and mountain pine beetle, *D. ponderosae* (Disrupt Micro-Flake® VBN), and can be applied by air or ground. The utility of verbenone-impregnated flakes for SPB management has not been evaluated, but they are currently not available with an enantiomeric blend that is suitable for SPB (see below). Their potential use will depend on efficacy, cost, convenience, and environmental effects relative to point-source devices.

26.3.4. Sharing Information on Releaser Performance

Many releaser designs have been developed by research and commercial entities with variable success. Improved dissemination and sharing of information on performance of elution devices (good or bad) is important for their efficient development and effective use. A Web page has been developed by the USDA Forest Service to promote exchange of this information (http://www.fs.fed.us/foresthealth/technology/elutionrate/).

26.4. ADVANTAGES OF SEMIOCHEMICALS FOR THE PROTECTION OF TREE RESOURCES

Semiochemicals are an attractive option for managing bark beetles, primarily due to their perceived lack of environmental intrusiveness, their flexibility, and their simplicity of application relative to other options. Standard practices for controlling SPB infestations are cut-and-remove and cut-and-leave. Pile-and-burn and cut-and-hand-spray with insecticides also have been utilized, but are labor-intensive and are used sparingly. Small infestations often are monitored until they become inactive or increase to a size requiring suppression. Insecticides were once commonly used in infestation suppression, but their use is currently limited to individual tree protection. Semiochemicals offer several advantages over these more traditional techniques.

26.4.1. Reduced Tree Felling

Current methods for infestation suppression all require tree felling. Tree felling is a particularly dangerous activity (USDL-OSHA), and is expensive if trees are not harvested. The development of new techniques incorporating semiochemicals could reduce the need for tree felling in response to bark beetle infestations or pressures, and if effective, would have broad management applicability, including use in special management areas where tree felling is prohibited or discouraged. Effective semiochemical treatments would also be beneficial during extended SPB outbreaks when sawyer availability becomes limited and/or when mills become saturated and low timber prices or lack of access preclude the utilization of cut-and-remove.

26.4.2. Host Specificity

Semiochemicals frequently are quite specific in their behavioral effects, reducing impacts on nontarget organisms as compared to synthetic insecticides or tree felling. Insecticides used against bark beetles are usually applied to the outer bole of either standing or felled trees, limiting nontarget effects in space when properly applied. However, insecticides affect a wide range of insects and may impact those that utilize the bole resource. Tree felling impacts not only SPB but all organisms that use standing trees for habitat and sustenance. Semiochemicals generally affect fewer nontarget species than insecticides, and even if behaviors of nontarget species are affected, individuals are not directly killed. Pheromones in particular tend to affect few species, usually the target insect along with co-occurring guild members and natural enemies. Competitors and natural enemies often use SPB pheromones as kairomones to find susceptible hosts or prey, so thoughtful positioning of SPB attractants can improve treatment efficacy. Salom and others (1995) report that verbenone treatments did not negatively affect SPB natural enemies. Host-based compounds tend to be less specific than pheromones, but are still much more specific than insecticides. Nontarget impacts of semiochemicals are more limited by species (to those that have altered behavior) but greater in space and perhaps time relative to insecticides.

26.4.3. Environmental and Human Safety

Human exposure to semiochemicals is generally low during applications for SPB management. Semiochemicals occur naturally, and related compounds are prevalent in forested environments, so neither the chemicals themselves nor their breakdown products are new to the ecosystems in which they are applied. Their targets are airborne, and significant quantities are not believed to lodge or persist in soil or water resources. The semiochemicals are enclosed within release devices, limiting the amount of human exposure. Proper handling and storage of the devices, plus care in their deployment, such as placing devices out of the reach of children, are essential for the safe application of semiochemicals. These practices are widely followed by forest health professionals.

Semiochemicals are believed to be less toxic to humans and other vertebrates than insecticides used for protective or remedial treatments of trees. For example, verbenone has been evaluated by Syracuse Environmental Research Associates, Inc. (2000). This report provides an oral LD_{50} in rats that ranges from 1 800 mg/kg (females) to 3 400 mg/kg (males). Dermal application of 2 000 mg/kg verbenone to rabbits did not result in any mortality. Synthetic insecticides with product labels for SPB include the active ingredients permethrin (Astro®, FMC, Corp.), with an oral LD_{50} of ~1 000 mg/kg (rat) and >2 000 mg/kg dermal (rabbit) and bifenthrin (Onyx®, FMC Corp.), which has an oral LD_{50} of ~150 mg/kg (rat) and >2 000 mg/kg dermal (rabbit).

Nontarget, nonacute impacts are difficult to evaluate and generally are considered less important than acute, more apparent effects such as toxicity. However, if semiochemical treatments shift from point-source release devices, which are usually removed following their use, to nonpoint-source broadcast applications of sprays, flakes, or beads, environmental impacts may require additional evaluation.

26.5. PROTECTION OF INDIVIDUAL TREES USING SEMIOCHEMICALS

Research into the use of disruptant semiochemicals for protecting individual trees from attack by aggressive *Dendroctonus* species has been ongoing since shortly after the discovery of scolytid disruptant pheromones in the late 1960s (Renwick 1967, Rudinsky 1968). It was quickly recognized that chemicals appearing late in the tree attack process may dissuade beetles from landing or constructing galleries, thereby providing the basis for a potentially useful management tool (Renwick and Vité 1970, Rudinsky 1969). In this realm, semiochemicals compete with insecticides, which can be effective but also expensive and environmentally intrusive. Evaluation of semiochemicals as tree protectants is usually limited to compounds with demonstrated disruptant activity in traps. Therefore, the question of primary interest with trees is not whether the treatment reduces attacks or even mortality; rather, it is whether or not effects are sufficiently large and consistent to prevent tree mortality at a useful level. Inherent in each evaluation are the environmental conditions of the study, especially the level of beetle pressure. To be most useful, studies must ascertain the conditions under which treatments succeed or fail. Semiochemicals have not fared well when two important efficacy criteria have been incorporated into their testing: evidence of demonstrated beetle pressure and a predetermined level of resource protection (efficacy) achieved (Shea and others 1984).

26.5.1. MCH

MCH (3-methylcyclohex-2-en-1-one) has been the most successful disruptant semiochemical used against bark beetles (Borden 1996, Ross and others 2002). It has been deployed primarily for the management of two species: the spruce beetle, *D. rufipennis*, and the Douglas fir beetle, *D. pseudotsugae*. It is well established that treatment of stands with MCH reduces the number of Douglas fir trees attacked by *D. pseudotsugae* (Ross and others 2002). The use of MCH to protect individual trees from *D. pseudotsugae* appears promising (Ross and Wallin 2008), but to date it has not been tested using standard protocols (Shea and others 1984). Applications of MCH for management of *D. rufipennis* are still only in the research and evaluation stage (Holsten and others 2003 and references therein), indicating that it is less effective in this system but its utility not yet elucidated.

26.5.2. Verbenone

Verbenone seems nearly ubiquitous among *Dendroctonus* and produces similar effects among other species when similar methods are used for evaluation. When deployed in traps in combination with attractants, verbenone typically reduces scolytid catch by 40-80 percent (see Borden 1996 for review). However, no published studies confirm the ability of verbenone to protect individual pines from SPB. Recent speculation that greater concentrations of R-(+)-verbenone provide greater disruptant activity than previously thought could renew interest in verbenone for this purpose, but the magnitude of its effects remain to be seen.

26.5.3. Nonpheromones

The most complete evaluation of a semiochemical tree protectant for SPB was done with the host-based disruptant 4-allylanisole (Strom and others 2004). This study evaluated efficacy under both major scenarios that cause tree susceptibility: proximity to attractants and compromised host resistance. 4-Allylanisole failed to provide efficacious protection of trees under either scenario. The inability of 4-allylanisole to deter all bark beetle species (e.g., *Ips*) may have contributed to treatment failure, particularly in trees with compromised resistance. To successfully protect these trees, a product must dissuade attack by numerous insect species, including those that may be more specialized for attacking decrepit trees. The disadvantages of semiochemical specificity are discussed below.

The recent commercialization of green leaf or nonhost volatile products may also affect semiochemical options for resource protection. However, extensive field testing has not yet been conducted, and there is no *a priori* reason to suspect these chemicals will improve upon the use of verbenone alone when deployed against SPB.

26.6. INFESTATION SUPPRESSION USING SEMIOCHEMICALS

The potential for using semiochemicals in suppressing bark beetle infestations has received considerable attention. In this application, managing the SPB is different than other

North American bark beetles because of SPB's affinity for spot formation. Spots provide a defined, biologically relevant unit to target for managing SPB and through which to evaluate success of applications. As discussed earlier, the predominant methods for suppressing infestations all include tree felling, so there is a need for identification and development of tactics that reduce or eliminate the need to fell trees. Even tactics that only slow resource losses until additional suppression activities can be applied may provide some benefit. New and evolving techniques using semiochemicals could fill these needs.

During outbreaks, SPB populations spend much of the year aggregated within expanding infestations. Therefore, semiochemical treatments can be targeted on known beetle locations and positioned according to semiochemical function and treatment objectives. Several tactics using semiochemicals have been tested or suggested for infestation suppression: trap and kill, spot disruption, and spot redirection.

26.6.1. Trap and Kill

Vité and Coster (1973) tested various trap designs for controlling SPB infestations. Traps were coated with sticky material and baited with frontalure, a 1:2 mixture of frontalin and α-pinene that was the standard attractant for SPB at the time. None of the tested designs attracted a sizable number of SPB, as beetles preferred to land on baited host and nonhost trees. The use of baited Lindgren multiple-funnel traps (Lindgren 1983), which provide an attractive vertical silhouette, has not been rigorously tested for infestation suppression. The consensus of SPB researchers and managers has been that baited traps cannot compete with the natural pheromone source surrounding trees under attack (although this is being revisited with the recent addition of *endo*-brevicomin to the attractant lure). Injections of trees with the herbicide cacodylic acid, or a combination of the fungicide metam-sodium and dimethyl sulfoxide (DMSO), have been proposed as techniques for suppressing spots (Roton 1987, Vité 1970). These injections render trees less suitable for brood development. Vité (1970) proposed a technique for utilizing cacodylic acid in spot suppression. Unattacked trees near the most recently attacked trees would be injected with cacodylic acid and baited with attractant to serve as trap trees, with the number of injected trees being approximately twice the number of currently infested trees. Copony and Morris (1972) tested this technique on 65 infestations. The closest unattacked pine to each currently infested tree was injected and baited with frontalure. In addition, every pine within 15 feet of a baited tree was injected. Additional treatments were only necessary on five infestations. Coulson and others (1973a) measured variables associated with the operational use of frontalure and cacodylic acid for SPB suppression in East Texas, and found that injected trees attacked by SPB still supported significant numbers of beetles (Coulson and others 1973b, 1975). As a result, this tactic has not been used operationally.

26.6.2. Spot Disruption

Halting the continued expansion of SPB infestations solely through the use of attractants has received little investigation. In one study, aerial applications of frontalure did not interrupt spot growth, and treatments appeared to increase beetle numbers on trees under attack (Vité and others 1976). Making applications from the ground, Richerson and others (1980) also tested frontalure treatments in active infestations. All trees with SPB larvae, pupae, or brood adults, as well as all nonhost trees within an infestation, were baited. Treatments successfully redistributed SPB within the infestation and prevented new trees from becoming attacked. Payne and others (1985) evaluated frontalure for spot disruption under intermediate and outbreak conditions; they concluded that the technique was more effective under intermediate conditions. This tactic has the potential to shift attacks to uninfested hosts near baited trees, and therefore may have more utility in spot redirection (described below).

Verbenone

Most SPB spot disruption tactics have focused on the use of the disruptant semiochemical verbenone. Early applications used a liquid polymer formulation (Payne and Billings 1989), but inconsistent release properties led to the use of a sponge or foam rubber pad sealed within a polyethylene pouch (Payne and others 1992, and similar to Figure 26.3).

In deploying verbenone against SPB, two tactics have been evaluated: verbenone-only and verbenone-plus-felling. In the former, all trees under attack plus a buffer of trees around the expanding edge of the infestation are treated with verbenone pouches. In the latter, all currently infested trees are felled and verbenone applied to a buffer around the infestation head. The size and shape of the buffers are similar to those applied in cut-and-leave treatments (Figure 26.6).

The elution device tested was a 4.5 x 7 cm cellulose sponge loaded with 5 ml of 34 percent R-(+): 66 percent S-(-) verbenone enclosed in a 6.5 x 10 cm pouch (1.5 mil thick white polyethylene; similar to the Contech/Phero Tech device shown in Figure 26.3). Pouches were tacked to trees at a height of 4 m using a Hundle hammer (Figure 26.7). Pouches were deployed so that they would be outside the reach of humans and approach the height of initial SPB attacks.

Field testing over several years supplied efficacy data from which treatment schedules were developed; Table 26.2 provides the number of devices required for efficacious treatment of infestations based upon these results.

The verbenone-only treatment was most effective on small to moderate-sized SPB infestations in pulpwood or plantations, while verbenone-plus-felling improved efficacy on larger infestations in sawtimber (Clarke and others 1999, Payne and others 1992). Large

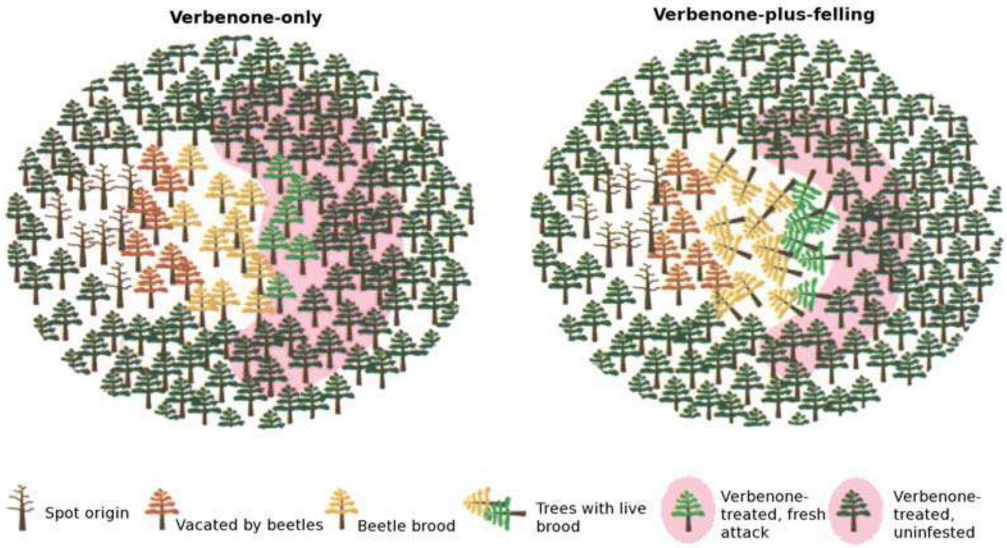

Figure 26.6—Diagrams depicting verbenone-only and verbenone-plus-felling treatments. (figure adapted from Clarke and others [1999])

Figure 26.7—The Hundle hammer (left), and pouch placement on treated trees (right). (photographs by S. Clarke)

infestations with large diameter trees are excluded from the table because the required number of pouches makes their treatment cost-prohibitive. These techniques have not been used operationally.

Hindrances to the operational use of verbenone

Operational use of verbenone with SPB has been hindered by a number of factors. Following the aforementioned efficacy trials, the sponge in the release device was replaced with a gel. The gel-based device was subsequently registered with the EPA by Phero Tech, Inc., and the application tables were no longer sufficient due to different release characteristics of the devices. This registration has subsequently lapsed, and the current Contech/Phero Tech verbenone pouches (Figure 26.3) have not been labeled for SPB. Synergy Semiochemicals Corp. has a verbenone device with a current EPA registration and a label for application against SPB (Figure 26.3). However, the label rates were determined for treating resources against mountain pine beetle, with an upper limit of 60 pouches per acre per year. This number is considered inadequate for most SPB applications (see Table 26.2). The enantiomeric ratio of verbenone that is necessary for effective deployment against the SPB has been researched (Salom and others 1995), and a 34 percent(+):66 percent(-) blend was used by Clarke and others (1999) to develop application schedules. There is recent concern that the most effective enantiomeric ratio of verbenone for SPB treatments may vary regionally or seasonally. It is hoped that an increased proportion of the R-(+)-enantiomer will reduce geographic sensitivity and required dosages, but this has not been tested, and the R-(+)-enantiomer is not as widely available as the S-(-)-enantiomer. Different formulations must be tested throughout the range of SPB to determine if significant increases in efficacy can be achieved through the use of regionally specific enantiomeric ratios. Treatment tables for SPB infestations will need to be developed for any registered verbenone products.

Table 26.2—Recommended number of pouches required to treat an SPB infestation, and their distribution by tree size. Large infestations with large diameter trees are outside of the range of the tables and are not recommended for treatment with verbenone. (Table adapted from Clarke and others (1999))

Verbenone-only

Average DBH (*in.*)	Number of Actively Infested Trees											
	10	20	30	40	50	60	70	80	90	100	110	120
6	50	50	50	63	79	95	110	126	142	157	173	189
8	50	56	84	112	140	168	196	224	252	280	308	335
10	50	88	131	175	218	262	306	349	393	437		
12	63	126	189	252	315	377	440	503				
14	86	171	257	342	428	513	599	684				

Verbenone-plus-felling

Average DBH (*in.*)	Number of Active Infested Trees											
	10	20	30	40	50	60	70	80	90	100	110	120
6	50	50	50	50	50	60	70	80	90	100	109	118
8	50	50	54	70	88	105	122	140	158	175	192	210
10	50	55	82	109	137	164	191	218	246	274	300	328
12	50	80	120	160	200	240	280	320	360	400	432	472
14	54	107	161	214	267	322	374	428	481	534	588	642
16	70	140	210	280	349	419	489	558	628	698	768	

Pouches per tree

DBH (*in*)	<4	8-May	14-Sep	15-17	18-19	>20
No. Pouches/tree	1	2	3	5	7	9

Semiochemical Combinations

Combinations of semiochemicals may improve the efficacy and/or reduce the cost of verbenone-based disruptant tactics while achieving the same or increased levels of effectiveness (Borden and others 2006). Combinations of verbenone and 4-allylanisole were tested on a small number of SPB infestations. The results were highly variable and the tactic was not pursued further (Clarke unpublished data). Green leaf volatiles can reduce SPB catch in attractant-baited traps (Dickens and others 1992), and nonhost chemical blends have been tested alone and in conjunction with verbenone against other bark beetle species (Huber and Borden 2001, Jakus and others 2003, Wilson and others 1996) with varying effects. Pheromones from competing species can disrupt the host selection process of more aggressive species. For example, (+)-ipsdienol serves as an attractant or disruptant for several species of *Ips* (Skillen and others 1997). *Dendroctonus brevicomis* males also produce (+)-ipsdienol, and *D. brevicomis* trap catch is significantly reduced when it is deployed in conjunction with verbenone (Bertram and Paine 1994, Byers 1982, Paine and Hanlon 1991, Strom and others 2001). The utility of nonhost volatiles or pheromones from other species for infestation suppression of SPB has not been tested.

26.6.3. Spot Redirection

Spot redirection seeks to shift the direction of spot expansion into areas that are more accessible for suppression or less suitable for continued spot growth. This tactic is equivalent to the push-pull management strategy used for many major insect pests (Cook and others 2007). In field trials, baiting uninfested trees with attractants in the direction of desired spot growth (pull), alone or in combination with a verbenone buffer around the previously expanding spot head (push), successfully redirected SPB infestation growth (Billings and others 1995). No operational use of this tactic has been reported. However, the increased attractiveness of SPB lures resulting from the addition of *endo*-brevicomin could rekindle interest in developing push-pull treatment methods for SPB, either for spot redirection or spot disruption.

26.7. AREA-WIDE SEMIOCHEMICAL TREATMENTS FOR POPULATION REDUCTION

Area-wide applications of SPB attractants or disruptants have been proposed as treatments for reducing the number and growth rate of infestations within a stand or forest. Gara and others (1965) suggest that field populations could be concentrated on trees or traps baited with attractants. Trees or traps could be arranged in groups or in grids, with trap trees being removed once they are colonized. Area-wide trapping or the timely removal of trap trees may also reduce numbers of natural enemies, so such treatments have been advocated for use during periods of low SPB population densities (Vité and Francke 1976), when impacts on the natural enemy community are presumed to be lower. Area-wide impacts of trap trees baited in the fall and spring during very low SPB population levels are under evaluation in East Texas. The proposed strategy is to concentrate populations of SPB on target trees during seasons when the developmental cycle of SPB is slowed by cool temperatures, thereby allowing more temporal flexibility for harvesting infested trees prior to brood emergence. Numbers of SPB in the western Gulf Coastal Plain have remained too low in recent years to adequately evaluate this strategy. Baiting trees following strip injection with cacodylic acid did not prevent the initiation of new infestations during outbreak conditions (Copony and Morris 1972). Vité (1970) proposed the baiting of trees scheduled for harvest to concentrate and then remove dispersing SPB; however, no tests of this tactic have been reported.

26.8. AREA-WIDE SEMIOCHEMICAL TREATMENTS FOR RESOURCE PROTECTION

Semiochemicals may be distributed throughout a stand or management area to reduce bark beetle attacks and tree mortality. For example, MCH has been applied in a grid pattern to prevent Douglas fir beetle infestations in susceptible stands (Ross and others 2002). Shea and others (1992) reduced mountain pine beetle attacks in lodgepole pine stands by using aerial applications of verbenone-impregnated beads. Borden and others (2003) suggest that a combination of verbenone and non-host volatiles deployed at points throughout a lodgepole pine stand may provide short-term protection from mountain pine beetles. A push-pull strategy to protect high-value lodgepole pine stands from mountain pine beetles has also been tested (Lindgren and Borden 1993). The development of experimental and operational techniques utilizing semiochemicals for this purpose against SPB has not received much attention, primarily because SPB forms discrete infestations during much of the year rather than infesting scattered individual trees throughout a stand. Individual tree protection and infestation suppression using semiochemicals appear to have more practical value at this time.

26.9. CONCERNS WITH SEMIOCHEMICAL-BASED CONTROL TACTICS

The development and application of efficacious techniques for SPB management using semiochemicals comes with an assortment of challenges and concerns. Most important is their inconsistent efficacy. Why this continues to be the case is not certain, but improving our understanding of the semiochemicals, beetle behavior, and role of heterogeneous environments are thought to be keys to increasing the value of semiochemicals for forest management. Many of these problems can be addressed through research and treatment development prior to operational applications. However, it is possible that the complexities inherent with targeted manipulation of beetle communication are too great to allow for simple and robust forest management tools. Regardless of the reasons, there remains no semiochemical-based tactic that is being used operationally with SPB. We have identified some of the challenges associated with semiochemical-based SPB management strategies and divided them into three categories: 1. semiochemical identification and determination of behavioral effects, 2. semiochemical product development, handling and delivery, and 3. design and analysis of experiments.

26.9.1. Semiochemical Identification and Determination of Behavioral Effects

The activities of semiochemicals in an insect community are complex. Even though significant resources have been expended to increase our understanding, semiochemicals remain poorly understood. Pioneering work can sometimes be misleading. Misinterpretations or uncertainties of testing methods or bioassay results, incomplete understanding of the chemicals themselves, activity of mixtures, lack of understanding of insect behavior, and haste for a usable product. all complicate the interpretation of the role of semiochemicals in host selection and mating processes. While applications cannot wait for complete understanding (which likely will never be achieved), knowledge guides the thoughtful deployment of semiochemicals.

The research process for evaluating disruptant semiochemicals is multifaceted. Typically a potential semiochemical is discovered or identified by gas chromatography and mass spectrometry, having originated from the target or related insect, the host, a nonhost, or a combination. Serendipity and market factors also play a role in suggesting new compounds. Once a compound is identified and obtained, the behavioral effects that it causes can be determined. A first step in this process is to test whether the chemical elicits antennal activity in the target insect. This approach can evaluate complex plant tissues as well as individual compounds. Responses to different concentrations and enantiomeric ratios of the chemical often are evaluated. This is an effective method for determining a necessary step in organism response (i.e., the ability to detect the chemical); however, antennal activity does not indicate insect behavior relative to the chemical or necessarily provide a correlation with varying concentrations and behavioral effects in nature. Insects are faced with myriad chemicals during host and mate selection, so antennal response to an individual compound in the laboratory is hardly an indicator of its effects in the field. However, as a tool to filter complex mixtures for potential semiochemicals, antennal detection is unsurpassed.

Once a compound has been identified as a potential semiochemical, the behavioral effects must be determined. There is a paucity of effective whole-organism laboratory assays for bark beetles. The primary method has been a walking olfactometer and its variants (Berisford and others 1990, Hayes and others 1994, Payne and others 1976), but interpretation of results of these bioassays has been uncertain (relative to field results) and is considered as much an art as a quantifiable science. Wind tunnels have been used intermittently with bark beetles (Salom and

McLean 1991), but they have not consistently predicted field behavior and are not commonly used with these species. Because laboratory assays with bark beetles have not consistently produced repeatable or useful results, this step is often bypassed, and field trials are heavily relied upon to evaluate behavioral effects. Field trapping studies are the primary assay through which the nature and extent of semiochemical effects are evaluated; semiochemical utility is predicted from these results until efficacy evaluations can be achieved (see below).

26.9.2. Semiochemical Product Development, Handling and Delivery

Before field trials, and ultimately application tactics, can be realized, an elution method must be selected. The types of semiochemical delivery systems are described earlier in this chapter. Some of the factors influencing the selection of an appropriate elution method are trial or treatment objective, availability, desired concentration, environmental and forest conditions, and cost. Each semiochemical formulation and delivery system has its own set of benefits and concerns.

Consistency

To be successful, semiochemical treatments must be able to suppress infestations or protect trees throughout a wide range of forest and environmental conditions. Treatment results must be robust; i.e., effective and reproducible throughout the range of SPB. Some of the factors affecting consistency are:

Elution rate

Target elution rates are developed over time from observations and research and development; elution devices must be able to deliver chosen rates predictably. Release rates from passive devices, such as pouches, are affected by variables such as temperature, humidity, and sun exposure. Such devices must be designed to elute the semiochemicals at a specified minimum threshold level at the appropriate time of day. Active devices deliver a more certain quantity of the semiochemicals over specified time intervals. Though the release rates of active devices may not be as subject to variations in their environment, the diffusion of semiochemicals into the atmosphere after release is affected by weather conditions and climate. Selecting the appropriate number and placement of the elution devices can help ensure that the target elution rate is achieved.

Enantiomeric ratio

Many of the semiochemicals used in SPB management have enantiomers. Beetles may respond strongly to one enantiomer, while the other enantiomer may elicit no or even an opposite response. Elution devices must contain and release the target enantiomeric ratio and its rate to achieve the desired behavioral result.

Longevity

Devices must release their semiochemicals over a length of time sufficient to accomplish treatment objectives. As a rule of thumb, devices utilized in spot disruption should release the target elution rate for a time period equal to or longer than the length of an SPB generation at the time of application. Devices could be replaced or refilled as necessary.

Chemical degradation

Some semiochemicals can degrade into other compounds over time, affecting treatment efficacy. Temperature and sun exposure can affect the conversion rate. The addition of stabilizers, the proper placement of the devices, and device design, including the use of construction materials that screen out wavelengths that accelerate degradation, can help alleviate this problem.

Storage

Storage of elution devices can be problematic. Commercially available, passive devices are usually preloaded, so will elute semiochemicals at a temperature-dependent rate; they should be kept in cold storage to reduce losses and undesired exposure. The need to purchase, power, and maintain refrigerators or freezers dedicated to the storage of semiochemicals increases costs and can limit their use. Active devices normally contain semiochemicals sealed inside as free liquids, and consequently may require storage in outbuildings with regulated access, similar to insecticide storage.

Durability

In addition to delivering a desired rate of semiochemical over a specified time period, elution devices must be able to withstand a variety of conditions. Point-source devices must be positioned and secured so they cannot be dislodged by wind, animals, rain, or other factors. Nonpoint-source (sprayable) products must hold up under adverse weather and release for a period of time considered adequate for the application.

Retrieval

Reusable devices must be retrieved, and even disposable devices often are collected due to environmental or esthetic concerns. Applying the devices in a safe and secure manner increases the time and effort of retrieval. If retrieval is not planned, then treatments should incorporate biodegradable or environmentally safe materials. For example, aluminum nails can be used to attach pouches rather than steel nails that could damage equipment when trees are harvested and processed.

Cost

Semiochemicals often are expensive, and their application, especially in forested environments, can be time-consuming. Methods to contain costs include: 1. use of less expensive blends (impure chemistries and/or enantiomeric ratios) if efficacious; 2. development of reusable elution devices; and 3. applications during initial ground checks when infestations are smaller, also eliminating the need for a separate treatment visit. The drive to reduce costs also affects consistency. For example, the polyethylene tubing used in device (pouches or sleeves) construction also has other, larger markets that demand low cost over consistency. The resulting differences in allowable film densities may be great enough to affect elution rates from products constructed with these films.

Multiple Sources

The semiochemicals and materials used in device construction may come from multiple manufacturers. Any change in the materials can lead to a change in consistency, efficacy, and cost. Uncertainties about product consistency result in increased research, development, and purchasing costs.

Product Regulation and Environmental Protection Agency Registration

Semiochemical products are shipped throughout the world. The crossing of international boundaries causes cost increases and delays. In North America, semiochemicals and devices used for bark beetle management require EPA registration in the United States and its equivalent in Canada. Registration is a resource- and time-consuming process, and even maintaining registrations can be costly. Any changes in the semiochemicals or devices used can trigger the need for a new registration. Currently there are two semiochemicals with registered products for bark beetles: verbenone and MCH. Verbenone pouches are currently labeled to include treatment for SPB, but product revisions that occurred after extensive field testing and the pouch/acre limitations mostly preclude their use in applications against SPB. The registration of Hercon flakes with verbenone includes SPB, but the product is not offered with an enantiomeric blend that is suitable for application against SPB. There was a prior registration for 4-allylanisole, but it is no longer current.

26.9.3. Design and Analysis of Experiments

Testing and application of semiochemical-based tactics in the field have a unique set of challenges, many related to the concerns with elution devices detailed above. Semiochemicals have been available for evaluation for several decades, and experiences gained over this period suggest areas of particular importance for improving application methods for managing bark beetles. To date, methods have not been particularly reliable in their ability to accurately forecast the utility of semiochemicals for management of bark beetles.

Experiments to evaluate the effectiveness of semiochemicals can be challenging, and have not always used adequate methods. This is true both for trapping studies, which are simpler to design and evaluate, and as management-oriented applications (sometimes referred to as application experiments or administrative studies), which are frequently more challenging in these aspects.

Trapping Experiments

Initial field testing is typically done using funnel traps. Potential attractants are usually judged on their ability to attract higher numbers of beetles into a trap than the standard monitoring lure—in the case of SPB, a combination of frontalin and host volatiles. Disruptants are added to attractant-baited traps to gauge their ability to reduce attraction. Though the results of these trials may be encouraging, they may not be indicative of what occurs when semiochemicals are deployed for resource protection. Synthetic attractants are seldom competitive with natural attacks, causing disruptants to appear more (or perhaps less) effective than they are when deployed operationally.

Trap placement during field trials also can affect results. Historically, traps in SPB semiochemical field trials have been positioned near or within active infestations to ensure adequate numbers of beetles, and traps have been placed fairly close together (Hayes and others 1994). Studies by Turchin and Odendaal (1996) suggest that active radii of traps are fairly large (0.1 ha), and more recently, work by B. Sullivan (personal communication) suggests that measurable interactions may occur between semiochemicals on neighboring traps and from infestations. Traps assessing the behavioral effects of semiochemicals should be widely separated from other sources of attraction or inhibition to be considered independent replicates (Shea and others 1984). Also, we believe that traps should be located a minimum of 7 m, and probably further, from any uninfested host to prevent spillover attacks and the possibility of creating an additional source of attraction. Therefore trapping studies should be interpreted cautiously and, ideally, conducted in large areas with significant background populations of SPB, and with open areas or hardwood inclusions for trap placement.

Statistical analyses of trapping studies are frequently done using inadequate methods (Reeve and Strom 2004). Researchers analyzing trapping studies generally err on the side of methods being too liberally applied (Reeve and Strom 2004), suggesting that treatments appear better than their effects actually indicate.

Application Experiments

The designing of application experiments (i.e., those that test treatments in a management application or scenario) and testing of semiochemicals for infestation suppression can be problematic. Variability tends to be high, and accounting for the variability difficult. Large areas are frequently needed, and untreated infestations may be hard to come by in a randomly assigned structure. Each infestation is different, so variability is high and unexplained error can be large. Therefore, extensive testing is required to document treatment efficacy. Adequate replication is very important, but it is also time- and resource-consuming to achieve. Factors that affect the consistency of elution rates also affect treatment efficacy: time of year, precipitation, temperature, semiochemical formulation, and others. Infestation size and mean tree diameter also impact results (Table 26.2), as large infestations and/or large trees decrease the chance of successful SPB spot suppression. Multiple spot heads complicate treatment, and usually only one spot head can be successfully suppressed at a time.

Treatment Evaluations

Field trials of semiochemicals for infestation suppression must utilize active infestations and prevent further spot growth within set time limits and/or a designated treatment area. Payne and Billings (1989) and Clarke and others (1999) instituted a 1-2 week pretreatment monitoring period to ensure that only expanding SPB infestations were selected for treatment, and to provide a baseline for comparison with post-treatment growth rates. Though the pretreatment monitoring period provides multiple benefits, it also influences successful spot suppression as it may allow spot size to increase. Billings and Upton (1993) predicted tree losses in the absence of semiochemical treatment using the Arkansas spot growth model (Stephen and Lih 1985) to analyze treatment effects.

Clarke and others (1999) established three categories of efficacy:

1. Total suppression. Spot growth is stopped within 6 weeks and the treated buffer is not breached.
2. Partial suppression. Spot growth is reduced by at least 50 percent in 6 weeks, but trees outside the treated buffer are attacked.
3. Ineffective. Treatment failed to reduce spot growth by at least 50 percent within 6 weeks.

Similar infestation selection and treatment efficacy standards should be incorporated into future semiochemical field tests to avoid treating spots that will not grow regardless of treatment, or those that have low probabilities for successful suppression. Acceptable target efficacy rates that indicate a potentially operational suppression method have not yet been firmly established.

Individual Tree Protection

For individual tree protection, candidate semiochemicals that have exhibited promise in trapping studies are applied to pines, either at the head of an active infestation or that have been baited with standard SPB lures. Although somewhat different, both scenarios can provide a rigorous, demonstrable challenge to the disruptant, the former due to the magnitude of attractant in the vicinity, and the latter due to an extended period of attraction. Unlike insecticides, semiochemicals have rarely succeeded in protecting trees in these trials. The similarity of these tests to real-world applications is debatable and varies by environment. However, most management applications occur when a resource is imminently threatened, so tests should incorporate this notion in their design and ensure a rigorous challenge. It can be difficult and costly to achieve tests that demonstrate both sufficient beetle challenge and adequate (useful) tree protection. Long-term trials using at-risk or highly susceptible individual pines could be implemented, but achieving an acceptable mortality level of untreated trees could prove formidable.

Statistical methods for studies of semiochemical efficacy for protection of individual trees have been thoughtfully determined (Shea and others 1984) and applied by many researchers in the forest entomology community. These methods require that two criteria be met for a successfully completed experiment: demonstrated beetle pressure through attack of control trees and a demonstrated, predetermined level of tree survival in the population of treated trees. These procedures require a significant investment of resources and can easily result in insufficient beetle pressure because one has to predict whether beetle activity will be sufficient ahead of time. This is especially true for univoltine species. These methods are also more difficult to apply to species that form spots, such as the SPB, because infestations can start at experimental trees when attractants are used to challenge treatments. Methods that simply compare survival of trees in treated vs. control treatment populations are akin to trapping studies (i.e., they are primarily testing behavioral effects rather than efficacy) and in our view are much less useful.

26.10. FUTURE USE OF SEMIOCHEMICALS FOR DIRECT CONTROL OF SOUTHERN PINE BEETLE

We expect the use of semiochemicals for direct control of aggressive bark beetles, such as the SPB, to increase. This is especially true for disruptants, assuming their availability, and it is likely that their application will be at least somewhat independent of their demonstrated efficacy. There is a paucity of tools for managing SPB, and proven, effective tactics that include cutting trees are dwindling in their availability. Semiochemicals have an allure based upon the behavioral effects they cause; changes in numbers of beetles caught can be very impressive. Their deployment and comparison against a no-treatment option is often relatively uninformative, but continues to be used as a standard. This approach also promotes the semiochemical treadmill in which a variety of compounds, each having some level of demonstrated ability for reducing catch of bark beetles in traps, are deployed in a stream of tests without much regard for their utility in management. Semiochemicals also appeal to public land managers who wish to demonstrate that they have done something to suppress infestations or save resources, even if applications do not provide the desired result.

On the positive side, semiochemicals do produce behavioral effects in the target insect and offer hope in a package that is relatively unobtrusive toward the environment. As we learn more about their deployment, increase our chemical options, and improve release devices and tactics, we may determine combinations that are more efficacious. Most important, we may measure a sufficient number of environmental factors to provide more effective guidance on when and where semiochemicals can be efficiently and effectively applied to achieve an acceptable management result. This is the major challenge facing effective deployment of semiochemicals for direct control of bark beetles.

27

Mechanical Control of Southern Pine Beetle Infestations

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Abstract

Periodic outbreaks of the southern pine beetle (SPB) may affect thousands of acres of commercial pine forests in the Southeastern United States, Mexico, and Central America. Accordingly, this species is the target of more aggressive and effective suppression programs than any other bark beetle pest in the world. The strategy for controlling the southern pine beetle during periodic outbreaks has changed in recent decades. Attempts to eradicate beetle populations by treating all infested trees with insecticides, the strategy prior to 1970, has been replaced with mechanical control tactics as a means to reduce resource losses. Once multiple-tree SPB infestations (spots) become established and exceed a certain size threshold (about 30 infested trees), they may rapidly expand and persist for multiple beetle generations, until lack of hosts, cold temperatures, direct control, or other factors intervene. The current strategy for suppression relies on identifying those SPB spots capable of rapid and prolonged expansion and treating these with mechanical control tactics to prevent loss of additional trees. Principal tactics are cut-and-remove (salvage removal) and cut-and-leave. A third tactic, pile-and-burn, is available but seldom used. Both cut-and-remove and cut-and-leave involve felling all brood trees plus a buffer of adjacent uninfested trees to disrupt further spot growth, the primary means of host tree colonization and beetle survival during summer months. In the case of cut-and-remove, felled trees are removed from the site and sold to a mill, further reducing the landowner's economic losses. The cut-and-leave tactic involves felling targeted trees (those containing SPB brood, fresh attacks, and adjacent buffer trees) toward the center of the infestation and leaving them onsite. Most spot disruption tactics are applied during the summer months when beetles are least capable of dispersing long distances or initiating large infestations. These tactics have proven effective in reducing tree losses up to 85 percent. Some mortality of SPB broods may occur in trees felled in cut-and-leave treatments, but this effect is not consistently achieved nor required for treatment success. Direct control, however, is just one option for effective management of SPB. A comprehensive pest management system also requires monitoring, prediction, early detection, and evaluation of infestations, as well as preventing beetle problems through silvicultural treatments of beetle-prone pine stands (discussed in other chapters of the Southern Pine Beetle II). This chapter discusses the rationale, methods of application, and effectiveness of mechanical control treatments (cut-and-remove, cut-and-leave, and pile-and-burn) for addressing SPB outbreaks.

Keywords

bark beetles
cut-and-leave
cut-and-remove
Dendroctonus frontalis
direct control
suppression

27.1. INTRODUCTION

Of the five pine bark beetle species that occur in the Southern United States, the southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB), is by far the most important tree killer (Coulson and others 1972, Dixon and Osgood 1961, Thatcher and others 1980). The other bark beetles—the six-spined engraver beetle, *Ips calligraphus*, the eastern five-spined engraver beetle, *I. grandicollis*, the small southern pine engraver beetle, *I. avulsus*, and the black turpentine beetle, *Dendroctonus terebrans*—are less aggressive pest species. These bark beetles usually limit their attacks to single trees and stands under severe stress or, in the case of *Ips* spp., to fresh slash or pine logs (Conner and Wilkinson 1983, Foltz and others 1984, Thatcher 1960). Direct control, other than removal of infested trees, is seldom applied to these secondary bark beetles in forest situations. In contrast, the SPB is the target of more aggressive, sustained, and effective direct control programs than any other bark beetle species in the world. This chapter describes the direct control strategy and various mechanical control tactics currently in use to address SPB outbreaks. Their effectiveness in suppression programs for reducing timber and other resource losses to SPB also is discussed.

27.1.1. Range of SPB

The range of SPB within the United States extends from New Jersey south to Florida, and west to eastern Texas, coinciding with the range of its principal host, loblolly pine (*Pinus taeda*). A population of *D. frontalis* occurs in southern Arizona (Wood 1963), along with a newly discovered population of a sibling species, *D. mexicanus* Hopkins (Moser and others 2005). The SPB also is found in Mexico, Guatemala, Belize, El Salvador, Honduras, and Nicaragua, where it is a major pest of native pine forests (Cibrián Tovar and others 1995, Vité and others 1975) and a target of suppression programs (Billings and Espino-Mendoza 2005, Billings and others 2004, Sanchez-Martinez and others 2007).

27.1.2. Causes and Duration of SPB Outbreaks and Declines

As documented by Price and others (1998), SPB populations in the Southern United States may reach outbreak levels every 6-10 years, with high populations occurring almost every year in different parts of its range. SPB outbreaks have been associated with a variety of predisposing factors. These include climatic factors that stress host stands at the landscape level (Craighead 1925, Kalkstein 1976, King 1972), an abundance of susceptible hosts (Coulson 1979, Hedden 1978, Mawby and Hain 1985), homogeneity of pine-forested landscapes (Coulson and others 1996b, 1999b), and other factors (Coulson 1980, Moore and Thatcher 1973, Turchin and others 1991). In the Southern United States, a typical SPB outbreak will last 3-4 years before populations decline to low levels, although some have persisted for decades (Price and others 1998). Resource losses during these periodic outbreaks may be severe, particularly if no direct control is applied (Figure 27.1B).

What triggers the collapse of SPB outbreaks is poorly understood, but contributing factors include an increase in natural enemies, interspecific competition with other bark and wood-boring insects, increase in blue stain fungi, lack of susceptible hosts, unfavorable weather, or a combination of these and other factors (Bridges 1985, Clarke and Billings 2003, Coulson 1980, Turchin and others 1991). Suppression programs for SPB in the Southern United States have been implemented since at least the 1920s with the goal of reducing potential timber and other natural resource losses during these periodic outbreaks (Billings 1980b, St. George and Beal 1929).

27.2. SEASONAL BEHAVIOR OF SPB AS RELATED TO DIRECT CONTROL

It is important to point out that, although closely related genetically to tree-killing bark beetles in other regions of the world (e.g., mountain pine beetle [*D. ponderosae*], western pine beetle [*D. brevicomis*], spruce beetle [*D. rufipennis*], European spruce beetle [*D. micans*]), the southern pine beetle is unique in many ways (Coulson 1979, Wood 1963). Knowledge of the unique dispersal and attack behavior of SPB and how this behavior changes with the seasons is essential for understanding how mechanical control strategies and tactics function to curtail SPB-caused losses.

27.2.1. Advantages of a Rapid Life Cycle

The SPB may complete up to seven generations per year in the Gulf Coast Region (Thatcher and Pickard 1967) and possibly 10 or more

(A) Small, expanding SPB spot **(B)** Large, expanding SPB infestation

(C) SPB spot controlled by savage **(D)** SPB spots controlled by cut-and-leave

Figure 27.1—Expanding (A and B) and controlled (C and D) southern pine beetle infestations (spots) in loblolly pine forests of East Texas. (photographs by Ron Billings, Texas Forest Service)

generations per year in Central America (Vité and others 1975). In contrast, other species of *Dendroctonus* bark beetles have just one or two generations per year (Wood 1963). This rapid life cycle accommodates a high reproductive potential and an attack behavior that is unique among bark beetles (Coulson 1979, 1980). During outbreaks, SPB tends to infest concentrated groups of trees, creating infestations that have the potential to continuously expand over time. These mortality centers, commonly called "spots," may range in size from a few trees at initiation to several thousand acres under favorable conditions (Figures 27.1A and 27.1B). As large SPB spots expand, beetles responding to aggregation pheromones often kill essentially every pine tree in their path over the age of 5 years, regardless of the tree's physiological condition (Payne 1980).

27.2.2. SPB Spot Dynamics

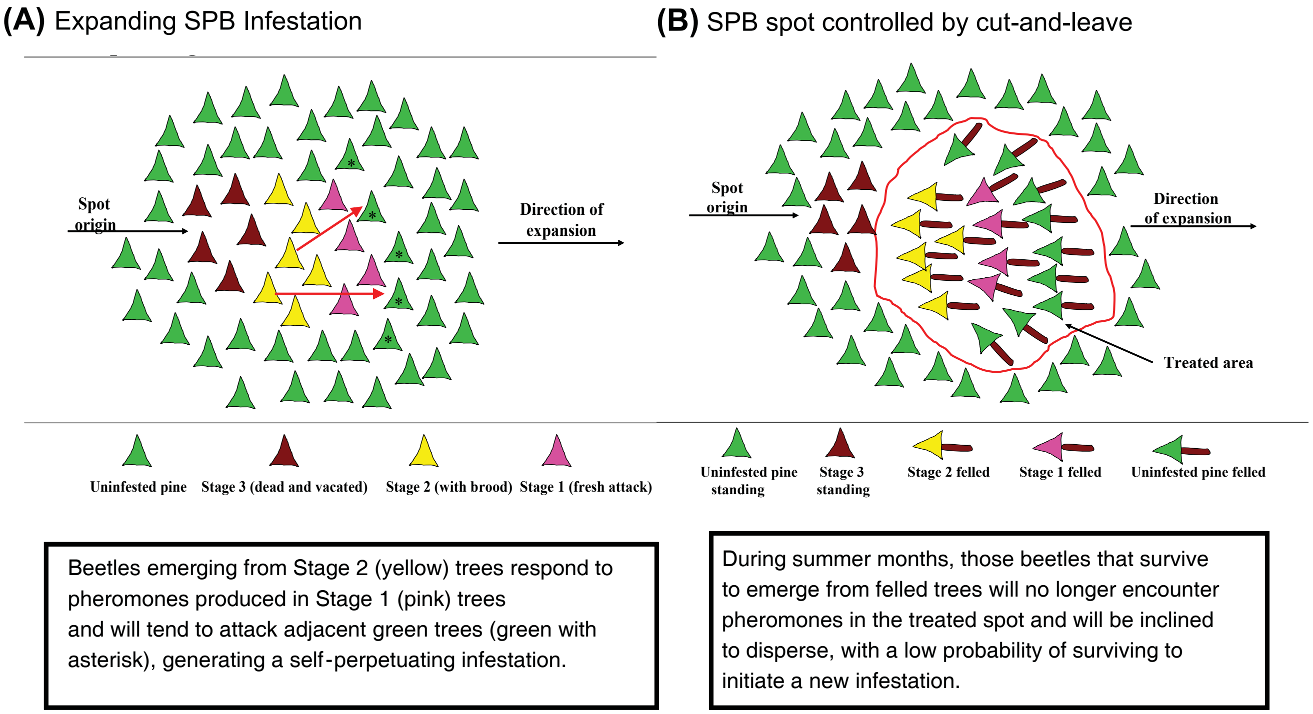
Research (Billings 1995; Billings and Kibbe 1978; Coulson 1980; Thatcher and Pickard 1964, 1967) and practical experience (Texas Forest Service 1978) have documented that SPB may be in flight and capable of attacking trees throughout the year. Yet the beetle's long-range dispersal capabilities, attack behavior, reproductive potential, and longevity, among other behavioral traits, vary with the seasons (Coppedge and others 1994, Coster and others 1977b, Hedden and Billings 1977, Thatcher and Pickard 1967). In the Southern United States, long-range dispersal begins in March or April, coinciding with the time when dogwoods bloom (Billings 1988, 1997).

In East Texas, and probably in other Gulf Coastal States, the progeny produced by SPB adults that attack trees during the 17-week period during November through February typically emerge in concentrated numbers during a 6-week period in March and early April (Billings and Kibbe 1978). This spring emergence event in the absence of pheromone production within overwintering infestations produces a large aerial population that leads to long-range dispersal and initiation of many new infestations (Coulson and others 1972, Texas Forest Service 1980).

During the spring, new SPB spots are initiated by pioneer beetles that locate and aggregate on weakened trees (Gara and Coster 1968), often on lightning strikes (Coulson and others 1983, 1985a, 1986; Hodges and Pickard 1971) and/or in over-crowded pine stands (Coster and Searcy 1981, Coulson and others 1974, Mason and others 1985). The attraction, a combination of the beetle-produced aggregation pheromone frontalin and host volatiles, generated by these initially attacking beetles as they colonize pines draws in other beetles flying in the area (Coster and others 1977a, Gara 1967). These new infestations are detected by aerial observers primarily in June, July, and August (Billings and Doggett 1980, Coulson and others 1972).

Presumably, a large, expanding infestation develops when pheromone production is successfully maintained within the newly created spot for a minimum of 30-40 days by beetles immigrating into the area and/or by re-emergent parent beetles. By then, beetle broods will have completed development within the first trees to be attacked at the spot origin, and the spot will contain brood trees with SPB in all life stages (eggs, larvae, pupae, and new adults). Under these conditions, new adult beetles and reemerging parent beetles will tend to attack additional trees on the periphery of the spot from which they emerged in response to the pheromones emanating from freshly attacked pines (Coster and Johnson 1979a, Gara and Coster 1968). In this manner, a required synchrony between beetle emergence and pheromone production is established, leading to the process known as spot growth (Gara 1967, Hedden and Billings 1979, Schowalter and others 1981b). When this synchrony is achieved, a self-perpetuating SPB infestation is established that no longer requires beetles immigrating from distant sources (Texas Forest Service 1978) (Figure 27.2A).

Spot growth, a phenomenon unique to SPB, is the primary mode of host colonization and SPB survival during summer months (June through September) (Coulson and others 1985a, Schowalter and Turchin 1993). During hot summer months, long-range dispersal of SPB adults is curtailed, and few new, expanding infestations are initiated (Cameron and Billings 1988, Hedden and Billings 1979). By attacking pines on the periphery of the spot from which they emerged, SPB adults effectively maximize their survival when temperatures are high (Schowalter and others 1981b). SPB broods emerging from expanding infestations avoid exposure to all the natural mortality factors associated with long-distance dispersal and initial host colonization (Coulson 1980). When SPB populations reach high levels, even healthy pines of all ages beyond 5 years are commonly infested on the periphery of expanding infestations due to the concentration of attacking beetles (Payne 1980).



Beetles emerging from Stage 2 (yellow) trees respond to pheromones produced in Stage 1 (pink) trees and will tend to attack adjacent green trees (green with asterisk), generating a self-perpetuating infestation.

During summer months, those beetles that survive to emerge from felled trees will no longer encounter pheromones in the treated spot and will be inclined to disperse, with a low probability of surviving to initiate a new infestation.

Figure 27.2—Illustration of an expanding southern pine beetle spot (a) and a similar infestation controlled by cut-and-leave (b). (illustration from Fettig and others 2007)

In the fall, as ambient temperatures become more moderate, emerging beetles tend to fly longer distances to attack individual trees and small groups of trees in adjacent stands. This seasonal behavior redistributes the population in the landscape prior to the winter (Thatcher and Pickard 1964). During the winter when temperatures exceed about 60° F, emerging SPB often attack uninfested portions of the same trees from which they emerged (Thatcher and Pickard 1967).

27.2.3. Why Do Many SPB Spots Go Inactive?

Large, expanding SPB spots cause most of the economic losses during outbreaks, and as a result, are the primary targets of suppression programs during the summer and fall months (Billings 1995, Redmond and Nettleton 1990). The majority of newly established infestations, however, do not exceed 50 trees in size (Leuschner and others 1976), and many are inactive (abandoned by SPB) even when first ground checked with no need for control (Billings 1974). So why do some spots become large while others remain small and soon go inactive?

The initiation and establishment of a continuously expanding SPB spot that is capable of sustaining itself for multiple SPB generations is a complex process that requires several critical events:

- A large aerial population of SPB adults
- Favorable weather for prolonged emergence and long-distance flight
- A susceptible host, often a lightning-struck pine, located in a dense pine stand having reduced host resistance to bark beetle attack
- Continuous production of aggregation pheromones and host odors over at least a 30-day period
- Immigration of adult SPB into the spot from distant brood sources for the same 30-day period (supplemented by parent beetles reemerging within the new spot), resulting in a spot with > 30 beetle-infested trees

Only when all these criteria are met will an SPB infestation become established and increase to a large size (Coulson and others 1985a, Hedden and Billings 1979, Schowalter and others 1981b). The fact that most large, expanding spots are initiated in late spring or early summer (Coulson and others 1974) provides evidence that the criteria listed above are most likely to coincide during this season. Inactive spots are those in which the beetles have failed to establish or maintain the synchrony between beetle emergence and pheromone production required for continuous spot growth (Gara 1967). Spots initiated after the spring dispersal season has ended and in pine stands with low densities are unlikely to persist or expand beyond a few trees (Cameron and Billings 1988, Coster and Searcy 1981, Hedden and Billings 1979, Johnson and Coster 1978, Schowalter and Turchin 1993). In such cases, all the criteria required for continuous spot growth were not met or sustained.

27.3. CONTROL STRATEGY FOR SOUTHERN PINE BEETLE

Expanding spots typically represent less than 25 percent of all spots detected during outbreaks but account for more than 60 percent of the timber losses (Lueschner and others 1976, Texas Forest Service 1980) (Figures 27.1A and B). These spots are the primary targets for current suppression programs (Billings 1980b, Redmond and Nettleton 1990).

The strategy for direct control of SPB outbreaks has changed over the years. Prior to 1970, the strategy was to eliminate SPB populations by killing developing broods within infested trees prior to emergence. This was first done by mechanical methods (St. George and Beal 1929) and later with use of chemical insecticides (Bennett and Pickard 1966, Dixon and Osgood 1961, Thatcher 1960). Despite dedicated efforts, this strategy was costly and of questionable effectiveness. Indeed, intensive use of chemical insecticides in the 1960s may have prolonged an SPB outbreak in East Texas by selectively eliminating the beetle’s natural enemies (Williamson and Vité 1971). The widespread use of chemical insecticides for SPB suppression was largely discontinued across the South in the early 1970s in favor of spot disruption tactics (Billings 1980b).

Since 1970, the SPB control strategy has been to reduce economic losses by mechanically disrupting the unique attack behavior of SPB that leads to development of continuously expanding infestations. Current suppression programs are aimed primarily at reducing the survival and success of the adult beetle population following emergence from brood trees. Reductions in survival of developing broods within infested trees, when and if they are achieved, are considered a secondary benefit of spot disruption tactics. Spot disruption tactics capitalize on the seasonal limitations of SPB by forcing emerging beetles to disperse from treated spots, greatly jeopardizing their survival, particularly during summer months. The result is reduced resource losses, compared to those in untreated infestations (Billings 1995, Clarke and Billings 2003) (Figures 27.1C and 27.1D).

27.4. SETTING PRIORITIES FOR CONTROL OF SPB INFESTATIONS

Direct control measures are applied differently for SPB compared to other *Dendroctonus* bark beetles. In the case of SPB, the strategy to minimize resource losses relies on identifying which infestations are most likely to expand, then treating this subset of the entire population of spots to assure that spot expansion is halted. The methodology developed over the years for distinguishing expanding spots from nonexpanding or inactive spots begins in the detection stage and continues with the ground evaluation phase (see chapter on aerial detection, ground evaluation, and monitoring SPB populations).

Aerial observers are trained to set minimum spot size thresholds (usually 5-10 yellow-and red-crowned trees), since experience has shown that spots with less than 10 dying trees have a high probability of being inactive (abandoned by beetles) upon subsequent ground check (Billings 1974). Furthermore, each spot that aerial observers record may be assigned a ground check priority during detection flights, based on the total number of visibly infested pines and presence of yellow-crowned trees (Billings and Doggett 1980, Billings and Ward 1984). The absence of trees with fading crowns indicates spots that are unlikely to expand or infestations caused by mortality agents other than SPB (Billings 1979).

In turn, during the ground evaluation phase, crews locate the infestation on the ground, confirm the causal agent, and evaluate the level of SPB activity, based on the number of Stage 1 (fresh attacks) and Stage 2 (SPB brood) trees (Table 27.1). Then a control priority is assigned to each spot, based on factors listed in Table 27.2 (Billings and Pase 1979a). High priority for control is given to those spots most likely to cause further economic losses if not treated (e.g., spots in expansion, particularly large spots in sawtimber stands). Indeed, several practical spot growth models have been developed that allow pest managers to predict tree losses within SPB spots in the absence of direct control. These range from simple one-page prediction tables (Billings and Hynum 1980) to more sophisticated mathematical models (Hedden 1985, Reed and others 1981, Stephen and Lih 1985).

27.5. DIRECT CONTROL TACTICS FOR SPB

Given the SPB's typical and unique seasonal attack behavior, direct control measures have been developed to disrupt spot growth within those spots most likely to expand. Since 1970, mechanical methods have been used almost exclusively for this purpose in forest situations. For information about SPB control in urban settings, see chapter 25 on chemical control.

27.5.1. Cut-and-Remove or Salvage

Cut-and-remove, also known as salvage removal (Morris and Copony 1974, St. George and Beal 1929, Swain and Remion 1981, Texas Forest Service 1976), one of the oldest SPB control tactics, continues to be the most recommended approach for suppressing SPB infestations. By harvesting and utilizing beetle-infested trees, plus a buffer strip of uninfested trees, landowners not only halt spot growth, but harvest the beetle-affected trees and thus reduce their economic losses (see Figure 27.1C). Also, SPB broods within trees are removed and eliminated at the mill if the infested logs are promptly processed.

How to Apply Cut-and-Remove

For cut-and-remove to be effective, SPB-infested material must be removed on a timely basis. An adequate buffer strip of uninfested trees also must be cut around the spreading edges of the spot. To apply cut-and-remove, the following steps are recommended (Billings 1980b, Swain and Remion 1981):

- Identify the active head(s) of the spot. The active head will contain Stage 1 trees—pines with green crowns and fresh pitch tubes and/or boring dust in bark crevices (Table 27.1).

Table 27.1—Symptoms associated with various stages of SPB-infested trees (from Billings and Pase 1979a)

Symptom	Stage 1 (fresh attacks)	Stage 2 (with SPB brood)	Stage 3 (vacated by SPB)
Foliage	Green	Green, fading to yellow before brood emerges	Red, needles falling, or bare
Pitch tubes	Soft, white, or light pink	White, hardened	Hard, yellow, crumble easily
Checkered beetles	Adults crawling on bark	Pink or red larvae about 1/2 inch long in SPB galleries	Larvae and pupae are purple; occur in pockets in outer bark
Bark	Tight, hard to remove	Loose, peels easily	Very loose, easy to remove
Color of wood surface	White, except near adult galleries	Light brown with blue or black areas	Dark brown to black
Exit holes on bark surface	None	Few, produced by re-emerging parent beetles	Numerous
Ambrosia beetle dust	None	White, localized areas at base of tree	Abundant at tree base, turns yellowish with age

Table 27.2—Guide for setting southern pine beetle growth and control priorities (May through October) (from Billings and Pase 1979a)

Key to spot growth	Your spot's classification	Risk-rating points
A. Stage 1 trees	Absent	0
(fresh attacks)	Present	30
B. Stage 1 and 2 trees	1-10 trees	0
(containing SPB brood)	11-20 trees	10
	21-50 trees	20
	More than 50 trees	40
C. Pine basal area (sq.ft/acre)	Less than 80 (low density)	0
(or stand density) at active	80-120 (medium density)	10
head or heads	More than 120 (high density)	20
D. Stand class by average	Pulpwood (9 inches or less)	0
d.b.h. (in inches)	Sawtimber (more than 9 inches)	10
	Total*	

* If total is 70-100, control priority = high

If total is 40-60, control priority = moderate

If total is 0-30, control priority = low

- Mark all SPB-infested trees or a boundary around them if there are many trees.
- If Stage 1 trees are present, mark a horseshoe-shaped buffer strip of green uninfested trees around each active head (Figure 27.3). A strip equal in width to the average height of trees in the stand is recommended for small to medium-sized spots. A wider buffer may be needed for large, expanding infestations. The horseshoe-shaped buffer strip typically includes those trees in proximity to all fresh-attacked pines (Figure 27.3).

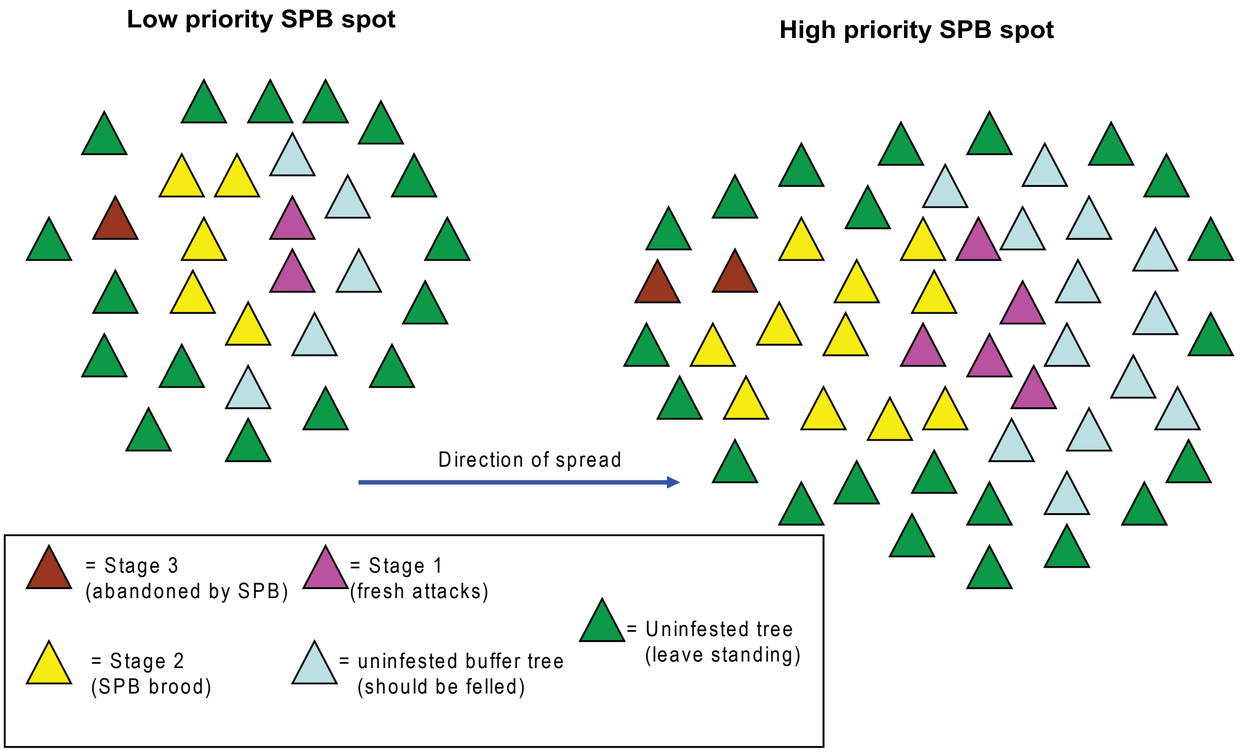


Figure 27.3—Diagram showing how to mark buffer strips for low- and high- priority SPB infestations (spots). All Stage 1 and Stage 2 trees, plus buffer trees, should be felled for cut-and-remove and cut-and leave applications.

- As soon as possible after ground checking and marking a buffer, all infested trees that can be utilized for wood products (those with green, fading, or red foliage) are felled and removed, along with the buffer strip of uninfested trees. Vacated trees (Stage 3) can be left standing, unless they can be utilized (Levi 1981).
- From May through October, buffer and fresh-attacked trees (Stage 1) should be removed first, followed by trees with SPB brood (Stage 2) and vacated trees (Stage 3). This will assure that spot growth processes are halted.
- During the remainder of the year (November through April), trees containing SPB brood (Stage 2) should be removed first to eliminate overwintering SPB broods prior to emergence.
- Infested trees (Stages 1 and 2) should not be decked next to green, standing pines to avoid initiating new infestations.
- Check salvaged spots for breakouts (re-infestations) after 2 weeks or during the next aerial survey (Billings 1979).

Limitations of Cut-and-Remove

Unfortunately, timely salvage operations frequently are not possible during SPB outbreaks for various reasons. These include lack of markets, mills that won't accept beetle-killed trees, lack of access for heavy equipment due to wet ground conditions, and the overwhelming numbers of spots detected during outbreaks that exceed the capacity of salvage crews to treat in a timely manner (Billings 1980b). In cases where prompt salvage is not feasible, the best alternative currently available to treat expanding SPB infestations is a tactic known as cut-and-leave.

27.5.2. Cut-and-Leave

Cut-and-leave (Billings 1980a, Texas Forest Service 1975) is a control method developed in Texas in the 1970s specifically to halt the expansion of SPB infestations that could not be promptly salvaged. This tactic has been commonly applied by other State and Federal agencies and private landowners faced with SPB outbreaks, and currently is second only to cut-and-remove as a recommended SPB control tactic (Price and others 1998, Redmond and Nettleton 1990, Thatcher and others 1982).

How to Apply Cut-and-Leave

To apply cut-and-leave, conduct a ground evaluation of the spot to identify the active head(s) and mark a buffer (Figure 27.3), as described for cut-and-remove in Section 27.5.1. Then fall all freshly attacked (Stage 1) and brood-containing trees (Stage 2); primarily these are infested trees with green or yellow crowns during summer months, toward the center of the infestation. In addition, a horseshoe-shaped buffer of uninfested trees at the spot's expanding front is felled to assure disruption of pheromone production (Figure 27.2B). Typically, the width of the buffer is equivalent to the height of the average tree in the stand, although actual buffer width will vary depending on infestation size and rate of spot growth. Vacated trees (Stage 3) should be left standing to favor development of the beetle's natural enemies and to provide nest sites for woodpeckers (Swain and Remion 1981). All infested trees are left onsite but may be harvested and utilized at a later date. Check for breakouts after 1 or 2 weeks or during the next aerial survey (Billings 1979).

If properly applied shortly after spot detection, cut-and-leave results in a small opening in the stand having little economic impact (Figure 27.1D). In an early version known as cut-and-top, the crowns of infested trees were severed after felling to more rapidly reduce the moisture content beneath the bark and further reduce brood survival (Ollieu 1969). This additional treatment is seldom applied and not necessary to attain control.

When to Apply Cut-and-Leave

Initially, cut-and-leave was recommended for application only during the hot summer months (May-October) on small spots with less than 50 infested trees (Texas Forest Service 1975). Clearly, only a narrow buffer of uninfested trees is required, and both reinfestation of adjacent trees (breakout) and proliferation of new spots are less likely if the spot is treated while still small during the hot summer months (Billings and Pase 1979b). Out of necessity, though, cut-and-leave (and partial treatments involving the felling of only freshly attacked trees and uninfested buffer trees) has been effectively applied at all seasons to spots of all sizes in Texas (Billings 1995, Clarke and Billings 2003) and Central America (Billings and others 2004). In contrast, merely cutting green uninfested pines at the leading edge of expanding SPB infestations is seldom effective since pheromone production is not halted and brood production in standing trees is not affected (Billings 1980b).

Effects of Cut-and-Leave on Brood Survival within Felled Trees

The initial rationale for applying cut-and-leave was to reduce brood survival in host trees by felling them (Ollieu 1969). Survival of beetle broods in felled trees may be reduced by direct solar radiation (St. George and Beal 1929), changes in moisture conditions beneath the bark (Gaumer and Gara 1967, Ollieu 1969, Palmer and Coster 1978), increased predation (Baker 1977), or competition from secondary bark beetles or wood borers. Significant reductions in SPB brood survival, however, have not been consistently observed as a result of cut-and-leave (Baker 1977, Hertel and Wallace 1983, Hodges and Thatcher 1976). No doubt, treatment effects on brood survival will vary by stage of brood development, season of the year, geographical location, bark thickness, local environmental conditions, and other factors. Also, during winter months, SPB adults have been observed to attack the underside of felled, green trees in Louisiana (Moser and others 1987), increasing the chance of brood survival in winter-felled trees.

Effects of Cut-and-Leave on Disrupting Spot Growth

Despite its questionable effectiveness for reducing brood survival in felled trees, cut-and-leave continues to be widely used on an operational basis throughout the range of SPB because the treatment has other desirable effects. If applied correctly, cut-and-leave disrupts the spot growth process, preventing further resource losses (Figure 27.1D). Felling freshly attacked trees and adjacent buffer trees serves to disrupt the production of aggregation pheromones and host odors required for continual spot growth (Billings 1980a, Gara 1967). Uninfested pine trees immediately adjacent to trees undergoing bark beetle attack are eliminated in the buffer strip, further discouraging spot growth (Johnson and Coster 1978). Beetles that survive to disperse from treated spots during summer months have reduced energy reserves (Coppedge and others 1994, Hedden and Billings 1977) and a low probability of survival (Coulson 1980). Finally, during summer months, the lack of a large aerial SPB population outside established infestations makes it difficult for emigrating beetles to initiate new, expanding spots (Billings 1980b, 1995). In summary, cut-and-leave is a simple and practical direct control tactic that effectively takes advantage of seasonal limitations in dispersal and aggregation behavior that are unique to SPB. It is not used nor recommended for other bark beetle species that have fewer generations per year.

Does Cut-and-Leave Cause Proliferation of New Spots?

Critics have suggested that cut-and-leave may aggravate rather than alleviate the pest problem by inducing surviving beetles to create one or more new spots in adjacent stands. Two independent evaluations of operational SPB records in Texas have provided evidence to the contrary. Billings and Pase (1979b) analyzed detection and control records in East Texas from the 1974-75 SPB outbreak. They found that the incidence of new infestations was significantly reduced in the vicinity of spots controlled by cut-and-leave or cut-and-remove (salvage) during summer months. Increased new spot proliferation was observed in proximity to uncontrolled infestations that remained active into the fall and those controlled after September.

Similarly, Fitzgerald and others (1994) analyzed data on SPB infestations detected and controlled on the Sam Houston National Forest in Texas from 1979 to 1989. These authors found no significant difference in proliferation between cut-and-leave and cut-and-remove treatments. Their results do not support the contention that SPB forced to disperse from treated spots establish increased numbers of new infestations.

In a more recent study, Cronin and others (1999) demonstrated that cut-and-leave may increase the numbers of SPB flying outside treated areas, compared to untreated spots, and suggested that emigrating beetles may survive by joining untreated infestations nearby. Beetle numbers decreased dramatically with distance from treated infestations. This finding does not negate the operational use of cut-and-leave, but supports the recommendation that all expanding infestations in a given area should be treated to eliminate natural pheromone sources that might attract dispersing beetles.

27.5.3. Pile-and-Burn

Felling, piling, and burning currently infested trees is one of the oldest SPB control methods, and is effective when used properly (Swain and Remion 1981, Thatcher and others 1982). All bark must be burned to achieve control and, unlike with cut-and-remove and cut-and-leave, felling a buffer strip of uninfested trees is not required. Because of high costs, the need for heavy equipment to pile large trees, the potential for wildfires, and air and water pollution, the practice is seldom used. Peeling the bark from SPB-infested trees after felling has been recommended in Honduras, primarily as a means to avoid transporting SPB populations to other forested regions (Billings and Espino Mendoza 2005). The infested bark should be promptly burned if SPB brood reduction within the spot is the goal.

27.6. CASE STUDIES ON EFFICACY OF TREE FELLING FOR SPB CONTROL

The most convincing evidence of the efficacy of spot disruption tactics (cut-and-leave, cut-and-remove) comes not from research studies, but from operational records in those regions where these tactics have been extensively applied for decades. A few examples follow.

Morris and Copony (1974) reported on the effectiveness of intensive salvage in reducing southern pine beetle populations in Virginia. During a 1973 SPB outbreak on the 15,000-acre Cumberland State Forest, salvage was promptly applied to all expanding spots, recovering 90 percent of the beetle-killed timber. As a result of this effort, spot density was reduced from 27.9 spots per 1,000 acres of host type in July 1973 to 6.3 spots by February 1974. In contrast, on adjacent private lands where little control was applied, spot density increased by 30 percent. Also, spot size was more than four times as large on the check area, compared to the state forest (26.9 trees vs. 6.3 trees), despite the presence of more susceptible stands on the state forest.

In early 1983, prompt direct control of SPB infestations on the Four Notch Further Planning Area, Sam Houston National Forest in Texas, was withheld for several months by protests from local environmentalists (Miles 1987). As a result, several small, uncontrolled SPB spots in a dense sawtimber stand of loblolly pine

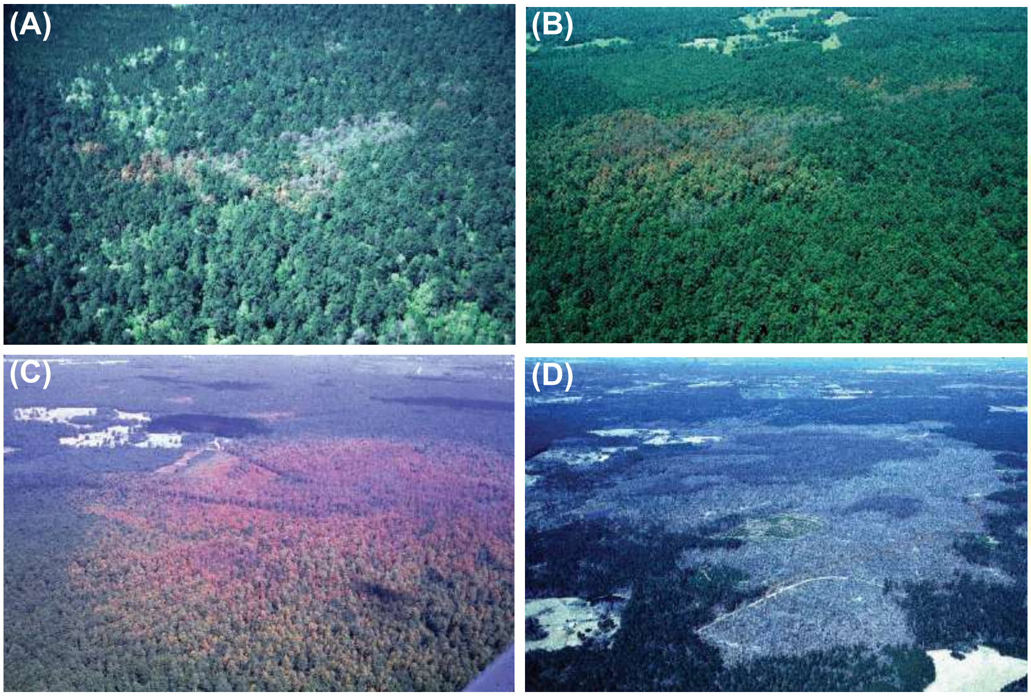


Figure 27.4—Development of a southern pine beetle outbreak on the Four Notch RARE II Study Area, Sam Houston National Forest, Walker County, Texas, in 1983-84. (A) April 1983, (B) June 1983, (C) August 1983, and (D) February 1984. (photographs by Ron Billings, Texas Forest Service)

converged to create a massive SPB infestation that grew by 50 feet per day along a 3-mile front (USDA Forest Service 1987). A sequence of photographs illustrating the rapid expansion of this uncontrolled SPB infestation on the Four Notch area during 1983-84 is shown in Figure 27.4. The infestation was finally halted by cutting a 250-foot-wide buffer strip of recently infested and uninfested trees around the periphery of the infestation, followed by helicopter logging to reduce the overwintering beetle population (Billings 1986). These delayed actions resulted in the loss of 3,700 acres of pine timber (valued at $4 million) by April 1984 and elimination of the area for wilderness consideration (Billings and Varner 1986).

In contrast, during the same year an SPB outbreak occurred on nearby Huntsville State Park, a 2,083-acre preserve of mature forest of 60- to 70-year-old loblolly pine. Infestation density averaged 20 spots per 1,000 acres of host type vs. seven spots per 1,000 acres on the Four Notch in June 1983. Unlike on the Four Notch, SPB infestations within the park were promptly controlled. Twenty-nine spots were salvaged, 7 were treated using cut-and-leave, and 13 were declared inactive with no need for control. Timber losses were limited to about 80 acres and the remaining natural pine stands within the park were protected (Billings and Varner 1986).

An economic analysis of SPB control across the South, based on operational records from the 1980s, revealed the economic benefits of suppression (DeSteiger and others 1987). Potential losses, in the absence of control, were estimated with use of the Clembeetle spot growth model (Hedden 1985). These authors confirmed that substantial benefits could be realized from optimal economic control of SPB damage to commercial forest stands. At a 4 percent rate to discount the value of timber losses, the optimal net benefits of control for the entire southern region were estimated at about $50 million, yielding a benefit: cost ratio of more than 6 to 1.

The 1985-86 SPB outbreak in the Gulf Coastal Plain was the worst in this region's history, resulting in the loss of almost 810 million board feet of timber in Texas alone (Price and others 1998). Redmond and Nettleton (1990) conducted an economic analysis of SPB suppression activity (cut-and-remove or cut-and-leave) on the national forests within the Gulf Coastal Plain (Texas, Louisiana, Mississippi, Alabama) during this outbreak. These authors compared actual suppression costs with estimates of potential timber losses without suppression obtained with use of the Arkansas spot growth model (Stephen and Lih 1985). They reported benefit cost ratios of 3.9 to 1 (based on a 4 percent discount rate) and 2.6 to 1 (based on a 7.12 percent discount rate).

Benefits of prompt direct control once again were dramatically demonstrated in the 1990-94 SPB outbreaks in East Texas. Losses on 31,656 acres of recently designated wilderness where little or no direct control was applied were compared to losses on the surrounding 600,000 acres of managed national forests where expanding spots were promptly controlled by cut-and-remove, cut-and-leave, and to a lesser extent, cut-and-spray with insecticides. Initial density of SPB infestations was higher on non-wilderness forests compared to wildernesses. Nevertheless, more than 40 percent of the host type was killed on the wilderness areas in the absence of direct control in 1990-93 vs. less than 2 percent of the host type on the 600,000 acres of managed national forests in Texas (Billings 1995, 1998; Clarke and Billings 2003).

Photographs documenting the rapid development of uncontrolled SPB infestations on Indian Mounds Wilderness in Sabine County, Texas, which eventually attained 7,500 acres, are shown in Figure 27.5. These photographs illustrate the magnitude of losses that can occur from SPB in a short period when a no-control policy is adopted or direct control is delayed. Interestingly, losses to SPB on these same wilderness areas during the 1984-85 outbreak before a no-control policy was implemented were held to 5.7 percent of the host type by prompt direct control (Billings 1995).

In Honduras, where *D. frontalis* also is the major bark beetle pest, cut-and-leave was implemented for the first time in 1984 to address a severe SPB outbreak. Prior to this time, SPB spots were treated with more traditional control methods of fell, pile, and burn or chemical insecticides. Prompt application of cut-and-leave from 1984-86 reduced average infestation size from 50 acres per spot in 1983 to about 1 acre. Total timber losses per year were reduced by 88 percent, despite higher numbers of spots in 1984-86 compared to 1983 (Billings and others 2004). Since that date, cut-and-leave has been routinely and successfully used in Honduras to halt the spread of expanding infestations and reduce resource losses except during years when financial sources were unavailable to fund suppression programs (Figure 27.6).

In 2001, the same cut-and-leave methods were successfully applied to halt a SPB outbreak in Nicaragua. In this case, buffer strips consisting of freshly attacked and green, uninfested trees had to be widened to about 300 feet and lengthened up to 6 miles to halt massive infestations that were progressing at 150 feet per day, prior to control (Figure 27.7). The SPB outbreak in Nicaragua collapsed at the end of 2001. Interestingly, across the border in Honduras, where direct control efforts in 2001-04 were largely withheld due to lack of financial resources, the same SPB outbreak continued for several years (Billings and others 2004).

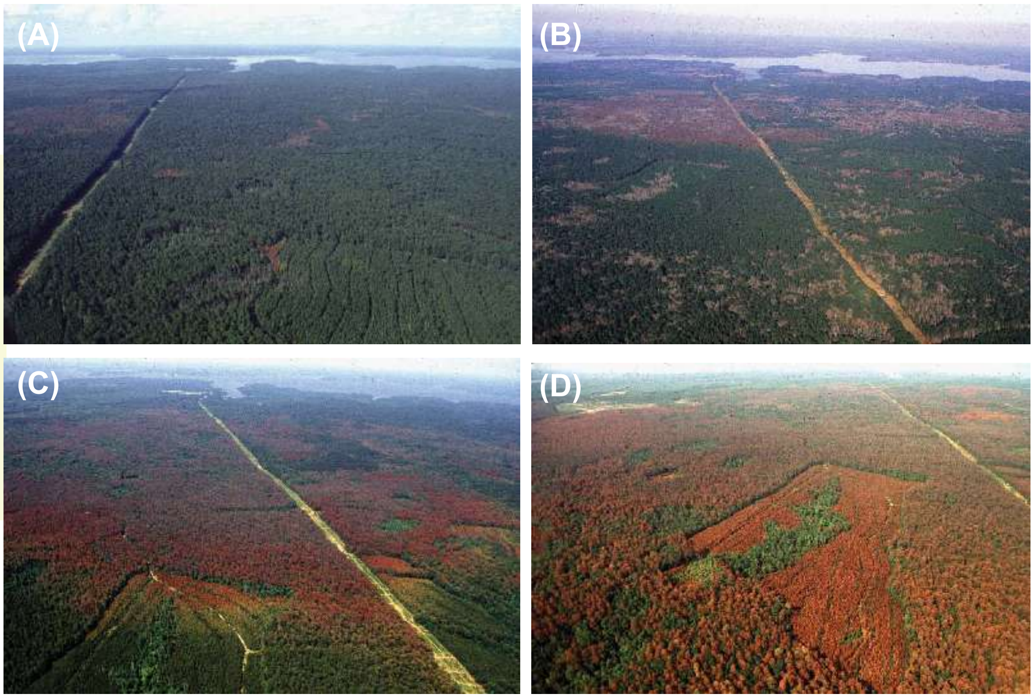


Figure 27.5—Development of a southern pine beetle outbreak on the Indian Mounds Wilderness, Sabine National Forest, Sabine County, Texas in 1992-93. (A) July 1992, (B) February 1993, (C) June 1993, (D) August 1993. (photographs by Ron Billings, Texas Forest Service)

In Belize in 2001, an outbreak of *Dendroctonus* spp. occurred for the first time in 50 years in the Mountain Pine Ridge Forest Reserve. Lacking experience with bark beetle outbreaks, the Belize Forestry Department took little or no action. As a result, 85 percent of the pine resource (more than 65,000 acres) was lost to uncontrolled beetle populations (Billings and others 2004).

27.7. LIMITATIONS OF DIRECT CONTROL PROGRAMS

Pest management programs involving prediction, monitoring, hazard rating, prevention, early detection, ground evaluation, and prompt direct control have been developed in recent years to better manage SPB populations (Branham and Thatcher 1985, Clarke 2001, Thatcher and others 1980). Although successful in reducing resource losses, these programs

Figure 27.6—Application of cut-and-leave used to successfully halt spread of SPB outbreak in Honduras in 2002. (photograph by Ron Billings, Texas Forest Service)

Figure 27.7—Large (250-foot) buffer consisting of freshly attacked trees and adjacent buffer trees felled to halt expansion of a 6,000-hectare southern pine beetle outbreak near Jalapa, Nicaragua, in 2001. (photograph by Ron Billings, Texas Forest Service)

have their limitations. SPB is a native forest insect and a natural component of southern forest ecosystems. Eradication is neither possible nor desirable, and periodic outbreaks will continue to occur as long as susceptible forests are present (Clarke 2001, Coulson and others 1999b, Mawbe and Hain 1985, Ward and Mistretta 2002). These outbreaks, which can develop extremely rapidly when optimal conditions prevail, are favored by several factors. These include:

- The preponderance of small private land ownerships in the South (more than 90 percent of the forest land is privately owned), with each private landowner having a different management objective, extent of SPB awareness, and level of interest in prevention or suppression (Billings 1980b, Mayfield and others 2006)
- The longer rotations and high basal areas on Federal forests that render these forests very susceptible to SPB outbreaks (Carter and others 1991, Clarke and others 2000)
- The situation on many southern national forests, where pressure and lawsuits by environmentalists often negate stand management practices and prompt direct control (Teich and others 2004, USDA Forest Service 1987)
- A spatial arrangement of susceptible landscape elements (extensive pine stands and abundant lightning-struck hosts) that favors SPB outbreaks (Coulson and others 1996b, 1999b)
- Presence of pine-dominated Federal wilderness areas where little or no direct control of SPB is allowed (Billings 1986, Clarke and Billings 2003)
- Lack of markets and chainsaw crews for applying salvage and/or cut-and-leave to large numbers of infestations in a timely manner in many areas (Billings 1980b)
- The occurrence of frequent climatic variations (e.g., droughts, floods, wind, and thunderstorms) that periodically stress trees at the stand and landscape level (Clarke and others 2000, Coulson and others 1983, Kalkstein 1976, King 1972)
- Changing land ownership patterns. In recent years, most forest industries have sold their lands to Timber Investment Management Organizations (TIMOs) or Real Estate Investment Trusts (REITs). These new owners are likely to lack the experience, trained manpower, and equipment that the forest industries had developed over many decades to address SPB outbreaks.
- The intermittent nature of SPB outbreaks, characterized by multiple years with essentially no SPB infestations (e.g., in Arkansas, Louisiana, Oklahoma, and Texas since 1998) that makes it difficult to maintain public awareness of SPB or pest specialists trained to deal with outbreaks when they do occur

Direct control or suppression is considered to be a short-term measure or last resort to reduce damage levels, once bark beetle outbreaks develop (Billings 1980b, Swain and Remion 1981, Thatcher and others 1982). There is little documented evidence that suppression of individual SPB infestations will terminate an outbreak or shorten its duration. Clearly, effective SPB management also involves other critical components such as hazard rating, prevention, and continual monitoring discussed elsewhere (see chapter 22).

27.8. FUTURE OF DIRECT CONTROL

For the reasons stated above, there is a need to develop new and more effective direct control strategies and tactics to address bark beetle outbreaks. Research in recent years has focused on use of behavioral chemicals and biological control as two promising approaches for direct control. For details, see the chapters on SPB behavioral chemicals and biological control in the Southern Pine Beetle II.

Clearly, until alternative suppression methodologies are developed, prompt application of mechanical controls shortly after detection will continue to be the principal means to reduce resource losses during SPB outbreaks. No chemical insecticides are currently available for suppressing these bark beetles in forest situations. Even if there were some insecticides registered for this use, their application would not be recommended. Chemical insecticides, although they have proven effective for killing beetles within infested trees (Bennett and Pickard 1966, Fitzpatrick and others 1979, Swain 1976), are costly and have undesirable side effects when applied at the landscape scale (Williamson and Vité 1971). In-depth knowledge of SPB behavior, coupled with a chainsaw, not an insecticide sprayer, are the land manager's most useful tools for managing the southern pine beetle in forest situations.

Prevention, rather than direct control, is considered the best long-term approach to avoiding SPB problems (Belanger and Malac 1980, Fettig and others 2007). Landowners should recognize those conditions that render pine stands prone to SPB attack (Coster and Searcy 1981) and apply silvicultural practices to avoid those conditions. Thinning dense stands to promote rapid growth and bark beetle resistance (Belanger and others 1993, Nebeker and others 1985) not only reduces the likelihood of beetle infestations (Hicks and others 1980, Mason and others 1985) but also minimizes the probability and rate of infestation growth once a spot is initiated (Brown and others 1987, Cameron and Billings 1988, Johnson and Coster 1978, Hedden and Billings 1979, Turchin and others 1991). Until SPB prevention programs become more widespread, however, early detection and prompt direct control will remain essential to reduce resource losses when SPB outbreaks do occur (Thatcher and others 1982).

27.9. CONCLUSIONS

The SPB is one of the most aggressive bark beetles in the world. Yet because of the multivoltine life cycle and seasonal limitations in the attack behavior of this species, SPB infestations are relatively easy to control with tree-felling tactics. This is particularly true when direct control is applied early in the development of a spot, before infestations exceed about 100 trees in size. Unfortunately, during regional outbreaks the sheer numbers of spots that develop and other factors may preclude prompt applications to all spots that warrant control. Also, spot disruption at the stand level does not assure control of the outbreak at the landscape level, and suppression programs may have little effect on the duration of SPB outbreaks.

Much has been learned in recent decades as a result of intensive research programs on southern pine bark beetles (Branham and Thatcher 1985, Thatcher and others 1980) and by pest managers addressing SPB outbreaks throughout the range of this beetle. Vegetation management in one form or another will continue to be the foundation for effectively preventing or suppressing bark beetle outbreaks (Fettig and others 2007). Foresters have long recognized that good forest management is good pest management—both require judicious and timely elimination of certain trees to protect and promote the survival and healthy growth of others in the stand and landscape. Still, there are many areas of SPB behavior and insect-host interactions that require more study if a permanent solution to the SPB problem is to be realized (Coulson and others 2003).

28

Biological Control of Southern Pine Beetle

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Abstract

Exotic invasive forest insects are frequently managed through classical biological control, which involves searching for, introducing, and establishing their exotic natural enemies. Biological control of native bark beetles, including the southern pine beetle (SPB), has been primarily attempted by conserving and manipulating their natural enemies. Knowledge of the role and biology of SPB natural enemies is increasing but is still limited, and is rarely well connected to coincident estimates of SPB host density. A rich complex of SPB native natural enemies exists, and these are discussed in greater detail in other chapters in this book. The cryptic nature of *Dendroctonus* species within phloem and bark, combined with the properties of many natural enemies (small size, highly aggregated distribution, lower density than their prey, and often acting late in the beetle's life cycle), results in challenging sampling problems that are difficult to overcome. Attempts to assess impact of natural enemies have often been presented as percent of mortality, but rarely do these assessments show variation in mortality. The manner in which mortality varies with host density is important in population regulation. Predators, parasitoids, and competitors of the SPB respond in varying degrees to SPB pheromones and tree volatiles during host selection. Variables such as bark thickness and SPB density influence parasitoid success. In making oviposition choices, parasitoids tend to select the host beetle and tree species from which they emerged. Short SPB generation times, continuous flight, and attack by SPB adults result in infestations containing all life stages of beetles and natural enemies. Opportunities for numerical response of parasitoids to epidemic population growth should be great but have not been confirmed. Manipulation efforts indicate that providing nutrients for parasitoid adults increases their longevity, stimulates production of additional eggs, and prevents resorption of existing eggs. Parasitoids do forage in canopies of both pine and hardwood trees, possibly to acquire honeydew as adult nutrition. Predators frequently are the most abundant and visible sources of SPB mortality, and their potential role as delayed density-dependent agents may be important in the cycles exhibited by SPB populations. Simulation models that experimentally remove mortality attributable to natural enemies show how rapidly infestations grow when natural enemies are absent. Experimental research on *Monochamus* spp. indicates that they can cause high mortality to SPB brood as competitors and predators, and field observations suggest that they may play an important role in the collapse of SPB epidemics.

Keywords

bark beetles
parasitoid competitors
population dynamics
predators
Scolytidae

28.1. INTRODUCTION

Infestations of southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) are a veritable hive of insect activity, and the majority of these insects are not SPBs. Observations from a field-based perspective of climbing hundreds of infested trees, sampling bark that contains different SPB life stages, and studying the multitudes of insect species searching on the bark surface and burrowing and developing within the inner bark and phloem, reveal the remarkable diversity of the SPB-associate complex. Many of these associated insects parasitize, prey upon, or compete for food and/or space with the SPB, and as such are considered natural enemies of the beetle. In five other chapters of this book detailed information is presented on SPB predators (chapter 10), parasitoids (chapter 8), competitors (chapter 12), and fungal and mite associates (chapters 9 and 11). Despite the extensive information that is known about SPB natural enemies, it is safe to say that we still know much less than we should about their roles and importance in suppressing SPB population density. The purpose of this chapter is to define the field of biological control as it relates to the SPB and to briefly summarize attempts made at SPB biological control.

28.2. BIOLOGICAL CONTROL

Human manipulation of natural enemies to effect reduction of pest populations has existed for millennia; however, the term "biological control" was first used by H.S. Smith (1919) to signify use of natural enemies, whether introduced or not, to control insect pests. Successful biological control of forest insects is well documented (Dahlsten and Mills 1999, Dahlsten and Whitmore 1989, Pschorn-Walcher 1977, Turnock and others 1976, Waters and others 1976), and biological control is today a primary tactic for management of many exotic forest insect pests.

28.2.1. Definitions

Natural control is a broad concept that encompasses the combined actions of abiotic and/or biotic environmental factors to maintain an organism's more or less fluctuating population density, within certain definable upper and lower limits, over a period of time (DeBach 1964). Although the term "biological control" is used in many ways by different authors, the most accepted and in our view the best definition is that of DeBach (1964), who considers biological control as a phase of natural control and defines it "as the action of parasites, predators, or pathogens in maintaining another organism's population density at a lower average than would occur in their absence." At its core, this definition implies that biological control is a natural process. The native complex of predators, parasitoids, and competitors associated with the SPB, for example, reduces to some extent SPB population density. This does not necessarily imply that natural enemies will maintain SPB population density below a level that is economically acceptable, but it does mean that without these natural enemies the SPB would be a more significant pest.

28.2.2. The Field of Biological Control

Biological control of insect pests can be considered an applied discipline; however, its foundations are based in ecological theory. Thus knowledge of insect ecology and ecosystem interactions is usually key to successful biological control. Although much is known, we still do not have sufficient knowledge to enact successful biological programs against the SPB. Biological control as a discipline is often separated by the origins of pests and of their natural enemies and by the approaches used to maximize the effectiveness of the natural enemies. These approaches can be distinguished as follows: 1. classical biological control – the importation and establishment of exotic natural enemies to control exotic or native pests; and 2. manipulative biological control – techniques that manipulate natural enemies to augment or enhance their effectiveness, or techniques that manipulate the environment to benefit and conserve existing natural enemies. Examples of these approaches in relation to the SPB are explained and discussed below. Disruption of naturally occurring biological control through human intervention can and does occur. This knowledge should further stimulate our efforts to gain more knowledge of forest / bark beetle / natural enemy interactions. Because successful biological control must be based on the fundamentals of scientific knowledge, it is essential to subsequently evaluate the reasons for success or failure of biological control programs.

Importation (Classical Biological Control)

The importation of natural enemies to control exotic (introduced) pests is by far the most common approach to biological control of forest insects (Dahlsten and Mills 1999). Invasive insects or other organisms that are accidentally or intentionally introduced from geographically distant areas into a new locale such as North America may reproduce without mortality from natural enemies or host resistance that normally evolves through generations of insect-plant interactions. The search for natural enemies of the pest in its native area, coupled with their importation, quarantined rearing to eliminate secondary parasitoids or diseases, in concert with release, establishment, and control of the pest in its new environment constitutes classical biological control (DeBach 1964). In forest systems, classical biological control should be considered as an essential management tool, particularly in light of the increasing numbers of invasive exotic pest species that are being discovered. If eradication of these exotic species fails, then management of their populations with classical biological control should be fully explored. Although there are many famous and successful biological control projects of forest pests that have involved importation and establishment of natural enemies (Dahlsten and Mills 1999, Huffaker and Messenger 1976, Pschorn-Walcher 1977, Turnock and others 1976, Waters and others 1976), for bark beetles the number of successful examples is quite limited.

A related approach that derives from the principles of classical biological control has been proposed (Hokkanen and Pimental 1984, Pimentel 1963). These authors suggest that because host-parasitoid relationships often tend to become less virulent over evolutionary time, new associations of natural enemies selected from species related to a particular pest may be advantageous. Pschorn-Walcher (1977) reports that this approach has not worked in forests, but suggests it should not be disregarded without more exploration. Indeed, predator introductions that are discussed below, *Thanasimus formicarius* (L.) (Coleoptera: Cleridae) and *Rhizophagis grandis* (Gyllenhal) (Coleoptera: Rhizophagidae), are both natural enemies of European bark beetles related to North American genera, and are thus illustrations of the new associations strategy.

Manipulation (Augmentation and Conservation)

Classical biological control may be an essential approach for managing invasive exotic pest species; however, manipulation by augmenting and conserving natural enemies is for native pests a strategy more important and more likely to succeed. Humans can act to augment numbers of natural enemies, and they can manipulate their habitats so as to increase natural enemy survival and effectiveness. Actions that manipulate insects themselves can theoretically be considered distinct from actions that alter the environment in which the insects live; however, in practice it can be difficult to distinguish the two (Rabb and others 1976). Conservation of natural enemies may be an approach that is highly appropriate in forest ecosystems, as they are longer lived, suffer fewer disruptions, and are generally more complex than agricultural systems (Dahlsten and Mills 1999).

Study

The phrase, "know your enemy," would seem to be essential to any commander of a military campaign, and may be an appropriate cliché in biological control programs. Successful biological control depends on knowledge of the biology and ecology of target hosts, natural enemies, and the ecosystems in which they will exist together. Although multiple lists of SPB natural enemies have been prepared (Berisford 1980, Franklin 1969, Goyer and Finger 1980, Linit and Stephen 1983, Moser and others 1971, Overgaard 1968, Stephen and others 1993), detailed information on their biology and impact is woefully lacking. There are many reasons for this circumstance. Bark beetles are difficult to observe. They spend most of their life cycle in phloem and bark tissues, and most of their natural enemies are also found in this cryptic environment. It is challenging to rear the SPB in the laboratory. Creating experiments with both the SPB and its natural enemies is even more difficult. Few controlled studies have succeeded in replicating environmental conditions encountered by the SPB and its associated species in the field. Sampling to estimate density of natural enemies is challenging, owing to their occurrence within bark and phloem tissue many meters above the ground in standing pine trees, their aggregated patterns of dispersion within trees in regard to their bark beetle hosts (Stephen and Taha 1976), and the timing of their arrival and development in relation to the SPB life cycle (Camors and Payne 1973, Dixon and Payne 1979b). Natural enemy abundance and distribution also varies seasonally (Goyer and Finger 1980, Stein and Coster 1977) and as a function of infestation age and size (Stephen and others 1989).

28.3. NATURAL ENEMIES OF SOUTHERN PINE BEETLE

Published literature that supports the importance of natural enemies in suppressing SPB populations traces its roots to A.D. Hopkins in the late 19th century (Hopkins 1899). Since then many other scientists have noted the abundance of natural enemy species and surmised that at times they must be extremely important mortality agents even if their overall importance in regulating SPB populations is unclear.

28.3.1. The Natural Enemy Complex

The complex of insect natural enemies that is associated with the SPB is extensive and may reach 150 species (Berisford 1980, Dixon and Payne 1979b, Franklin 1969, Goyer and Finger 1980, Linit and Stephen 1983, Moser and others 1971, Overgaard 1968, Stephen and others 1993). Organisms other than insects may also be key agents of mortality, and can include birds, particularly woodpeckers (Kroll and Fleet 1979), mites (Klepzig and others 2001a, Moser 1975, Moser and Roton 1971), fungi (Barras 1970, 1973; Bridges 1983; Hofstetter and others 2006a; Klepzig and others 2001a, Paine and Stephen 1988) , and nematodes (MacGuidwin and others 1980, Moore 1971, Sikorowski and others 1979). Other chapters in this text on SPB population dynamics within trees (chapter 4), SPB competitors (chapter 12), SPB parasitoids (chapter 8), SPB predators (chapter 10), and SPB mites and fungi (chapter 11) address details of mortality to SPB from this diverse group of enemies.

28.3.2. Natural Enemy Impact Assessment

Evaluating the impact of mortality caused by natural enemies has been varied and often innovative. Basic approaches to assessing the importance of natural enemies are often through some variation of either excluding them or adding them to an experiment, then comparing the resultant mortality to control situations. Adding predators and manipulating SPB host density showed that *T. dubius* can influence SPB attack density (Reeve 1997). Exclusion studies, both in the laboratory and field, provide estimates of mortality to the SPB by natural enemies (Linit and Stephen 1983, Miller 1984, Reeve and others 1998, Riley and Goyer 1986). Estimates of mortality or percent of parasitism obtained by rearing bark beetles and natural enemies are common, but provide very rough estimates. Correctly attributing mortality to a particular species, obtaining accurate density estimates, timing of tree felling, or caging, all contribute to errors in estimation. A life table approach to sampling on trees, where density of all bark beetle life stages can be found, and corresponding amount of stage-specific mortality by known natural enemies is a remarkably difficult and expensive operation, and rarely conducted. Experiments with direct observation of natural enemy / host interactions can be obtained using the valuable technique of phloem sandwiches (Dodds and others 2001, Kinn and Miller 1981). Trapping with the synthetic aggregation pheromone frontalin and turpentine can be used to estimate ratios of the SPB to its predator *T. dubius*, yielding predictions for SPB population trends but not impact from predation (Billings 1988).

Measured Impact

Linit and Stephen (1983), by sequential, on-tree exclusion studies, estimated within-tree mortality caused by the SPB natural enemy complex at 23-28 percent; this is certainly sufficient to be considered as potentially important in population regulation, particularly as much of it comes late in the SPB life cycle. Multiple factors are involved in determining natural enemy effectiveness. The success of eight species of SPB parasitoids was studied in relation to bark thickness and SPB host density (Gargiullo and Berisford 1981). In regions of thinner bark all species were found at higher densities, illustrating the importance of this variable to parasitoid success. These authors also determined that in seven of the eight species studied, parasitism increased as SPB host density increased.

During a 4-year period in Arkansas, Stephen and others (1989) sampled within-tree populations of the SPB and their natural enemies during years when overall SPB population levels were increasing (1975), epidemic (1976), and collapsing (1978). Over those years they found that egg density increased; however, numbers of eggs per attack remained fairly constant at about 28-30 (Table 28.1). Numbers of natural enemies increased 3 fold, and the proportion of natural enemies to late-stage immatures increased in a similar manner, from 0.18 to 0.57. Percent of mortality, calculated as the percentage of change in density from eggs to late-stage immatures, rose from 67 percent to 82 percent, suggesting that natural enemies were important in the collapse of this outbreak.

Table 28.1 — Changing relationships among SPB within-tree life stages and natural enemies as overall SPB population levels increase to epidemic status and then collapse. Data adapted from Stephen and others (1989)

Year (pop. level)	SPB *attacks/dm2*	SPB *eggs/dm2*	*Eggs/attack*	Late stage *larvae/pupae/dm2*	Natural enemies *(NE)/dm2*	Proportion NE	Percent mortality *egg-larvae/pupae*
1975 (increasing)	3.7	107.7	29.1	35.1	6.2	0.18	67.4
1976 (epidemic)	5.7	157.4	27.6	43.2	12	0.28	72.6
1978 (collapsing)	5.7	172.8	30.3	31.9	18.3	0.57	81.5

Larvae of the SPB guild and *Monochamus* spp. are commonly found together in phloem of SPB-attacked trees. Quantitative evaluations of mortality resulting from interactions between *Monochamus* and the SPB were investigated in the 1970s in East Texas, and interspecific competition was confirmed (Coulson and others 1976a, 1980a). They found that foraging by *Monochamus* reduced bark beetle survival when both co-existed, but that frequently the timing of their occurrence, coupled with the tendency of the SPB to move to the outer bark to form pupal chambers, often diminished that interaction. They further concluded that the observed levels of mortality had a significant influence on within-tree SPB survival, averaging 14 percent on a per tree basis and reaching 70 percent in specific areas where *Monochamus* was foraging (Coulson and others 1980a). Dodds and others (2001) experimented with interactions of bark beetle larvae (*I. calligraphus*) and their common associates, *Monochamus carolinensis* (Olivier). They established that *Monochamus* larvae are facultative predators upon the bark beetles, and when encounters occurred, cerambycid larvae usually attacked, killed, and frequently ingested the bark beetles. The importance of competition in SPB population dynamics appears critical, yet not fully understood (chapter 12).

Moore (1972) reported that in *P. taeda* L. parasitoids and predators of the SPB caused an average of 24 percent mortality to developing brood. He also reported that 22 percent of the SPB contained potentially pathogenic bacteria (Moore 1971). Given their potential importance to SPB population dynamics (Sikorowski and others 1979), it is surprising that more research on diseases has not been undertaken.

Models and Analysis of Impact

Simulations were made using SPBMODEL (Stephen and Lih 1985) to predict growth of SPB populations in several infestations that had been monitored and sampled during 1975 and 1978. The model was used to simulate growth of observed populations, and those populations were also surveyed and monitored by counting infested numbers of trees during the periods when growth was occurring. Mortality rates in the model were then conservatively modified to remove the estimated impact caused by parasitoids (one SPB larva for each parasitoid), and predators (two SPB immatures for each predator) to the SPB, and the simulations were again conducted. In all cases the predictions showed that when mortality to the SPB caused by those natural enemies was removed, infestation growth was dramatically increased (Stephen and Lih 1985).

A frequently cited paper by Turchin and others (1991) reports that both time-series and regression analysis of an index of SPB population levels in East Texas (spots greater in number than 10 trees) over time shows population change to be a result of as yet unknown delayed density-dependent process. The authors suggest that natural enemies, particularly predators, may be the causal agent. While their conclusions as to the importance of natural enemies in the cyclic dynamics observed to occur with SPB populations may be correct, their reasoning and methodology raise questions. Two are worth mentioning. First, data used in the analyses are infested spots (as an index of SPB numbers) counted on a yearly basis, and the best fit to their model was a 2-year time delay. Given that the SPB may undergo seven generations per year (Payne 1980), and some natural enemy species even more than that (Jones and Stephen 1994), a time delay of 2 years may encompass about 14 generations of the beetle and perhaps significantly more generations of its natural enemies. That fact confounds the biological interpretation of their perceived interactions with the SPB and its natural enemies. Second, the Texas Forest Service, private landowners, and at times the USDA Forest Service, did their best to prevent and minimize damage from the SPB during most of those years. The predominant control tactics were salvage and cut-and-leave (Billings and Pase 1979a, Swain and Remion 1981). The impact of these control procedures on survival and population dynamics of the SPB is not known; however, the unknown density-dependent process response, hypothesized by Turchin and others (1991), unfortunately cannot be separated from the density-related suppression efforts of foresters and pest managers.

28.4. BIOLOGICAL CONTROL OF SOUTHERN PINE BEETLE

Attempts at biological control of the SPB have been limited in scope but fall into two basic groups: those that deal with introductions of natural enemies, and those that seek to manipulate or conserve existing natural enemies. The latter efforts to enhance naturally occurring biological control are the more common and may show the most promise for the future. As with many complex systems, a primary concern should be to avoid forest or insect pest management tactics that negatively affect existing natural enemies, thus disrupting a system that may be working better than we realize. Human interventions in forest ecosystems can lead to unexpected disruption of naturally occurring biological control (Luck and Dahlsten 1975), and such results merit wise planning in regard to forest management decisionmaking.

28.4.1. Introduction of Exotic Natural Enemies

The most noteworthy and successful attempts at classical biological control of bark beetles involve the greater European spruce beetle, *Dendroctonus micans* (Kugelann) (Dahlsten and Mills 1999). This bark beetle, native to Eurasia, became a problem in the Massif Central region of France in the 1970s and was later discovered in 1982 in spruce plantations in Wales. In France, *Rhizophagus grandis* was relocated from Soviet Georgia, mass reared, and released. The predators became established and are at least partially successful in reducing populations of the bark beetle (Dahlsten and Mills 1999, Gregoire and others 1989). *D. micans* was accidentally introduced to Great Britain from continental Europe and became a serious pest of spruce there in the absence of natural enemies. Again, its major predator, *Rhizophagus grandis*, was imported and released, and appears to be limiting populations and minimizing impact of the outbreaks (Fielding and Evans 1997). About 220 of these predatory beetles were introduced into Southern United States for biological control of *D. terebrans* (Miller and others 1987, Moser 1989), but successful colonization was not reported.

The earliest attempt at introduction of an exotic bark beetle natural enemy was made in West Virginia by A.D. Hopkins, who collected '*Clerus*' (*Thanasimus formicarius* (L.)) with assistance from the German scientists Eichhoff, Schaufuss, and Strahmeyer (Hopkins 1899). He traveled with his beetles to England to avoid cholera in Germany and France (and to keep his belongings—and insects—from being fumigated on board ship) and brought them home in his luggage. In October 1892 he released 50 adults and about 25 larvae "on and in the bark of a group of dying scrub pines on Mayfield Hill, about 7 miles from Morgantown, this colony being the first examples liberated in America" (Hopkins 1899). The sudden disappearance of the SPB in 1893, however, meant he had no target population for his planned releases in spring of that year, a fact he believed may have contributed to the apparent failure of his releases. In total more than 2,000 *T. formicarius* were released between 1892 and 1894, but none were recovered.

Although not a *Dendroctonus* species, the five-spined engraver beetle, *Ips grandicollis* (Eichhoff), a species native to the Southeastern United States, was discovered in the exotic pine plantations of Australia in 1943, and in the early 1980s became the focus of a biological control program (Waterhouse and Sands 2001). C.W. Berisford and D.L. Dahlsten collected and transported several species of North American hymenopterous parasitoids to Australia, where they were cultured and some subsequently released. The most successful releases were of the species *Roptrocerus xylophagorum* (Ratzeburg), and *Dendrosoter sulcatus* Muesebeck, with the former species becoming established in all States and reducing host populations on average 25 percent and up to 70 percent in some situations (Waterhouse and Sands 2001). The predators *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae) and *Temnochila virescens* (Fabricius) (Coleoptera: Trogositidae) also were introduced from the Southeastern United States to Australia. Although *T. dubius* may have been established in the mid-1980s (Berisford and Dahlsten 1989), subsequent evaluations report that neither species is considered established (Waterhouse and Sands 2001). *Ips grandicollis* remains a serious pest of pine plantations in Australia, particularly during periods of severe drought.

28.4.2. Conserving and Enhancing Naturally Occurring Biological Control

Natural enemies are abundant in SPB infestations (Stephen and others 1997) and collectively help in regulating SPB population abundance. It seems clear, however, that they do not always regulate populations below economically acceptable levels, a fact vividly illustrated by numerous large-scale SPB outbreaks in multiple southeastern States in the past 20 years. When massive outbreaks do occur, natural enemies may, however, be critical both in their termination and in maintaining endemic populations, and extending the period between outbreaks. What may be most important in maintaining bark beetle populations is a collective effort to properly manage forest stands (chapter 23) while working to conserve and enhance natural enemy effectiveness.

Suppression Tactics and Conservation

Direct control for suppression of SPB includes four techniques that are approved for use by the Final Environmental Impact Statement for the Suppression of the SPB (USDA Forest Service 1987). These tactics are cut-and-remove, cut-and-leave, cut-and-hand-spray, and pile-and-burn (see chapters 25, 26, and 27). Development time of most natural enemies is either longer than the SPB or they attack the SPB late enough in its life cycle that they will emerge from trees after emergence of the majority of the SPB brood adults. Trees from which SPBs have emerged will still harbor rich natural enemy populations, and therefore their removal, cut-and-spray, or pile-and-burn will needlessly kill natural enemies. The suggestion that bark beetle natural enemies can be conserved through cultural practices is long-standing (Berryman 1967, DeLeon 1935, Moore 1972). Manuals describing SPB control techniques such as cut-and-leave, in which SPB infested trees are felled and left on the ground, include recommendations for conserving natural enemies by leaving trees from which all SPBs have emerged, thus allowing natural enemies to complete development (Swain and Remion 1981). The fate of natural enemies in cut-and-leave trees is dependent primarily on solar radiation and temperature, and has not been fully explored.

Suppression of the SPB by use of chemical pesticides is limited to a practice known as cut-and-hand-spray (USDA Forest Service 1987). In national forests in Texas, during the period 1990-99, about 5,600 infestations covering 2900 ha (~7,200 acres) required suppression treatments. Of these treatments, cut-and-hand-spray for SPB suppression was used on about 3,000 trees on about 7.6 ha (~19 acres). Use of pesticides for SPB suppression, more prevalent in previous pest management recommendations than in current ones, has been indicted as harmful to its natural enemies and potentially causal in creating chronic bark beetle problems (Williamson and Vité 1971).

Semiochemicals

It is well known that natural enemies of bark beetles respond to host tree and beetle odors as they attempt to locate their prey (Mizell and others 1984, Payne 1989, Raffa 2001). Synthetic chemicals such as frontalin, *trans*-verbenol, *endo*- and *exo*-brevicomin or verbenone attract or repel SPB and may also affect populations of many of their natural enemies (Dixon and Payne 1980, Payne 1989). *Monochamus titillator* (F.), probably the most important SPB competitor, is also attracted to pheromones for the southern pine engravers, *Ips* species (Billings and Cameron 1984). Suppression and prevention programs for bark beetles that have used semiochemicals in trap-out strategies report that, in addition to the target bark beetles, large numbers of predators were also captured (Bedard and Wood 1981).

The effects on natural enemies of stand treatments using the SPB inhibitor, verbenone, were tested for *T. dubius* (Johnson and Coster 1980), and in a well-planned field study for all important SPB natural enemies by Salom and others (1995). Both studies concluded that there was a negligible effect of the verbenone suppression tactic on natural enemies, and that no unusual dispersal of the natural enemies from the treatment areas was detected. However, the fact that natural enemies are intimately tied to the semiochemicals, particularly attractants, associated with bark beetles implies that any management technique using these compounds should be evaluated carefully to ensure that they are not negatively affecting natural enemies.

28.4.3. Parasitoid Manipulation

Research to more fully understand the biology and role of parasitoids in SPB population dynamics, and to enhance their effectiveness in suppressing SPB population growth, was conducted in a series of experiments in the 1990s by F.M. Stephen and students at the University of Arkansas, in collaboration with L.E. Browne of Entopath, Inc. Their ideas and research efforts are summarized below.

Why SPB Parasitoids Should Be Important

There are several reasons, discussed below, that explain why the SPB parasitoid complex may be unique and more able than enemies of other *Dendroctonus* species to rapidly respond to bark beetle population growth. Berisford (1980), Goyer and Finger (1980), and Moser and others (1971) indicate that there are eight common parasitoids of the SPB. This includes the pteromalids *Roptrocerus xylophagorum* (Ratzeburg), *Heydenia unica* Cook and Davis, and *Dinotiscus dendroctoni* (Ashmead), the eurytomids *Eurytoma* species, and the braconids Meteorus species, *Coeloides pissodis* (Ashmead), *Dendrosoter sulcatus* Muesebeck, and *Spathius pallidus* Ashmead. Intensive sampling in a wide variety of infestations between 1975 and 1992 revealed that the parasitoid species named above were present in most infestations most of the time (Stephen and others 1997) (Figure 28.1).

Developmental times for SPB generations in the warmer parts of the South may be about 1 month in duration (Wagner and others 1984b), resulting in as many as seven to eight generations per year (Thatcher and Pickard 1967). A large proportion of the attacking adult population reemerges shortly after oviposition is completed (Coulson and others 1978), and these reemerging adults, in concert with emerging brood adults, produce a continual allocation of beetles (Coulson and others 1979c) that attack and produce pheromones in adjacent trees (Coster 1970). The continual presence of a pheromone source results in infestations forming as cohesive "spots" that serve to concentrate both the SPB and its natural enemies (Franklin 1970b). In large infestations SPB hosts are abundant and parasitoids do not need to disperse further than adjacent trees to find them. It has also been commonly observed that those parasitoid adults aggregate at SPB-infested trees with susceptible hosts (Camors and Payne 1973, Dixon and Payne 1980, Sullivan and others 1997) and generally parasitize later larval stages (Kudon and Berisford 1980, VanLaerhoven and others 2002). Field and laboratory experiments with five common SPB parasitoid species revealed that at temperatures near 30 °C, the average development time was about 2 weeks, or approximately one-half the time required for their SPB hosts (Jones and Stephen 1994).

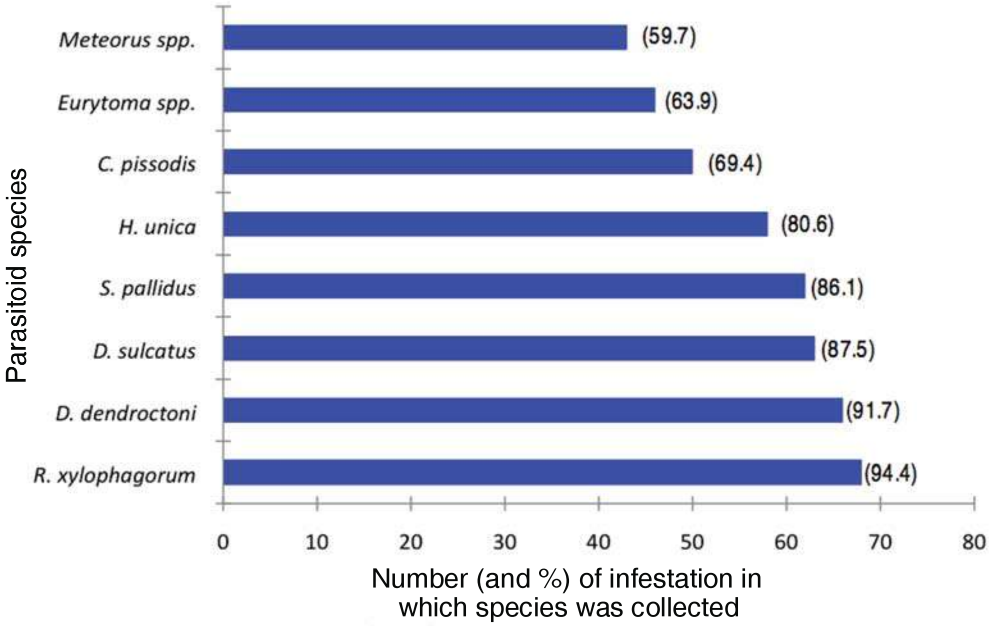


Figure 28.1—Constancy of occurrence of eight common parasitoids in SPB infestations. The bars reflect number of times each parasitoid species was collected, by intensive within-tree sampling, from a total of 72 infestations studied between 1975 and 1992. The values in parentheses are percentage of occurrence of those parasitoid species. (adapted from Stephen and others 1997)

Within a large spot that has been growing for several months, the SPB population age structure has beetle immatures in all stages of development that can serve as hosts for parasitoids. It therefore seems probable that over time, in large SPB infestations, parasitoids should have higher population growth rates than their SPB hosts and through numerical response be effective regulators of SPB populations. However, most SPB infestations are fewer than 10 trees and usually decline (Billings 1980b). In these small infestations the host resource is patchy and ephemeral, and parasitoid dispersal to other infestations is critical.

Evidence Parasitoids Are Not Suppressing SPB

Research is extremely limited that provides estimates of parasitoid-caused mortality to SPB populations. Those data that do exist support the conclusion that parasitoids do not cause high amounts of mortality. A large SPB infestation was intensively monitored in 1991 and 1992 by within-tree sampling of infested pines and concurrently counting total numbers of infested and cumulative dead trees on the Indian Mounds Wilderness Area in East Texas. In April 1991, the infestation contained 74 currently infested trees. Rapid growth occurred throughout the summer until by late September 1991, 895 currently infested trees (and nearly 2,600 cumulative dead trees) were counted. Beetle population numbers declined in winter, but infestation growth began again in spring. Population estimates of the SPB in April 1991 showed approximately 2.8 million SPBs present in the infestation, which grew quickly until there were an estimated 33.5 million SPBs present in November. February 1992 estimates indicated about 15.8 million beetles, with fast growth leading to a population of nearly 42 million SPBs by May 1992 (Figure 28.2). The total parasitoid population grew from less than 200,000 in April 1991 to about 1.2 million in November, declined over winter, then grew to about 1.45 million by May 1992. A visual comparison of increase and decrease in parasitoid numbers in relation to the SPB numbers indicates that patterns of change are closely related. Although parasitoid population abundance continually increased throughout spring and summer, average percentage of parasitism was between 6 and 7 percent in both April and September and fluctuated at about those levels in all intervening months, suggesting that although actual numbers of parasitoids increased in relation to changing beetle numbers, a numerical response probably did not occur (Figure 28.3).

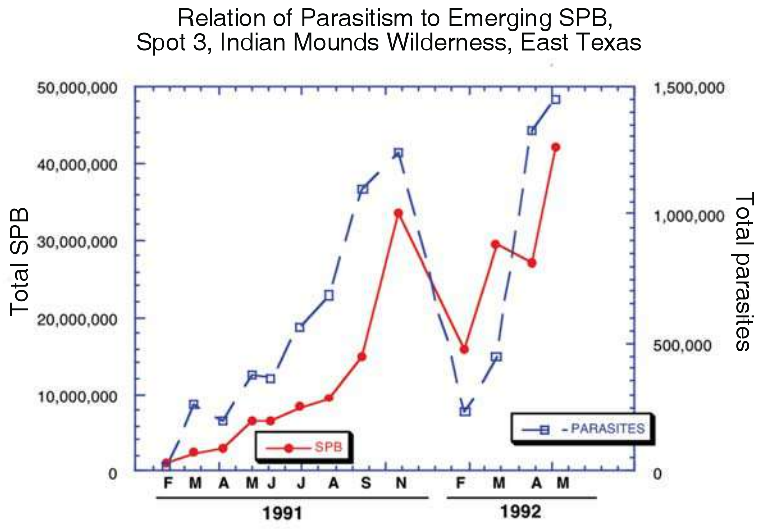


Figure 28.2—Estimated total numbers of adult SPB and adults of its parasitoid complex in a single large SPB infestation sampled intensively from February 1991 to May 1992. Numbers of SPB are shown in red, scaled on the left axis, and total parasitoids are shown in blue, scaled on the right axis. (adapted from Stephen and others 1997)

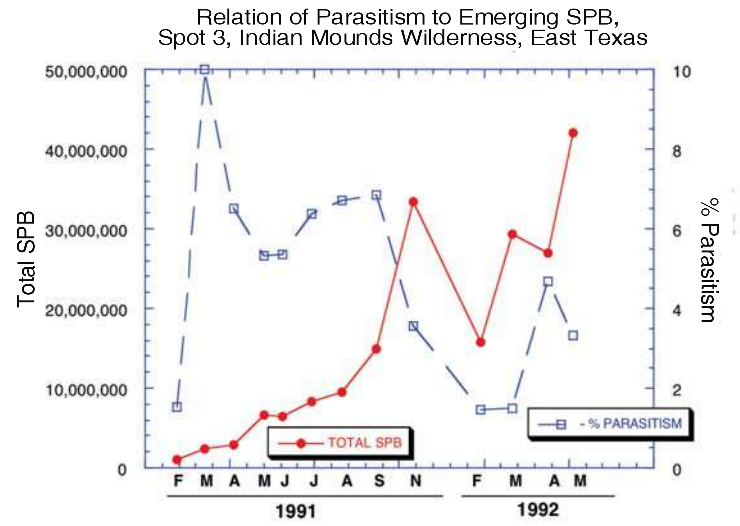


Figure 28.3—Estimated total numbers of adult SPB and percent parasitism from its parasitoid complex in a single large SPB infestation sampled intensively from February 1991 to May 1992. Numbers of SPB are shown in red, scaled on the left axis, and total percent parasitism is shown in blue, scaled on the right axis. (adapted from Stephen and others 1997)

It appears from the East Texas data that parasitoids inflicted variable but relatively low mortality, and did not exhibit a numerical response to increasing SPB populations. When this conclusion is examined in relation to: 1. superabundance of continuously available

SPB host larvae; 2. parasitoid adults needing only to traverse minimal distances between trees within spots to locate these hosts; 3. observed parasitoid aggregation at trees with suitable host larvae; and 4. Parasitoid immature development rates that are nearly twice as rapid as their hosts, it seems remarkable that over several months of infestation growth a proportionally greater amount of parasitism did not occur. Unfortunately data of this same type were not collected in this area for the next several years as SPB populations remained high in 1993 but collapsed in 1994 (Clarke and Billings 2003).

Hypothesis of Adult Parasitoid Nutrition

From these and additional observations Stephen (1995) proposed a hypothesis that parasitoids are not effective in regulating SPB populations because parasitoid adults, in improperly managed southern pine forests (those which are overstocked, homogeneous in age and species composition, and protected from fire), are limited in reproductive capacity and longevity by lack of suitable nutrition from natural sources. This hypothesis evolved over time as scientific evidence was accumulated in support of the importance of nutrition to parasitoid effectiveness.

Natural sources of food for adult parasitoids could be in the form of flower nectar or honeydew secreted by forest Homoptera. Laboratory studies demonstrated that parasitoid adults would take flower nectar if it were readily available (Drumtra and Stephen 1999). Flowering plants are rare in intensively managed pine forests, and in field studies artificially placed flowers within SPB infestations were not visited (Drumtra and Stephen 1999). VanLaerhoven and others (2005) reported that SPB parasitoid adults will feed on artificial food applied to the bole of host pines. Those parasitoid adults also move considerably away from potential host larvae, located in subcortical tissues of infested pines, and forage in the forest understory and in the canopies of pines and hardwoods. Foraging in locations where their hosts do exist suggests these locations may provide a source of adult nutrition, and indeed a significant amount of honeydew is produced, especially by hardwoods, in those locations (VanLaerhoven and others 2005, VanLaerhoven and Stephen 2008). It is also possible that foraging in tree canopies may provide a corridor for parasitoid movement and dispersal within SPB infestations.

Testing the Hypothesis

Parasitoids of SPBs employ a reproductive strategy, termed "synovigenic," in which adult females have large, nutrient-rich eggs that are few in number but can be resorbed by the adult if hosts are not available (Figure 28.4). If adults do find nutrition they can produce more eggs and they live longer (Mathews and Stephen 1997, VanLaerhoven and others 2002). In the mid-1990s Lloyd E. Browne (Entopath Inc. Easton, PA) developed a nutritionally complete, environmentally safe, artificial food for SPB parasitoids that he named Eliminade®. In laboratory trials, Mathews and Stephen (1997) tested more than 2,800 individual SPB parasitoids of seven species, reared from field-collected SPB infested logs, by exposing them to water only or water plus the Eliminade® diet (Figure 28.5). All seven species fed on the diet and all had significantly greater longevity when they consumed artificial diet (Mathews and Stephen 1997). Further experiments also showed that under more extreme laboratory conditions designed to more closely mimic hot summer field conditions, particularly in high temperature-low humidity situations, parasitoid adults only lived a very short time, but that with nutrients and moisture their longevity was significantly improved (Mathews and Stephen 1999).

To further explore manipulation of parasitoid effectiveness by augmenting adult nutrition, plastic paint balls each were filled with 2.1 g Eliminade® to which blue dye was added as a means to visually identify diet on trees and in guts of parasitoids. Field experiments were conducted in which food balls were shot from compressed air rifles onto the boles and into the crowns of SPB-infested trees (Stephen and Browne 2000). Parasitoids searching for hosts or ovipositing on SPB-infested tree boles (Figure 28.6) were subsequently collected using modified Dustbuster® vacuums (Figure 28.7), and dissected to determine if they had Eliminade® and dye in their guts (Figure 28.8). Adults from all eight species of parasitoids (Figure 28.1) fed on Eliminade® in field trials (Stephen and Browne 2000). Application of food via compressed air rifles and food balls was too labor-intensive and slow for operational suppression, thus prompting aerial spray trials of Eliminade® from helicopters into the pine canopy of an SPB infestation. Following aerial application 514 parasitoid adults were collected on boles of infested trees and dissected. Nearly 75 percent showed evidence of feeding on

Eliminade® (Stephen and Browne 2000) (Table 28.2). Stephen and Browne (2000) proposed that aerial application of Eliminade® could be a direct control for SPB by enhancing longevity, fecundity, and effectiveness of SPB parasitoids. Subsequent field experiments to validate this idea were hampered by epidemic SPB population levels, coupled with unpredictable movement of adult SPB among infestations, plus lack of funding for aerial Eliminade® treatments and simultaneous area-wide monitoring of the SPB and their natural enemies in multiple infestations across the landscape.

28.4.4. Predators and Competitors

The clerid beetle, *Thanasimus dubius* (F.), has captured the attention of forest entomologists since the time of A.D. Hopkins (Hopkins 1893, 1899). Its response to the SPB aggregation pheromone (Dixon and Payne 1979a, Thatcher and Pickard 1966), coupled with its abundance and highly visible habits as a predator of SPB adults on the bark of newly infested trees and larval predation of SPB immatures, has made it a prime candidate for study and possible manipulation (chapter 10). Reeve suggests that *T. dubius* may, under field conditions, slow the attack process of the SPB and help regulate SPB populations, as he noted an inverse relationship between year-to-year growth rate of the SPB and *T. dubius* populations (Reeve 1997). Miller and others (1987) suggest that predators, specifically the North American clerid *Thanasimus undatulus* Say and the palearctic predator of *D. micans*, *Rhizophagus grandis*, may be suitable for colonization and manipulation as they respond to aggregation pheromones of the SPB.

Massive outbreaks of the SPB in East Texas slowed and collapsed in 1994, and analysis of causes suggested that available host trees were still abundant, and the collapse was probably a function of predation, plus competition from pine engravers (*Ips* species) and long-horned wood borers (*Monochamus* species) (Clarke and Billings 2003). Although their assessment as to the cause of the collapse was speculative, other scientists who have observed the rapid decline of bark beetle infestations in the South have also alluded to the importance of competition from *Monochamus* species in particular (Dodds and others 2001, Hain and Alya 1985). The roles and impact of predation (chapter 10) and competition (chapter 12) deserve additional study and must be more clearly defined in order to adequately understand SPB population dynamics.

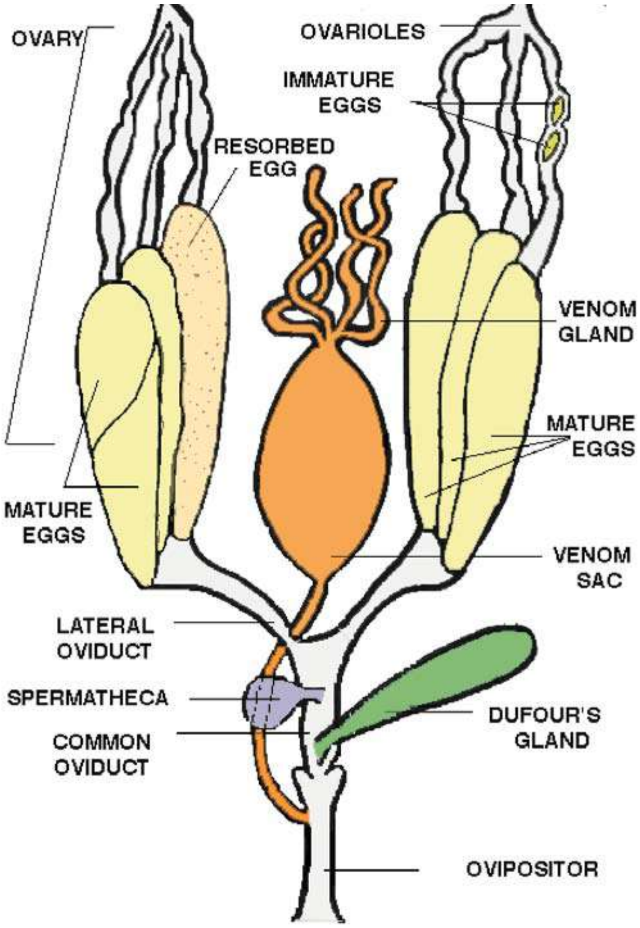


Figure 28.4—Stylized rendering of the reproductive system of an adult female synovigenic parasitoid, showing ovaries containing immature, and mature, large nutrient-rich eggs, plus a partially resorbed egg. (adapted from Gauld and Bolton 1988. The Hymenoptera. Oxford University Press)

Figure 28.5—*Roptrocerus xylophagorum* adults in the laboratory feeding on a drop of blue-dyed Eliminade®

Figure 28.6—*Coeloides pissodis* adult ovipositing on surface of pine bark

Figure 28.7—Dustbuster® cordless vacuum, modified for parasitoid collection

Figure 28.8 —*Coeloides pissodis* adult, dissected to show blue-colored mid-gut resulting from feeding on Eliminade®

28.4.5. Natural Enemies Share a Host Resource

A long-noted and important observation associated with SPB infestations is that a complex of bark beetles is commonly present in the same infested trees (Berisford 1980, Dixon and Payne 1979b, Paine and others 1981). This complex of bark beetles is attacked by many of the same natural enemies, and this is true in general for bark beetles throughout North America. Wasps in the braconid genus *Coeloides*, for example, parasitize six species of *Dendroctonus*, three species of *Scolytus*, and seven *Ips* species in North America (Stephen and others 1993). Long-legged flies, *Medetera* (a bark beetle predator), are reported to attack six *Dendroctonus*, two *Scolytus*, and five *Ips* species. Similar patterns of host utilization occur with many predators and parasitoids, and better information on host prey selection and rearing records would further confirm this fact. This information is important because as populations of the SPB shift in abundance, their natural enemies still can locate *Ips* species or even other bark beetle or weevil genera in their habitat that will serve as suitable hosts and maintain a natural enemy complex in the forest. Research conducted by Kudon and Berisford (1980) confirmed that the most common hymenopterous parasitoids of the SPB also are found parasitizing *Ips* engraver beetles, and even the eastern juniper bark beetle, *Phloeosinus dentatus* (Say). They suggest that when SPB populations are low and *Ips* bark beetle populations are high, *Ips* could serve as reservoir hosts for these parasitoid species, and during SPB epidemics *Ips* bark beetles may compete as alternate hosts for SPB parasitoids. Although SPB parasitoids are not host-specific, they do prefer to oviposit on the host bark beetle species and host tree species from which they emerged (Berisford 1974b, Kudon and Berisford 1980). A model describing possible host choice and patterns of resource use during shifting levels of SPB and *Ips* abundance in forest stands has been proposed and is illustrated by Berisford, chapter 8.

28.5. RESEARCH NEEDS

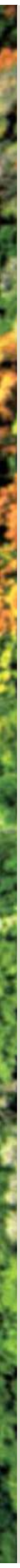
Considerable research has been done that strongly implies parasitism, predation, and competition are important causes of mortality to the SPB throughout all life stages and may alter the trajectory of population growth within infestations and on a wider scale across landscapes. Field-based studies during all phases of bark beetle population cycles, from endemic to epidemic, coupled with laboratory experiments and systems modeling are still needed to confirm the roles and impact of naturally occurring biological control in SPB population dynamics.

A further need is for area-wide assessment of SPB populations. Sampling of bark beetles and their natural enemy populations has been accomplished in individual infestations (Stephen and Taha 1976), but during epidemic SPB infestations field experience suggests that movement of adult beetles among infestations occurs (F.M. Stephen and L.E. Browne unpublished data), and that the only way to adequately assess manipulation of natural enemies is to evaluate total populations of the SPB over a wide area. If, for example, parasitoids are important in killing a significant number of beetles in a single infestation but immigration of SPB adults from nearby infestations occurs, it may swamp the effects of manipulation. The costs of field-based sampling programs are high and the efforts involved great, but this type of field assessment must be supported if we are to understand these interactions sufficiently to take full advantage of this naturally occurring biological control.

Long-term studies of bark beetle population dynamics are needed, and bark beetle natural enemies and associates should be included in these long-term efforts. There are too few examples of individual research efforts that address population dynamics of bark beetles and associates during endemic/epidemic population levels and the transition phases between them. Research relating seasonal phenology of both beetles and their natural enemies should be coupled with tracking infestations through low-level, endemic phases, and on to increasing and epidemic outbreaks and subsequent decline. Studies which target natural enemy biology, behavior, and density must not be conducted in isolation, but rather be related clearly to population dynamics of the bark beetles upon which they are dependent.

Table 28.2—Results of parasitoid foraging tests with Eliminade®. Aerial application, by helicopter, of 8 L. Eliminade® on day zero to foliage of tree crowns in Alabama SPB infestation. Parasitoids collected on bark surface of SPB-infested trees containing late-stage immatures on the day of treatment and for 4 subsequent days. Dissections were made to confirm Eliminade® feeding.

Day of treatment	SPB *attacks/dm2*	SPB *eggs/dm2*
0	48	0
1	161	75
2	157	76
3	143	78
4	82	61



Section V

V. Integrated Pest Management

Section V addresses the theory and practice of the concept of integrated pest management (IPM) as applied to the southern pine beetle. This unit contains one chapter. *Integrated Pest Management* is defined to be the maintenance of the southern pine beetle populations at tolerable levels by the planned use of a variety of preventive, suppressive, or regulatory tactics and strategies that are ecologically and economically efficient and socially and politically acceptable. It is explicit that the actions taken are fully integrated into the total forest and environmental management process–in both planning and operation. The practice of IPM incorporates information from many of the preceding chapters in *The Southern Pine Beetle II*. An implemented IPM System for the southern pine beetle is defined. Input from 11 separate components is required: climate change, population dynamics of the insect, tree and forest dynamics, impact assessment, monitoring, diagnosis, treatment tactics, environmental assessment, the forest database, management planning, and decision and execution. The relation of these various compartments and the types of information needed for each are defined.

29

Integrated Pest Management of the Southern Pine Beetle

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Abstract

Integrated pest management (IPM) is the maintenance of destructive agents, including insects, at tolerable levels by the planned use of a variety of preventive, suppressive, or regulatory tactics and strategies that are ecologically and economically efficient and socially and politically acceptable. It is explicit that the actions taken are fully integrated into the total forest and environmental management process –in both planning and operation. The concept, methodology, and practice evolved from extensive research and development projects conducted during the 1970s and 1980s. In this chapter we 1. provide a general overview of the IPM concept, 2. place IPM in the broader context of a multitiered management hierarchy, 3. define the forest settings where the southern pine beetle (SPB) is considered to be a pest, 4. examine the structure and component activities of an SPB IPM system, and 5. summarize the major research, development, and management actives in need of further study and elucidation.

Keywords

climate change
decision support
forest dynamics
integrated pest management
treatment tactics

29.1. INTRODUCTION

Integrated pest management (IPM) is a concept, methodology, and practice that was formulated from extensive research and development conducted during the 1970s and 1980s. Impetus for the forest component of this work came as a result of cyclic outbreaks of several prominent forest insects; e.g., southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB); the western pine beetle, *D. brevicomis* LeConte; the mountain pine beetle, *D. ponderosae* Hopkins; the gypsy moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae); the Douglas-fir tussock moth, *Orgya pseudotsugata* McDunnough (Lepidoptera: Lymantriidae), the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae); and the western spruce budworm, *C. occidentalis* Freeman. Much of the work on the SPB centered on ways to manage the economic, ecological, social, and political impact of the insect on southern forests (Branham and Thatcher 1985, Coulson 2003, Thatcher and others 1980). Attributes of the natural history of the SPB, particularly the occurrence of infestations in spatially discrete patches (spots), and the innovations of the digital age (e.g., global positioning systems, geographic information systems and related technologies, Internet delivery systems) greatly facilitate application of IPM concepts for the SPB in southern forest landscapes. Accordingly, in this chapter our goal is to examine IPM as related directly to the SPB. The specific objectives are: 1. to provide a general overview of the IPM concept; 2. to place IPM in the broader context of a multi-tiered management hierarchy; 3. to define the forest settings where the SPB is considered to be a pest; 4. to examine the structure and component activities of an SPB IPM system, and 5. to summarize the major research, development, and management activities in need of further study and elucidation.

29.2. INTEGRATED PEST MANAGEMENT

The term "pest" is an anthropocentric designation given to certain forest insects and other organisms when they adversely affect ecological, economic, social, and political values associated with the resources and conditions of the forest environment. The philosophy, concept, and methodology of IPM evolved over a period of years, and therefore, so has the definition. Our working definition of IPM is as follows: Integrated pest management is the maintenance of destructive agents, including insects, at tolerable levels by the planned use of a variety of preventive, suppressive, or regulatory tactics and/or strategies that are ecologically and economically efficient and socially and politically acceptable. It is explicit that the actions taken are fully integrated into the total forest and environmental management process –in both planning and operation (Coulson 2003).

The definition of IPM contains four key points of emphasis. First, the foundation of IPM is based on the principles of ecology. Second, the methodology involves a combination of tactics; that is, discrete techniques aimed at suppression or prevention of population growth. When combined, several tactics constitute a strategy for regulating or modifying population distribution and abundance. In some instances more than one strategy can be applied. Third, the functional goal of IPM is to reduce or maintain pest populations at tolerable levels. Economic, ecological, social, and political values are used in judging what tolerable levels are. Fourth, IPM is a component of forest protection, which is a component of forest management, which is a component of environmental management (Coulson 1981).

29.3. MANAGEMENT HIERARCHY

To manage is to take charge of or care of. Management is a directed activity. IPM is the approach used to manage destructive agents in the forest environment by the planned use of preventive, suppressive, and/or regulatory tactics and strategies. The effects of IPM are propagated through a management hierarchy consisting of three levels of activity: forest protection➔forest management➔environmental management.

The base of the management hierarchy is forest protection, which we define as the applied component of forest management that deals with the agents that cause undesirable change in the conditions and resources of the forest landscape. The actual practices of IPM are part of the domain of forest protection. However, forest protection is a component of the next level in the hierarchy, forest management, which we define as follows: the orchestrated modification or manipulation of landscape structure, function, or rate of change. The specific type of forest (e.g., extensively managed, intensively managed, specialized forest setting, urban/suburban) and the impact of the pest species will dictate the need for and extent of IPM. The effects of IPM must be considered in the context of specific forest management goals. Finally, forest management is a component of environmental management. Herein we define the term, environment, as the external conditions and resources, living and nonliving, that affect an organism or other specified system (e.g., a forest) during its lifetime. Environmental management is defined broadly to mean the orchestrated modification or manipulation of the chemical, physical, and biological surroundings of an organism or other specified system during its lifetime. The tactics and strategies of IPM are directed to specific pest organisms, but the effects are often distributed through the forest landscape. For this reason, IPM actions are often evaluated through a formal environmental impact assessment (EIS) prior to implementation. In the United States, the EIS procedure is a formal process defined by NEPA (National Environmental Policy Act of 1969 as amended) legislation. A multivolume EIS has been prepared for the SPB (USDA, FS, EIS 1987).

29.4. WHERE IS THE SOUTHERN PINE BEETLE A PEST?

There are several different kinds of forests where the SPB is considered to be a pest. The prominent types are intensively managed forests, specialized forestry settings, and urban/suburban forests. Each forest type varies in the degree of human intervention involved in management (Figure 29.1). As IPM is a costly and complicated endeavor, application of the approach is often reserved for those circumstances where forest resources and conditions have extraordinary value. Although the SPB is associated with conservation forests (e.g., wilderness areas) and extensively managed forests, IPM in these environments is reduced and tailored to meet unique management objectives. In the following sections, we examine SPB in intensively managed forests, specialized forestry settings, and urban/suburban forests.

29.4.1. Intensively Managed Forests

Much of the impetus for the research into principles and procedures of IPM came from interest in protecting the valuable resources associated with intensively managed forests. Although these forests are managed for multiple values, maximizing timber and fiber production is often the overriding goal. Specific attributes of forest sites and stands have a great impact on forest productivity. The effects that insects have on forest trees are related to site and stand conditions (Figure 29.2).

Southern Pine Beetle and Site Relationships

A site can be considered as a localized area within a forest landscape where a particular tree species, along with associated vegetation, grows. The site consists of both abiotic (nonliving) and biotic (living) components. Our focus here is centers of sites predominately stocked with southern yellow pine (*Pinus* spp.) as these species are the main host of the SPB. The condition of the site has a major influence on productivity of a pine forest. The concept of site is expressed in production forestry in a variety of ways; e.g., site class, site index, site quality. A pine forest landscape consists of a mosaic of different site conditions. The condition of the site changes throughout the life cycle, or rotation time, of a tree species.

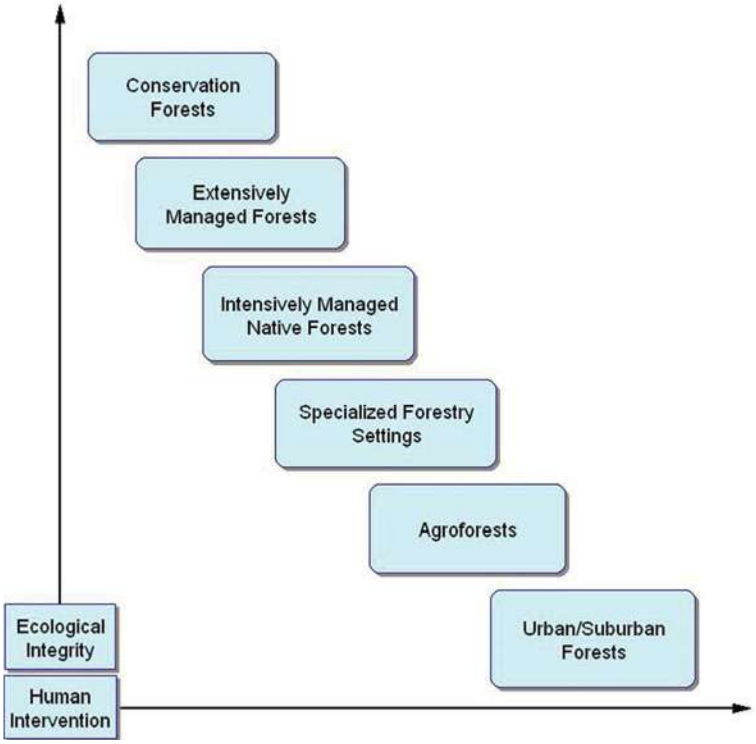

Figure 29.1—Types of forests illustrating a range of human intervention from modest to great. IPM is practical in intensively managed forests, specialized forestry settings, urban/suburban forests, and (to some extent) agroforests. (KEL image)

Figure 29.2—Southern pine beetle infestation on an intensively managed forest (Indian Mounds Wilderness, northeast, Texas). (photograph by Ron Billings)

Site condition is an important consideration in IPM of the SPB for two reasons. First, the site contains the host material, *Pinus* species, in various stages of growth that the SPB utilizes for food and habitat. The availability of suitable preferred host species is a primary requisite for the development of SPB populations. The opportunity for SPB populations to grow in size varies on different sites. Second, site condition, in combination with weather, determines the rate of growth and general vigor of host trees present. To initiate infestations the SPB exploits trees that are physiologically weakened as a result of stress created by nutrient deficiencies, drought, flooding, overcrowding, and so on.

Southern Pine Beetle Stand Relationships

In production forestry, the basic unit of management is the forest stand. A stand is a somewhat arbitrary subdivision of a forest landscape. It is an aggregation of trees and other vegetation occupying a specific area. It is sufficiently homogeneous in species composition, age, size, structure, and condition to be distinguishable from the forest and associated vegetation on adjoining areas.

Certain activities involved in the cultivation of pine forests create conditions that enhance or reduce the likelihood that the SPB will have a significant impact on forest resource values. In circumstances where we are attempting to maximize wood or fiber production, forest structure is tailored in a number of specified ways: 1. generally one pine species will be planted; 2. within a particular stand, the species selected will be planted at or about the same time—that is, the stand will be even-aged; 3. there will usually be an attempt made at controlling unwanted hardwood species; and 4. the density of the trees will be prescribed. Each of these conditions is conducive to the buildup of large populations of the SPB once the stands mature. Variations in site quality, that is poor site quality, and stand conditions within the forest, taken together, often create the opportunity for large SPB populations to develop (Figure 29.2).

29.4.2. Specialized Forestry Settings

There are several different types of specialized forestry settings where tolerance of SPB infestation is much lower than even the intensively managed forests. These settings include seed orchards, recreation areas, arboretums, and research plots. The SPB is commonly a pest in these settings because of the high value of the product sought (or function, in the case of recreation areas) relative to traditional forest values. The strategies taken in managing the SPB in these settings are more closely aligned with the practices used in traditional agriculture than in forest landscapes. For example, pest management practices are more intensive and generally warrant a greater expenditure of capital than is practical in a forest over an entire rotation. There is also a much greater dependence on the use of pesticides in the specialized settings than in forest landscapes, where economic, ecological, social, and political constraints often limit widespread application (Figures 29.3A and B).

29.4.3. The Southern Pine Beetle in Urban/Suburban Forests

The urban/suburban forest can be defined to include trees growing in residential areas at the interface between managed forests and centers of commerce, in yards at residences, along city streets, in city parks, and in recreational areas. Conceptually, the problems with the SPB in urban/suburban forests are similar to those in intensively managed forests and specialized forestry settings. The main difference is that trees in urban areas are cultured primarily for aesthetic purposes and because of their usefulness in buffering the effects of weather.

Urban areas throughout the range of the SPB periodically have outbreaks of the insect. The commercially valuable pine species are common ornamental trees, and residential developments are often built in remnant mature forests. Cultural disturbances to sites and trees in urban/suburban forests often trigger local SPB outbreaks and infestations of individual hosts trees. Examples of common disturbances include road construction; power transmission line clearing; photochemical oxidation injury; building construction, including site clearance and dressing, placing of sidewalks, driveways, and conduits; and modification of water drainage patterns. Once infestations occur, pest management generally involves use of remedial tactics to remove infested hosts.

29.5. COMPONENT ACTIVITIES OF SPB IPM

The major impetus that fueled the development of concepts of IPM came from concern for managing forest insect pest outbreaks on intensively managed public and private forest lands. The research and development projects of the 1970s and 1980s and subsequent investigations have provided a well-formulated IPM concept and approach. However, the issue of implementation of IPM within the managerial hierarchy of forest protection➔forest management➔environmental management remains a challenging task. The concepts, practices, technologies, and legal statutes of forest protection, forest management, and environmental management have changed significantly since the architects of IPM crafted the initial principles. Following, we present an overview of the basic activities associated with the practical application of IPM for the SPB in forest landscapes.

IPM in forests can be defined, from a functional perspective, to consist of a number of specific but related activities as illustrated in Figure 29.4 (Coulson 2003, Saarenmaa 1992). This activity

Figure 29.3A—Aerial photograph of southern pine beetle infestation in an urban landscape in North Florida. (photograph by J. Meeker)

Figure 29.3B—Remedial suppression tactic, involving the use of pesticides applied to infested pines in an urban landscape. (photograph by J. Meeker)

model is a concise overview of the concept and practice of IPM. It represents a significant advancement over previous constructs in that the research and development components of IPM are integrated with activities needed for implementation of the concept in a real-world forest environment. Figure 29.4 represents IPM to consist of 11 separate activities that are related as illustrated by connections and directions of arrows. The basic activities include the following: effects of climate on the forest environment, assessment of pest population dynamics, assessment of tree and forest dynamics, impact assessment, evaluation of control alternatives, monitoring, database management, diagnosis, environmental assessment, management planning, and decision and execution. Each of these activities is examined below.

There are eight fundamental principles of IPM in forests conveyed in Figure 29.4 that pertain to the SPB specifically and forest insect pests in general. These principles include the following:

- The basic premise of IPM is that there is a resource or forest condition in need of protection from pests. From a management perspective, the state of the resource is evaluated through an examination of tree and forest dynamics. This examination usually involves use of simulation models that approximate the expected growth and yield of a valued tree species over at least a rotation period. The condition of the forest is evaluated by integration and interpretation of spatially referenced tabular databases that describe a specific environment. The types of data needed for this purpose include themes such as tree species composition, age, and density; terrain elevation and slope; and soil type.
- Some insect species are periodically pests because they become sufficiently numerous to damage a valued resource or desired forest condition in some way. Generally, there is a direct relation between population size and impact on forest resources and conditions. IPM, therefore, requires evaluation of pest population dynamics. Again, this evaluation can be facilitated through the use of simulation models.
- The actual or potential importance of a pest species is judged by evaluating its economic, ecological, social, or political impact on values we associate with the resource or forest condition.

- In order to assess the actual or potential impact of a pest species, it is necessary to gather contemporary information about the state of insect populations and the resources and conditions of the forest environment. This activity requires monitoring. To monitor is to observe critically in ways that do not affect the resources and conditions of the forest environment. The information collected during the monitoring activity becomes a part of the forest database. The forest database contains spatially referenced and tabular data that describe the forest resources and condition.
- The contemporary information gained through the monitoring activity is used in diagnosis of the cause and extent of a pest problem. This diagnosis is used to establish the need for directed suppression or prevention actions. Human judgment by experienced individuals is often an important component of the diagnosis.
- Pest population size can be modified (e.g., pesticides) or regulated (e.g., natural enemies) by the application of treatment tactics. The procedures may be targeted to suppression of existing populations or prevention of forest conditions that lead to pest outbreaks.
- Decisions to consider application of specific control tactics must be evaluated for their effect on the forest management plan and their environmental impact. These activities link forest protection to the higher levels of the management hierarchy; i.e., to forest management planning and environmental assessment.
- Decision and execution of an IPM program follows from interpretation of the environmental assessment and an evaluation of the effects on the forest management plan. Typically, this activity (decision and execution) requires integration and interpretation of both qualitative and quantitative information, and computer-based decision support is often a necessity. The results of the decision and execution activity directly affect the pest population and forest tree dynamics.

In the following subsections we examine each of the basic activities associated with IPM of the SPB. The interrelations of the various elements of the activity diagram (Figure 29.4) are also illustrated.

29.5.1. Climate and the Forest Environment

Climate is the combination or aggregate of weather conditions experienced in a particular area. It includes both averages and extremes measured over an extended period of time. The most important determinates of climate are temperature and precipitation. Climate affects the population dynamics of host species and the SPB (Figure 29.5). Climatic conditions

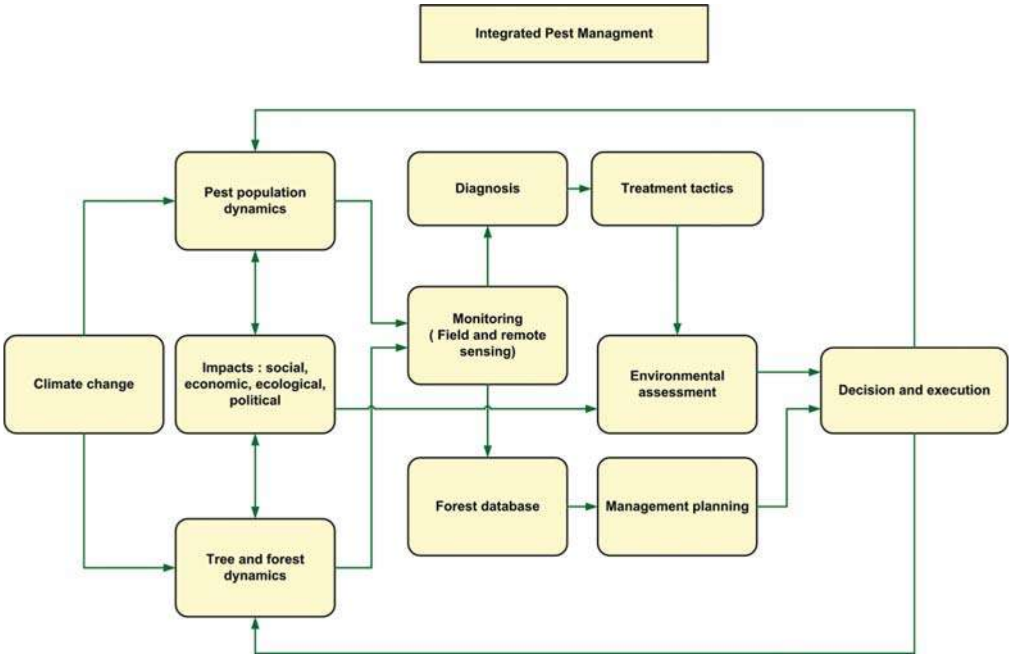

Figure 29.4—Activities associated with integrated pest management and their relation to one another. (modified from Coulson 2003)

influence the host/insect interactions directly. Climate also establishes the geographic range in distribution of preferred *Pinus* hosts and the SPB. Global climate change has greatly expanded the traditional geographic range of the SPB (Ayers and Lombardero 2000), and this circumstance must now be factored into IPM decisionmaking.

29.5.2. Pest Population Dynamics

Pest population dynamics (Figure 29.6) is the change in the distribution and abundance of an organism through space and time. The spatial framework for the SPB encompasses a range of square centimeters to hectares, and the temporal framework may vary from minutes to years. Within this spatial-temporal framework, it is possible to focus attention on populations of the SPB within a unit of habitat (a tree), within a stand, or within a forest landscape, and within an ecoregion (Coulson and Wunneburger 2000).

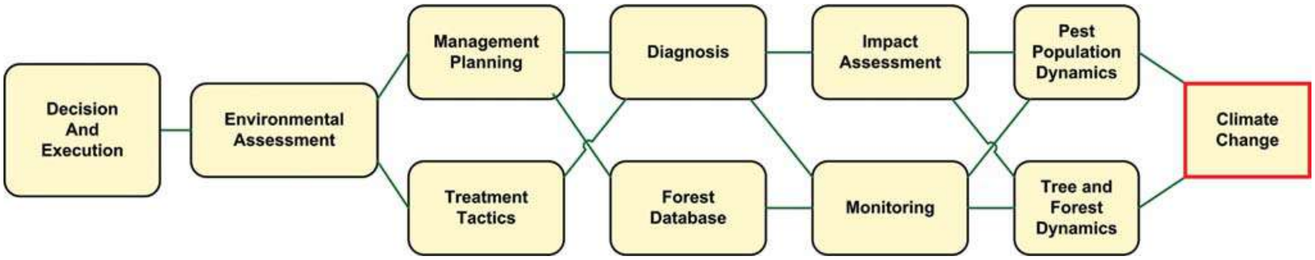

Figure 29.5—Dependency network for the Climate Assessment IPM activity.

The SPB is of major importance in forest management because it consumes resources, alters the conditions of the forest landscape, and disrupts management plans and schedules. Our interest in managing the SPB includes immediate short-term response to outbreak conditions involving current population levels and damage as well as long-term planning to anticipate and prevent population levels that lead to outbreaks. Obviously, the approaches used in population management under these two circumstances are quite different.

When one considers all the variables that affect birth, death, immigration, and emigration in a population of the SPB, it is not surprising to find that mathematical models of population systems are utilized to abstract key elements (Coulson and others 1989, Feldman and others 1981a, Lih and Stephen 1989, Stephen and Lih 1985). The accuracy and precision of predictive models of population dynamics are related to space-time resolution. Both accuracy and precision diminish as the space-time framework is enlarged, primarily because of the difficulties in forecasting weather over long periods of time. Therefore, best results in modeling populations have been obtained at the stand level of organization and in a period of time ranging from several weeks to several months. In management planning for potential SPB outbreaks, variables such as stand age, species composition and density, localized site conditions, physiographic conditions, and climatic zones within the range of the insect are used in predicting the likelihood of pest problems occurring at various age intervals of forest growth.

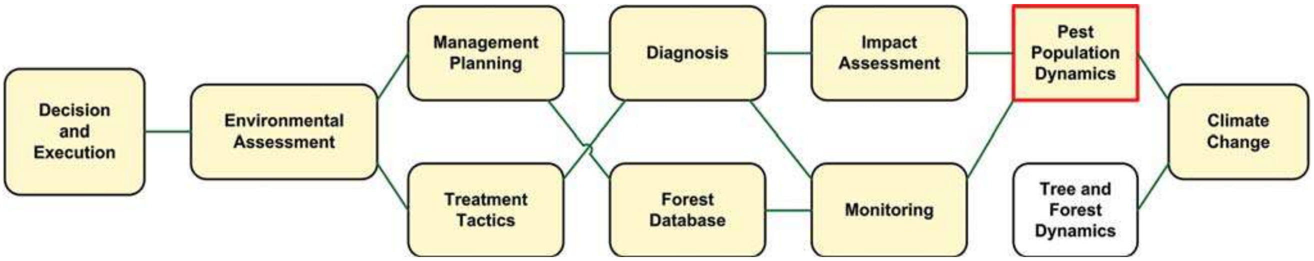

Figure 29.6—Dependency network for the Pest Population Dynamics IPM activity.

29.5.3. Tree and Forest Dynamics

The forest stand is often the focal point of IPM because it is the basic unit used by foresters for inventory, planning, and operations. Tree and forest dynamics (Figure 29.7) include consideration of causes for changes in the distribution, abundance, and size of a host tree species through space and time. In the context of IPM, we may be interested in either 1. the role of the SPB in the population dynamics of the host tree species or 2. the role of the host in the population dynamics of the SPB. In the first case, where interest is in the role of SPB in the population dynamics of the host, the temporal framework spans the rotation time for a particular tree species, which can range from about 6 to 150 years. Typically the SPB begins to affect pine forest stands at about 35-40 years. The spatial framework will normally be in hectares. In the second case, where we are interested in the role of the host in the population dynamics of the SPB, the spatial framework can range from a single tree, to stands, and to forests composed of stands in different age classes. The temporal framework can span from hours to several years. Host trees vary in susceptibility to colonization by the SPB and suitability as food and habitat. Tree species, age, and general vigor are variables that influence both susceptibility and suitability. Furthermore, many tree species possess defense mechanisms that deter insects; for instance, the resin system of pines is considered to be a primary defense against certain bark beetle species.

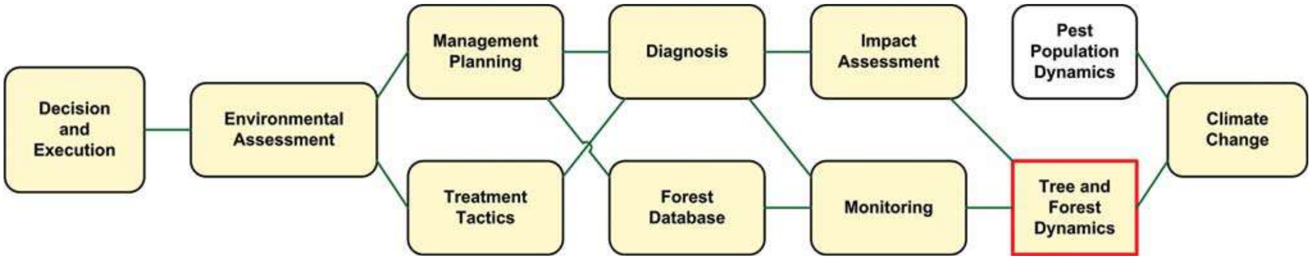

Figure 29.7—Dependency network for the Tree and Forest Dynamics IPM activity.

Foresters have developed mathematical models to predict forest stand growth and yield for many of the commercially important tree species. Data for these models are collected as part of the normal forestry inventory conducted on Federal, State, and private lands. Growth and yield models have proved to be useful in IPM, particularly when we are interested in defining costs associated with tree mortality or growth reduction resulting from the activities of pest species.

Significant advances in both the theory and practice of spatial modeling of forest landscapes have been made in recent years (Cairns and others 2008a, 2008b; Gustafson 1998; Mladenoff and Baker 1999; Rauscher and others 2000; Xi and others 2008). Major emphasis has centered on advancing scientific understanding of forest landscapes (e.g., forest succession and disturbance, vegetation dynamics, impact of deforestation, harvesting effects on landscape structure) (Lafon and others 2007, Mladenoff and Baker 1999, Waldron and others 2007) and on applications to enhance forest management practice (e.g., forest management decisions for wildlife, decision analysis for forest ecosystem management, assessment of watershed condition) (Rauscher and others 2000).

29.5.4. Impact Assessment

The concept of pest impact on forest resources and conditions is a central issue of IPM. Impact (Figure 29.8) is broadly defined to mean any effect on the forest environment resulting from the activities of insects. From an ecological perspective forest insects can act as herbivores, carnivores, or detritivores. Through these activities insects can cause changes in forest conditions (the abiotic environment, biotic environment, and forest configuration) and valued forest resources (timber production, hydrology, fish and wildlife, recreation, grazing, real estate, biodiversity, endangered species, cultural resources, and nonwood forest products). The degree of insect impact is evaluated using ecological, economic, social, and political criteria.

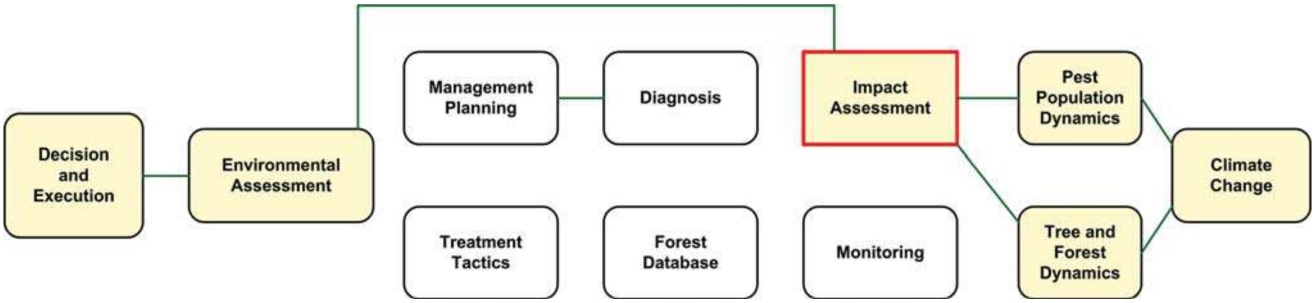

Figure 29.8—Dependency network for the Impact Assessment IPM activity.

Typically, for an insect or other organism to be considered a pest in a forest management context, the impact must be substantial; i.e., of sufficient magnitude to cause a human reaction. Because any reaction will involve expenditure of capital (human or monitory), pest management programs are often associated with high value forest environments; i.e., intensively managed forest, specialized forestry settings, and urban/suburban forests. In these environments, the reaction is to suppress or prevent the activities of the pest.

Evaluating impacts of the SPB can be extremely complicated. The insect can have both negative and positive impacts, depending on the criteria used in judgment and the particular forest management goal. For example, herbivory by the SPB serves to truncate community development at a time when the forest has become senescent, and thereby it reinitiates the process of ecological succession. At the same time, herbivory also causes economic loss at the stage in the rotation of the pine stand when the trees are most valuable. Because of the difficulties involved in assessing impacts, it is not surprising to find, again, that mathematical models are used for interpretative, as well as predictive purposes.

In the activity dependency diagram for IPM (Figure 29.4), impact evaluation involves a reciprocal interaction with the pest population dynamics and tree and forest dynamics components. The results of the impact evaluation feed directly to the environmental assessment component. This flow illustrates how forest protection activities link directly to the upper echelons of the management hierarchy.

29.5.5. Monitoring

Recall that to monitor is to observe critically in ways that do not affect the resources and conditions of the forest environment. Monitoring (Figure 29.9) involves collecting data about the forest environment. Forest landscapes are monitored for a variety of reasons; e.g., 1. to inventory the resources and conditional states of the forest environment, 2. to demonstrate compliance with legal forest management statutes, 3. to evaluate the impact of disturbance events, and 4. to survey the activities of pest organisms.

In the context of IPM, surveys involve monitoring tree and forest dynamics and the distribution and abundance of actual or potential pest insects or the damage they cause. There are several types of insect surveys

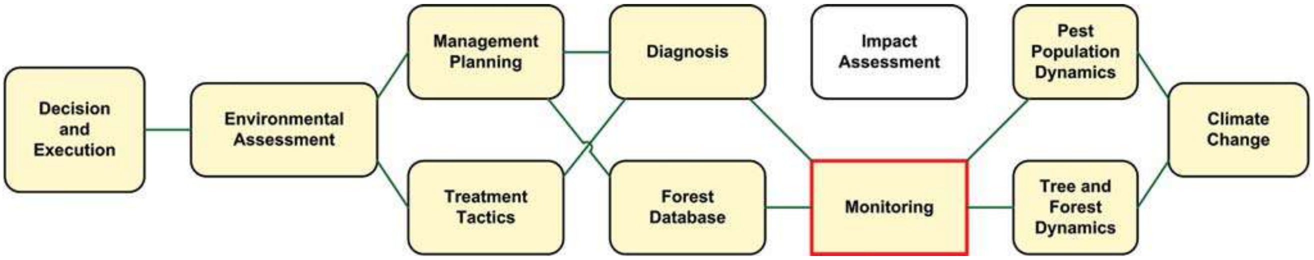

Figure 29.9—Dependency network for the Monitoring IPM activity.

that can be applied in intensively managed forests, specialized forestry settings, and urban/suburban forests. Forest surveys can be quantitative or qualitative with regard to the type of data collected. Surveys are often classed according to their purpose in the following way: 1. detection surveys, 2. biological evaluations, 3. loss or damage surveys, 4. pest control evaluations. The specific procedures used depend on the type of forest situation being sampled, the type of survey being conducted, and the intended use of the data collected.

The data collected in a survey are used for two purposes: to diagnose the nature and extent of the pest problem, and to enrich the forest database. Because of the importance of correct and contemporary information for use in IPM decisionmaking and the high costs associated with surveying pest populations, advanced technologies are often used to capture (remote sensing), analyze (spatial statistical procedures) (Gustafson 1998), display (geographic information systems or GIS), and interpret (decision support systems or DSS) (Coulson and others 1999c) survey data.

29.5.6. Diagnosis

To diagnose is to recognize and identify by examination and observation. There are two aspects of diagnosis (Figure 29.10): the first involves identification of the cause of the pest problem, and the second involves evaluation of the extent of damage. Monitoring forest insects through the various types of surveys provides basic information about the activities of pest species. The surveys often are routinely scheduled for important pest species. For example, most of the States in the Southern United States conduct aerial surveys to detect the presence and estimate the abundance the SPB. These surveys are usually initiated in April and May. Diagnosis is closely coupled with monitoring. It involves inspecting infestations on the ground (ground checking) and verifying the causal agent after pest activity has been detected. The pest species could be the SPB or another bark beetle species. Verifying the pest to be the SPB is important, as this insect is capable of causing significant tree mortality. Diagnosis involves examination of the host material to identify the causal agent and an appraisal of the extent of damage that occurred.

Forest entomologists and forest pathologists diagnose the cause and extent of pest problems. Their diagnoses are based on fundamental understanding of insect pests and the damage they cause. This understanding is founded on knowledge of the natural history of the pest species.

Diagnosis often includes consideration of experiential knowledge provided by foresters who are familiar with a particular forest environment; i.e., diagnosis is a collaborative activity that may involve the technical expertise of more than one specialist. Because it is often difficult to assemble technical specialists to address each forest pest problem, computer-based technologies have been employed to capture the heuristic knowledge of experts. Expert systems, which are computer programs designed to mimic the reasoning process of human experts, are suitable for this purpose (Coulson and Saunders 1987, Saarenmaa 1992, Saarenmaa and others 1994, Saunders and others 1993, Stone and others 1986).

29.5.7. Treatment Tactics

One outcome of the diagnosis activity can be that an insect pest is causing sufficient impact to warrant human intervention. Treatment tactics (Figure 29.11) are planned procedures that are used to modify or regulate the distribution and abundance of a pest species. As with the other elements of IPM, treatments have time and space components. That is, we are interested in ways and means of suppression of

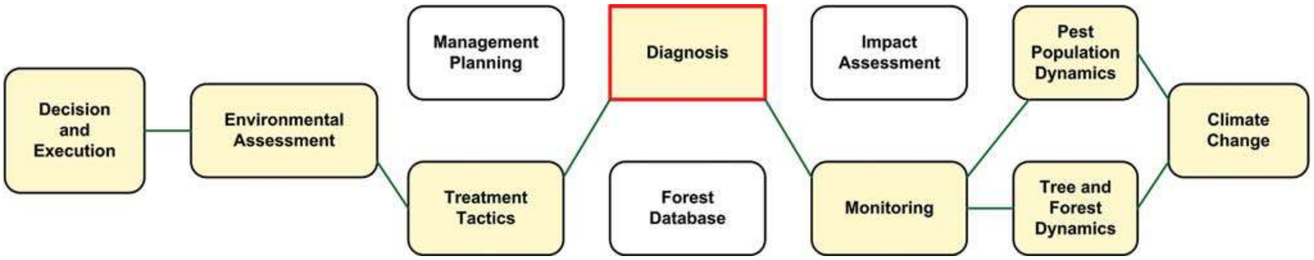

Figure 29.10—Dependency network for the Diagnosis IPM activity.

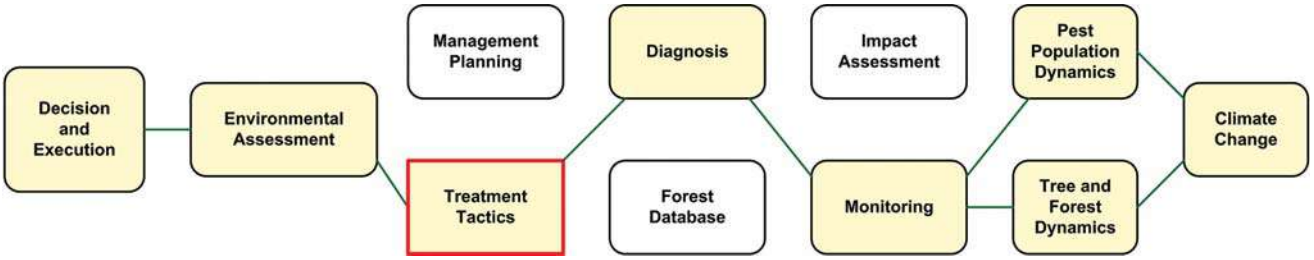

Figure 29.11—Dependency network for the Treatment Tactics IPM activity.

an existing pest population and in prevention of potential pest population outbreaks. In the case of suppression, the timeframe may range from several weeks to months, and the space framework from single trees to stands. However, more than one stand within a forest landscape can be affected. In the case of prevention, our time framework may span the rotation period for a tree species, and the space framework may include stands within forest landscapes. Obviously, the procedures used in suppression and prevention are quite different.

Historically, a great deal of attention has been given to development of treatments for specific pest problems. As concepts, these tactics affect reproduction, mortality, immigration, and emigration. There are numerous ways to manipulate these population system components. The specific procedure is often referred to as a control procedure or control tactic. Billings (see chapters 25 and 27, this volume) reviews the procedures used against the SPB. Following are several examples that illustrate various tactics used in suppression and prevention.

Suppression tactics are directed to existing pest populations. Examples of tactics are: 1. biological control, including augmentation of insect parasitoids, insect predators, avian predators, and disease; 2. chemicals, including various pesticides and herbicides; 3. behavioral chemicals (semiochemicals), including compounds that result in attraction and dispersal; 4. utilization, which involves harvesting of infested host materials; 5. various mechanical procedures, including felling infested hosts and burning infested hosts; and 6. use of genetically altered (transgenic) host plants.

Techniques used in prevention of insect outbreaks include: 1. regulatory controls, which are designed to prevent introduction of pests into uninfested forests or contain them through quarantine in localized areas, and 2. cultural or silvicultural controls that include management of stand characteristics such as species composition, age, and density; site maintenance; and avoidance of disturbances to both stands and sites.

The concept of IPM stresses that a variety of tactics can be used simultaneously to manage pest populations. These tactics collectively constitute a strategy. It is possible to develop strategies for both suppression and prevention goals. For a particular treatment tactic to be included as part of a strategy, it must be efficacious, safe, cost-effective, legal, and socially acceptable. Reference to Figure 29.4 indicates that treatment strategies are directly linked to environmental assessment.

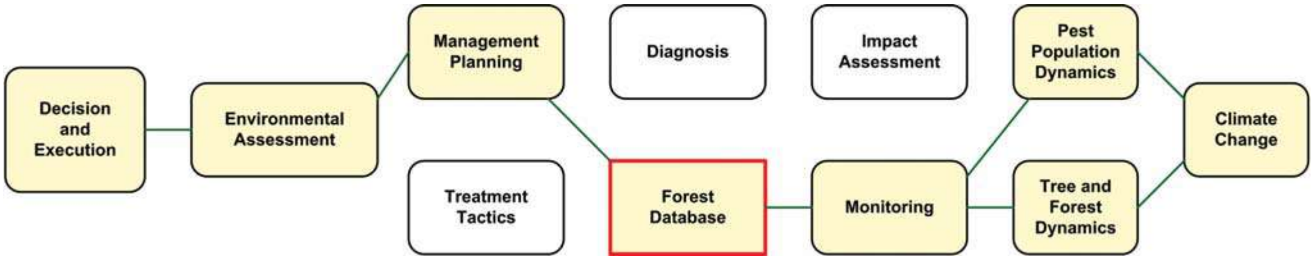

Figure 29.12—Dependency network for the Forest Database IPM activity.

29.5.8. Forest Database

Accurate information on the state of the environment is a critical component of all forest management programs. The data that provide information about the forest environment are collectively referred to as the forest database (Figure 29.12). The database contains numerical data that describe different attributes of the biotic and abiotic forest environment. The database can also include data on the condition of the atmosphere. Historically, forest landscapes have been organized for management purposes using a hierarchical system. For example on national forests in the United States, the basic unit of organization is the stand. Stands are aggregated into compartments. Compartments are combined to form a ranger district. Ranger districts are combined to form a national forest. Commercial timber companies use a similar system for private forest lands. The basic unit of forest management does not have to be the stand. Landscape management practices could, for example, use the boundaries of a watershed to delimit a management unit. Multiple watersheds could be clustered in manner analogous to the compartment configuration. However, the specific numerical data comprising the various themes of the database are associated with a basic management unit.

Because the forest database is complex, GIS and database management technologies are used to organize, integrate, and display information. Typical spatially referenced themes represented in the database include: a base map, vegetation types, forest tree inventory, terrain features, hydrography, road corridors, and so on. Very detailed data about the management unit can be stored in a separate database management system and accessed, manipulated, and displayed in the GIS. The forest database is used to store the results of monitoring and to guide management planning.

29.5.9. Management Planning

The goals of forest management vary among the different types of forest environments. The management plan (Figure 29.13) for a specific forest environment will be based on accomplishing defined goals. For example, the management plan for a commercial seed orchard would emphasize profitability. The details of the plan to achieve this end will include ways to maximize production of high quality seed that the customers require, while minimizing the costs associated with the operation. The management plan employed by a city government for an urban forest might emphasize scenic beauty as its management goal. The details of the plan to achieve this end would be substantially different from those used by the seed orchard manager. In the United States, the management goal for public forests is sustainability, while providing goods and services to citizens. The National Forest Management Act of 1976 (as amended) specifies this goal. How to achieve this goal is defined by the National Forest System Land and Resource Management Planning rule (as revised). The current rule describes the framework for National Forest System land and natural resource planning (Federal Register 2000). The principal goal for privately owned intensively managed forest properties is profit from the sales of goods and services. The plan to achieve this goal typically will emphasize ways to maximize growth and yield, minimize taxation liability, and minimize negative environmental impacts. The certification programs for sustainable forest management and legal statutes provide boundaries that constrain the management plan.

Pest insects are associated with all of the forest environments, and therefore, management plans must consider their impact. In production forests, insect consumers directly compete with humans for resources. IPM is the approach

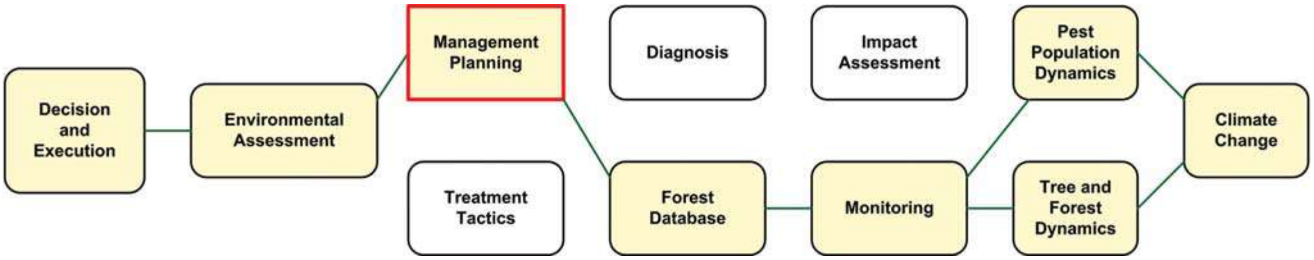

Figure 29.13—Dependency network for the Management Planning IPM activity.

used to deal with insect pests when they disrupt our planned uses of the forest environment.

29.5.10. Environmental Assessment

Environmental assessment (Figure 29.14) deals with evaluating change to the environment resulting from human actions. In the context of IPM, assessment centers on evaluating change in the environment resulting from suppression or prevention activities associated with forest protection. In particular, we are interested in the effects of proposed SPB IPM actions on the forest environment. The terms effect, impact, and consequence are used interchangeably.

In the United States, the substance of environmental assessment is defined by the National Environmental Policy Act of 1969 (as amended) (NEPA). This act requires that Federal agencies assess the environmental impact of implementing their major programs and actions. For projects or actions that are expected to have a significant effect on the quality of the environment, the responsible agency is required to file a formal environmental impact statement (EIS) (Jain and others 1993). The EIS is a substantial undertaking and involves the preparation of a document that addresses the following key issues for a proposed action (Jain and others 1993):

- The environmental impact of the proposed actions
- Any adverse environmental effects that cannot be avoided should the proposal be implemented
- The alternatives to proposed actions
- The relationship between local short-term uses of the environment and the maintenance of enhanced long-term productivity
- Any irreversible and irretrievable commitments of resources that would be involved in the proposed action should it be implemented

The environmental assessment activity follows from the selection of specific treatment tactics and consideration of the impact of the pest species on forest resources and conditions (Figure 29.14). The need for IPM actions is often a result of an SPB outbreak that was not anticipated or predicted. In these instances, it is difficult for the responsible Federal agency to develop an EIS and provide for protection of valued forest conditions or resources in a timely manner. This dilemma is one of the challenges of forest protection. Environmental assessment is a complex, costly, and slow process.

It is noteworthy that the initial models of IPM did not explicitly address the issue of environmental assessment. This activity is a key component of the contemporary view of IPM that is addressed formally for public lands through the NEPA–EIS mechanism. It is dealt with directly on private forest lands through the sustainable forestry certification programs and specific environmental statutes.

29.5.11. Decision and Execution

The final component of the IPM activities model is decision and execution (Figure 29.15). This activity involves both judgment and directed action. The issues associated with these two components are quite different, and we discuss each in turn.

The judgment (decision) component of IPM is an integrative step. To reach this position in the IPM model, we have had to participate in 10 other activities (see Figure 29.15). The data and information that form the knowledge base for a specific forest management problem involving pest insects and diseases often come from several different domain specialties

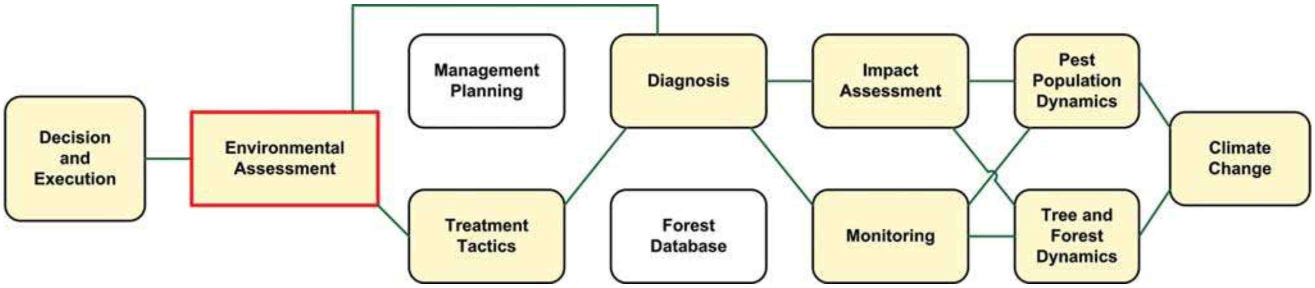

Figure 29.14—Dependency network for the Environmental Assessment IPM activity.

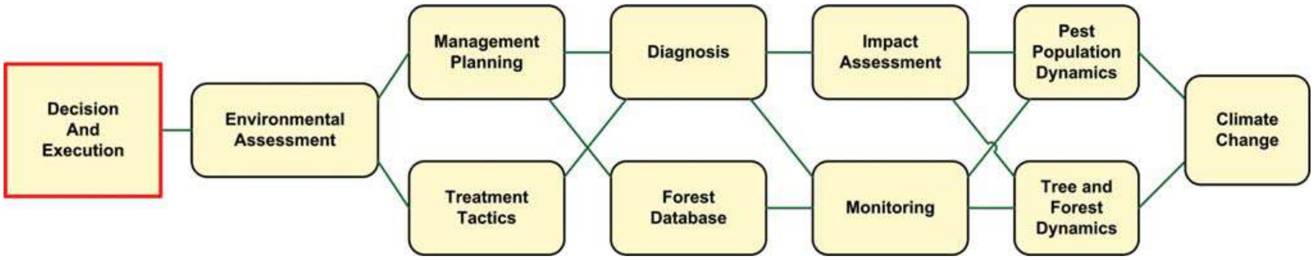

Figure 29.15—Dependency network for the Decision and Execution IPM activity.

such as entomology, forestry, ecology, geography, sociology, and economics. The knowledge base can exist in several forms: 1. tabular information, usually stored in a database management system; 2. spatially referenced data themes, usually associated with a geographic information system; 3. numerical output from simulation models and mathematical evaluation functions; 4. unstructured paper and hypertext documents; and 5. heuristics of experts based on corporate experiences of humans (Coulson and others 1996a). Given this complexity, integrative computer-based technologies have been used to aid in supporting the decisionmaking process of the forest manager (Coulson and Saunders 1987). A variety of approaches have been employed, and Schmoldt (2001) reviews applications developed specifically for insects and diseases; e.g., Potter and others 2000 - (gypsy moth), Power and Saarenmaa (1995) - eastern hemlock looper, Reynolds and Holsten (1996) - spruce beetle. Synthesis for planning, problem-solving, and decisionmaking support involves the use of both qualitative and quantitative information. It is a challenging task that is the focus of considerable ongoing research and development.

The directed action (execution) component of IPM involves application of one or more of the tactics available for pest population suppression or prevention of damage. The arsenal of weapons includes chemical pesticides, biological control with natural enemies, mechanical or physical methods (e.g., trapping, habitat destruction), silvicultural practices, and regulatory (legal) procedures (e.g., quarantines). These actions can be combined to form a strategy for protection that can be integrated into the forest management plan. In some instances, the evaluation phase may suggest that the best response to the pest activity is no action. For example, the cost of an insecticide application may exceed the value of the trees in the forest stand, or the environmental impact may be greater than desirable.

29.6. THE RESEARCH, DEVELOPMENT, AND APPLICATIONS AGENDA FOR SOUTHERN PINE BEETLE INTEGRATED PEST MANAGEMENT

The SPB persists in causing catastrophic economic, social, and ecological impacts across the South. The existing knowledge base for the insect is inadequate to explain the causes for epidemics or provide insight into how they can be managed. Outbreaks cycle within the southern region, and we cannot anticipate when or where they will occur or predict their severity. Consequently, when outbreaks do occur the effects on forest health are devastating. Because of the persistent impact of the SPB on public and private forests throughout the South, this insect is a specific target of the Healthy Forests Initiative and the Healthy Forests Restoration Act, which President George W. Bush signed into law on December 3, 2003. The IPM concept, presented above, is generally acknowledged to be the framework for addressing the depredations caused by the insect.

Managing the impact of the SPB within tolerable limits is a realistic expectation that can be accomplished through a focused research, development, and applications (RD&A) program. To this end, representatives from the Southern State Agricultural Experiment Stations, USDA Forest Service, State Forestry Agencies, and technical specialists from the research community participated in a workshop (held in Mountain Lake, VA, August 11-14, 2003) to define in detail the agenda for an SPB RD&A program and to develop a plan for implementing the RD&A program. The organizing theme for the RD&A program was Integrated Pest Management (IPM) (Coulson 2003). The workshop resulted in the following conclusions:

- The persistent impact of the SPB on public and private forests throughout the South places this destructive pest species at the forefront of the Healthy Forest Initiative. The Healthy Forestry Restoration Act provides the means for addressing the depredations caused by the insect through a comprehensive RD&A program directed to SPB IPM.
- The significant economic, ecological, and social impact of the SPB on the forests resources of the South can be reduced and losses caused by the insect managed within tolerable limits. However, the current knowledge base for the insect is inadequate, and significant new technologies are not being used in the context of contemporary forest and environmental management practices. A substantial and targeted RD&A program will address these issues.
- The IPM concept and methodology provides a framework suitable for structuring an SPB RD&A program that will lead to clearly defined products and procedures needed to reduce economic, ecological, and social impacts.
- Participants in the SPB workshop (scientists, practitioners, and technical specialists from State, Federal, and private agencies and organizations) critically and systematically examined and defined the agenda needed for an SPB RD&A program organized around the IPM approach. This activity resulted in the four products reported in this proceedings: 1. an evaluation of each of the 10 IPM activities, 2. a definition of RD&A questions for each activity, 3. a prioritization of the RD&A activities, and 4. a list of deliverable products that will follow from an SPB IPM program. These products provide an objective and consensus-based agenda for the RD&A program (Adams and others 2003).
- The technical expertise needed to conduct an SPB RD&A program is dispersed among a variety of State, Federal, and private agencies and organizations. A centrally organized and specifically targeted RD&A program will provide the mechanism needed to coordinate and focus human resources needed to address IPM of the SPB.
- There is solidarity among the scientists, practitioners, and technical specialists from the various agencies and organizations in State, Federal, and private sectors regarding the need for a centralized RD&A program to address SPB IPM. Participants in the SPB workshop acknowledged that implementation of a program could be accomplished using a model that includes a high degree of coordination and peer-reviewed evaluation.
- The agenda for the IPM program involved a blend of priorities distributed among research (38 percent), development (40 percent), and application (22 percent) (Table 29.1).

Table 29.1—The priorities for the SPB IPM program involve a blend of activities associated with research, development, and applications

Proportion of effort needed in the SPB RD&A Program		
Research	Acquisition of new knowledge	38%
Development	Integration and interpretation of new and existing knowledge	40%
Application	Use of knowledge for planning, problem solving, decision support	22%

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Species Index

Dendroctonus frontalis, *Thanasimus dubius*, and *Ophiostoma minus* appear throughout the book; thus have been excluded from the species index.

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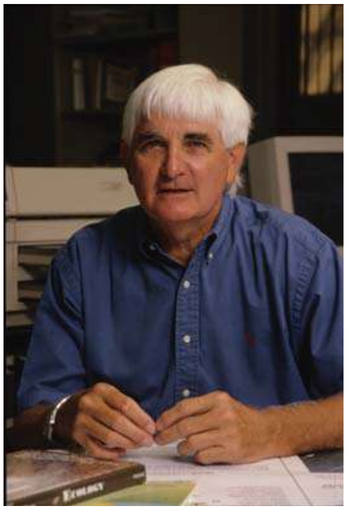
Subject Index

Editors



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BIOGRAPHY | Robert N. Coulson is Professor of Entomology at Texas A&M University. He earned the BS degree in biology (1965) from Furman University and MS (1967) and Ph.D (1969) degrees in entomology from the University of Georgia. After a year of post doctorate study at the Institute of Ecology at the University of Georgia, he joined the Texas A&M University System where he was initially employed as Principal Entomologist with the Texas Forest Service and Assistant Professor with the Texas Agricultural Experiment Station. In 1973 he received an academic appointment with the Department of Entomology at Texas A&M University. Dr. Coulson's research has been transdisciplinary in approach and directed to investigations of the activities and impacts of insects and other taxa in forest, prairie, savanna and agricultural landscapes. The research addresses issues of significance to ecological science as well land-use management. In 1984 he co-founded the Knowledge Engineering Laboratory (KEL) to facilitate research and development of computer applications for planning, problem-solving and decisionmaking in environmental science and management. Focus of KEL research is directed to landscape problems that require integration, interpretation, and use of different representations of knowledge. Special emphasis has been placed on ways and means of blending qualitative heuristic knowledge of experts with quantitative information that results from scientific investigations. His research accomplishments have been recognized at local (Former Student Association Faculty Achievement Award for Research, Texas A&M University), state (Award of Merit in Recognition of Outstanding Achievements in Forest Research, Texas Forestry Association), regional (A. D. Hopkins Award, Southern Forest Insect Work Conference), and national (J. E. Bussart Award and Fellow of Entomological Society of America) levels. Dr. Coulson teaches undergraduate courses in insect ecology and forest protection and a graduate course in landscape ecology. He is a member of the Entomological Society of America, International Association for Landscape Ecology, and the International Union of Forestry Research Organizations. He is a regular contributor to the scientific agenda of these societies.

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BIOGRAPHY | Kier D. Klepzig is Assistant Director for Research for the USDA Forest Service, Southern Research Station. He earned his BS degree with a double major in biology and reclamation (1986) from the University of Wisconsin-Platteville. He earned his MS (1989) and Ph.D (1994) degrees, both with double majors in entomology and plant pathology from the University of Wisconsin-Madison. In 1994, he was hired as an Assistant Professor in the Urban Forestry program at Southern University – Baton Rouge. One year later, he joined the USDA Forest Service, Southern Research Station, Southern Pine Beetle Research Work Unit in Pineville, LA. Initially employed as a Research Entomologist, he became the Project Leader of the Unit in 1998, holding graduate faculty adjunct appointments at Louisiana State University and Southern University. Dr. Klepzig's research has drawn from his background in entomology, pathology and microbial ecology. He has concentrated on the complex interactions among the microbial associates of the southern pine beetle. In 2006, Dr. Klepzig assumed leadership of a newly created research work unit: Insects, Diseases and Invasive Plants with Southwide responsibility for addressing biotic threats to forest health. In 2008, Kier was hired as Assistant Director for Research for the Threats Science Area. Located at Station Headquarters in Asheville, NC, he supervises three Southern Research Station research programs: Insects, Diseases and Invasive Plants; the Center for Forest Disturbance Science; and the Eastern Forest Environmental Threat Assessment Center. He is an internationally recognized authority on bark beetle-fungal interactions, with over 60 peer reviewed publications. He is a member of the Entomological Society of America, the and the International Symbiosis Society.

THE TEAM | The Southern Pine Beetle II was produced and edited by the staff and partners of the Knowledge Engineering Laboratory, Department of Entomology, Texas A&M University. The individuals responsible include (from right to left): Audrey Bunting (production editor), Shruti Gupta (graphic design artist), Maria Tchakerian (project manager), and Amy Krupa (language arts editor). Not pictured, Linda Anderson (copy editor).

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The knowledge base for the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae) has increased dramatically since the last comprehensive and interpretative summary (Thatcher and others 1980). This insect continues to be a significant pest affecting the forest environment of the Southern US and adjoining states and it is also the subject of considerable ongoing basic research. The knowledge base for the southern pine beetle is therefore broad-based and ranges from practical information that forms the foundation for integrated pest management (IPM) to basic discoveries that define our scientific understanding of the roles this organism plays in the natural environment. Accordingly, the goal of *Southern Pine Beetle II* is to provide a synthesis of new and existing knowledge to address both practical application as well as advancement of scientific understanding. *Southern Pine Beetle II* consists of 29 chapters divided into five basic sections: Ecology, Impact, Silviculture and Management, Treatment Tactics and Strategies, and Integrated Pest Management. The 22 first authors who contributed the individual chapters of *Southern Pine Beetle II* are recognized authorities in the respective domains of their contributions. The authors represent a blend of individuals who have, in some cases, devoted a significant portion of their professional careers to investigations of the southern pine beetle and new personalities who have brought fresh perspectives to the research arena.

Keywords: Southern pine beetle, Population Dynamics, Impact Assessment, Silviculture, Management, Treatment Tactics and Strategies, Integrated Pest Management

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