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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.

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 *intraspecific* competition, and competition for resources with individuals from other species is termed *interspecific* 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).

Bark Beetles

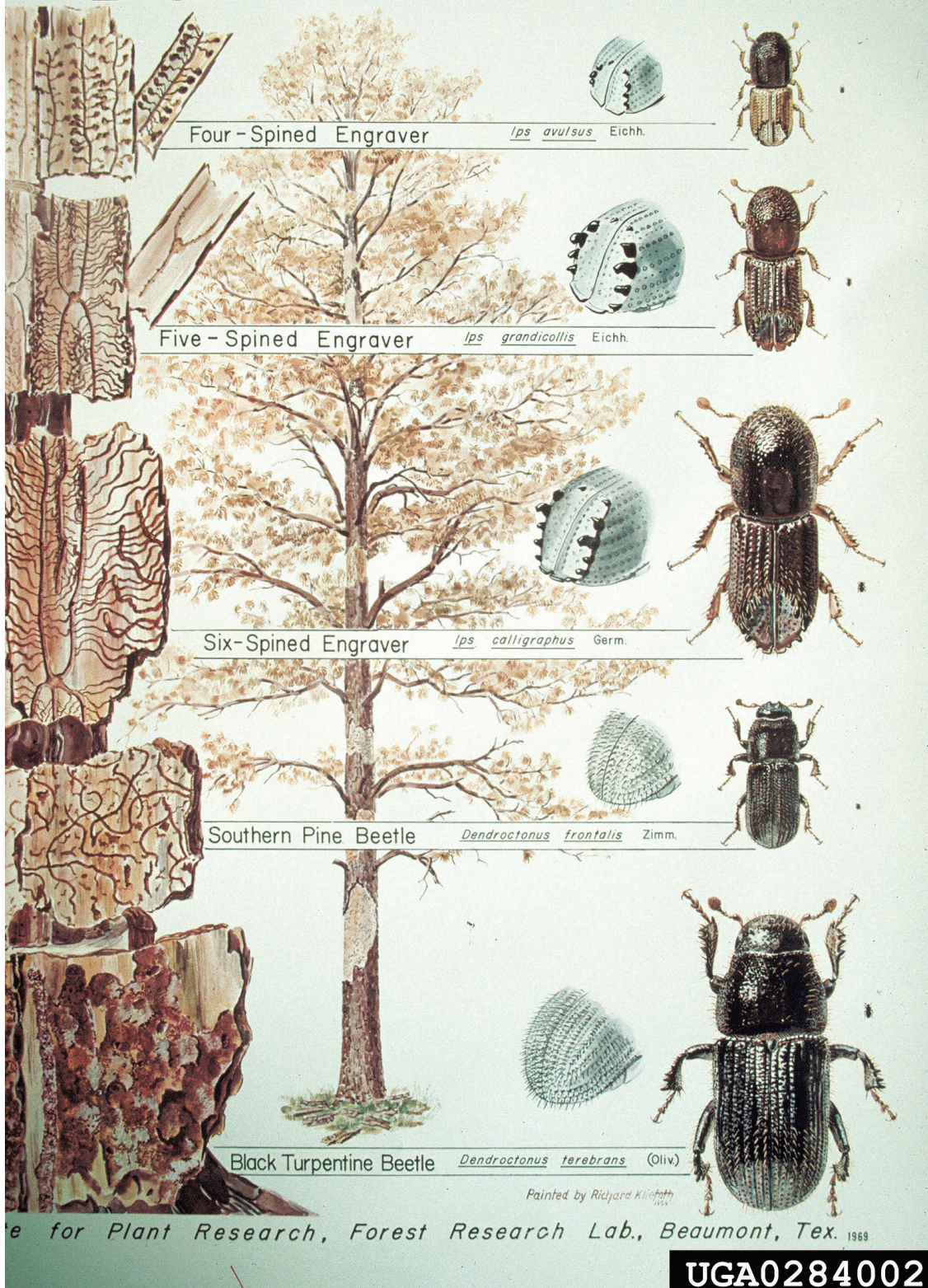


Figure 12.1—Classic painting, by Richard Kleifoth; Southern Forest Research Institute, of the southern pine bark beetle guild showing spatial preferences within trees, gallery patterns under bark, relative size, and elytral characteristics. (photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

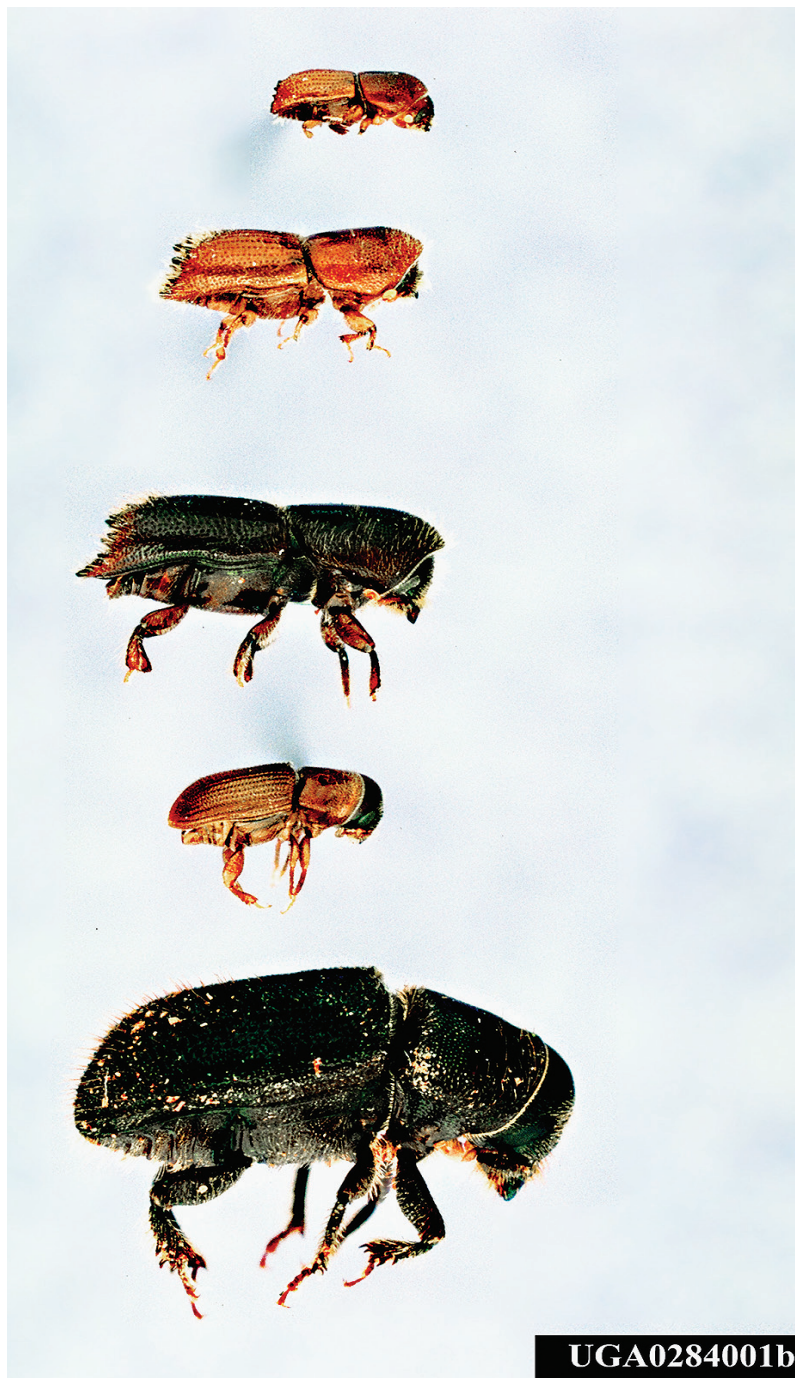


Figure 12.2—Adults of three species of southern pine engravers (top to bottom), *Ips avulsus*, *Ips grandicollis*, *Ips calligraphus*, plus the southern pine beetle, *Dendroctonus frontalis*, and the black turpentine beetle, *Dendroctonus terebrans*. Note relative size differences of each species, and 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 (Tschamtké 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

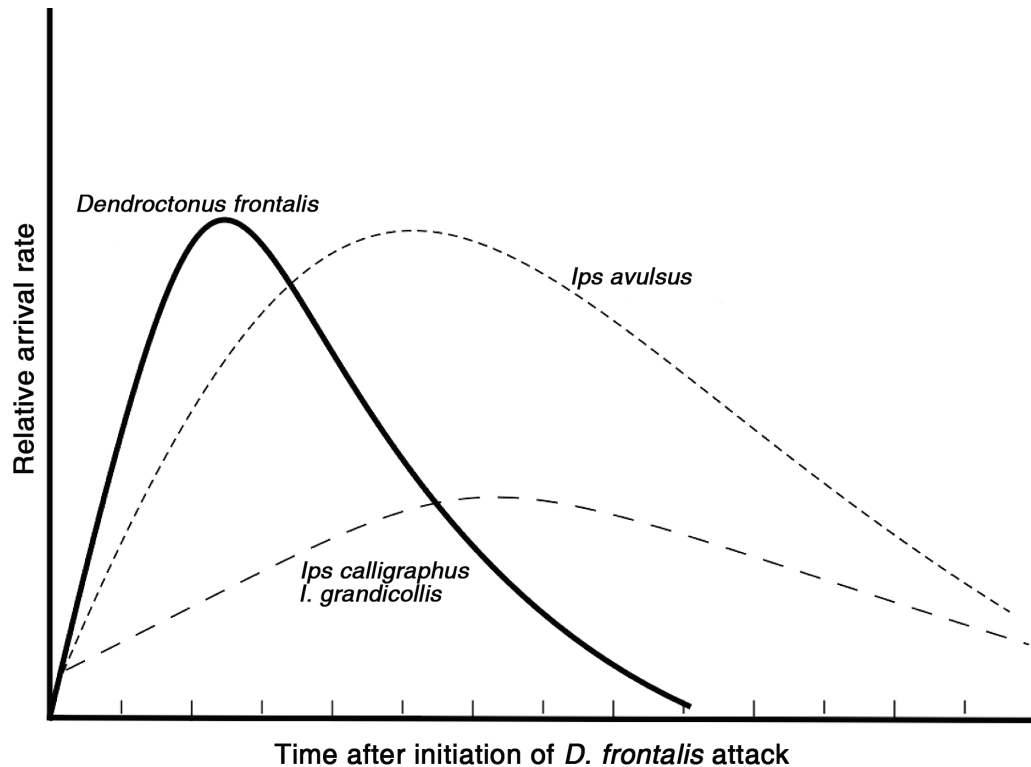


Figure 12.3—Generalized temporal patterns of arrival of *D. frontalis* and the southern pine engraver complex. (adapted from Berisford and Franklin 1971, Coster and others 1977a, Fargo and others 1978, Wagner and others 1985, Flamm and others 1987b, Stephen and others 1993)

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/dm² (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

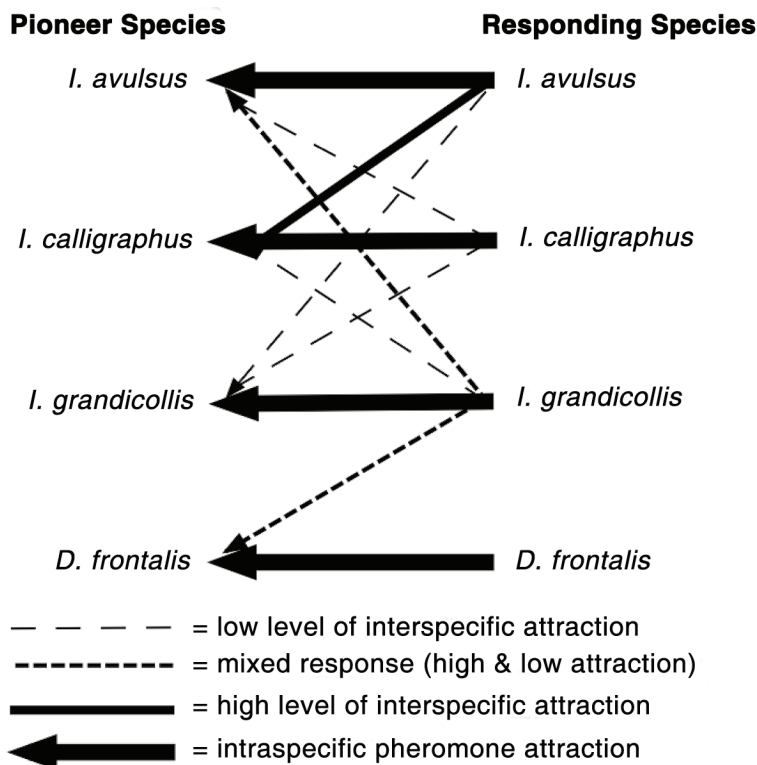


Figure 12.4—Summary of interspecific attraction within the southern pine engraver guild and SPB. A pioneer species produces pheromones as individuals of that species arrive at host resource. A responding species may respond to pheromones of one or more of the pioneer species. (abstracted from data in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

Payne 1979b). *Ips calligraphus* (Germer) 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

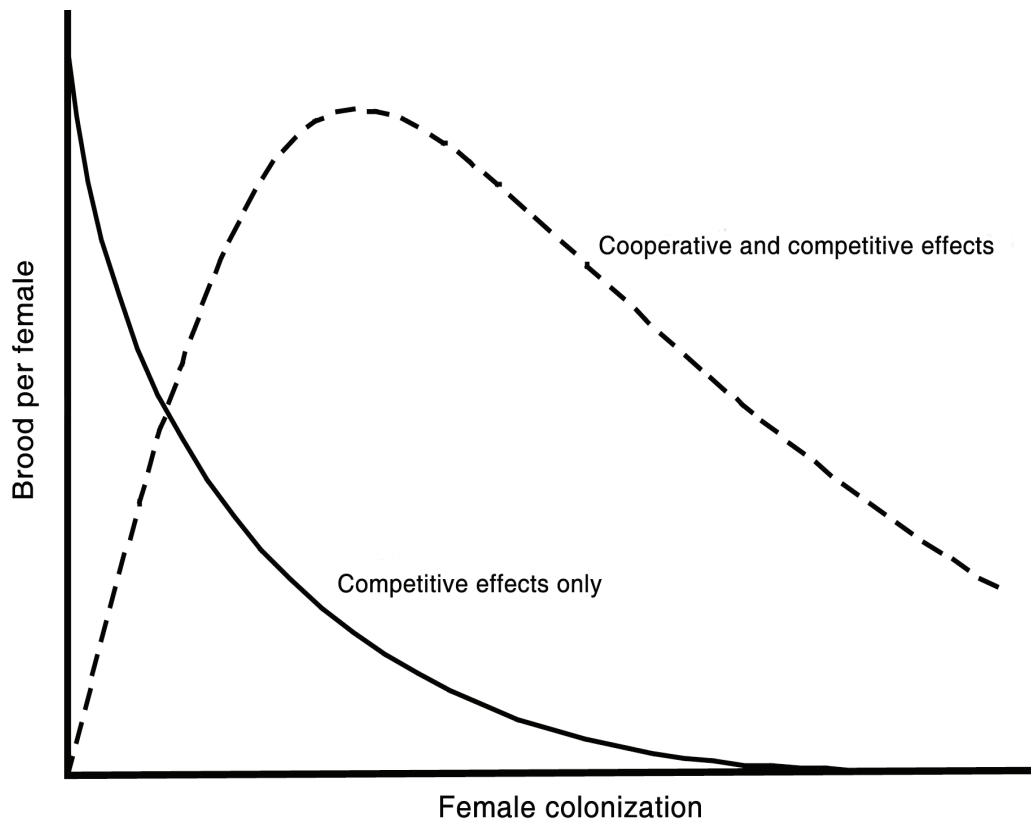


Figure 12.5—Proposed model of the effects of aggregation on individual beetle fitness, adapted from Raffa (2001). The solid line illustrates the hypothetical effects on numbers of females produced per female with bark beetle species such as the complex (*Ips avulsus*, *I. grandicollis* and *I. calligraphus*) 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 cm² (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).

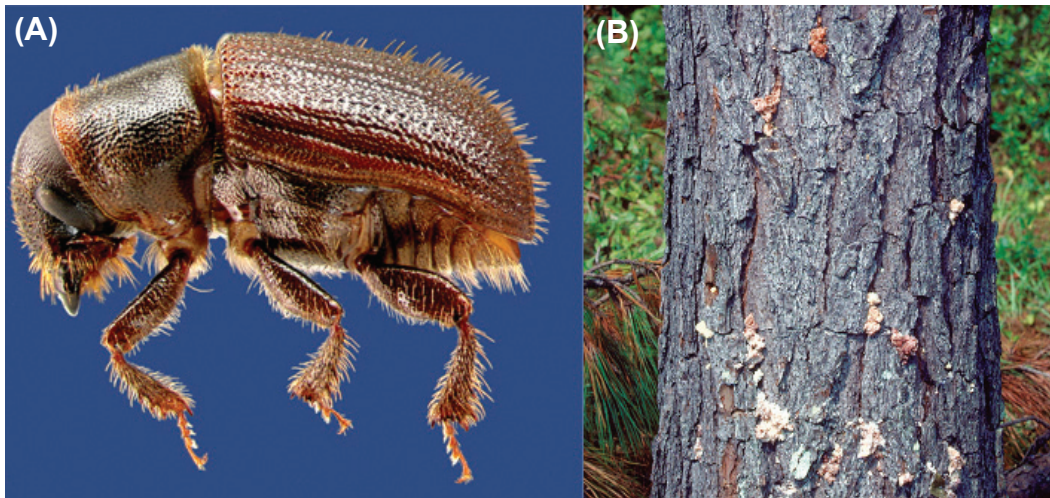


Figure 12.6—(A) Side view of black turpentine beetle, *D. terebrans* (Olivier), taken using an Auto-Montage digital microscopy system. (Photograph by David T. Almquist, University of Florida, www.forestryimages.org). (B) Basal region of a southern pine showing pitch tubes from black turpentine beetle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

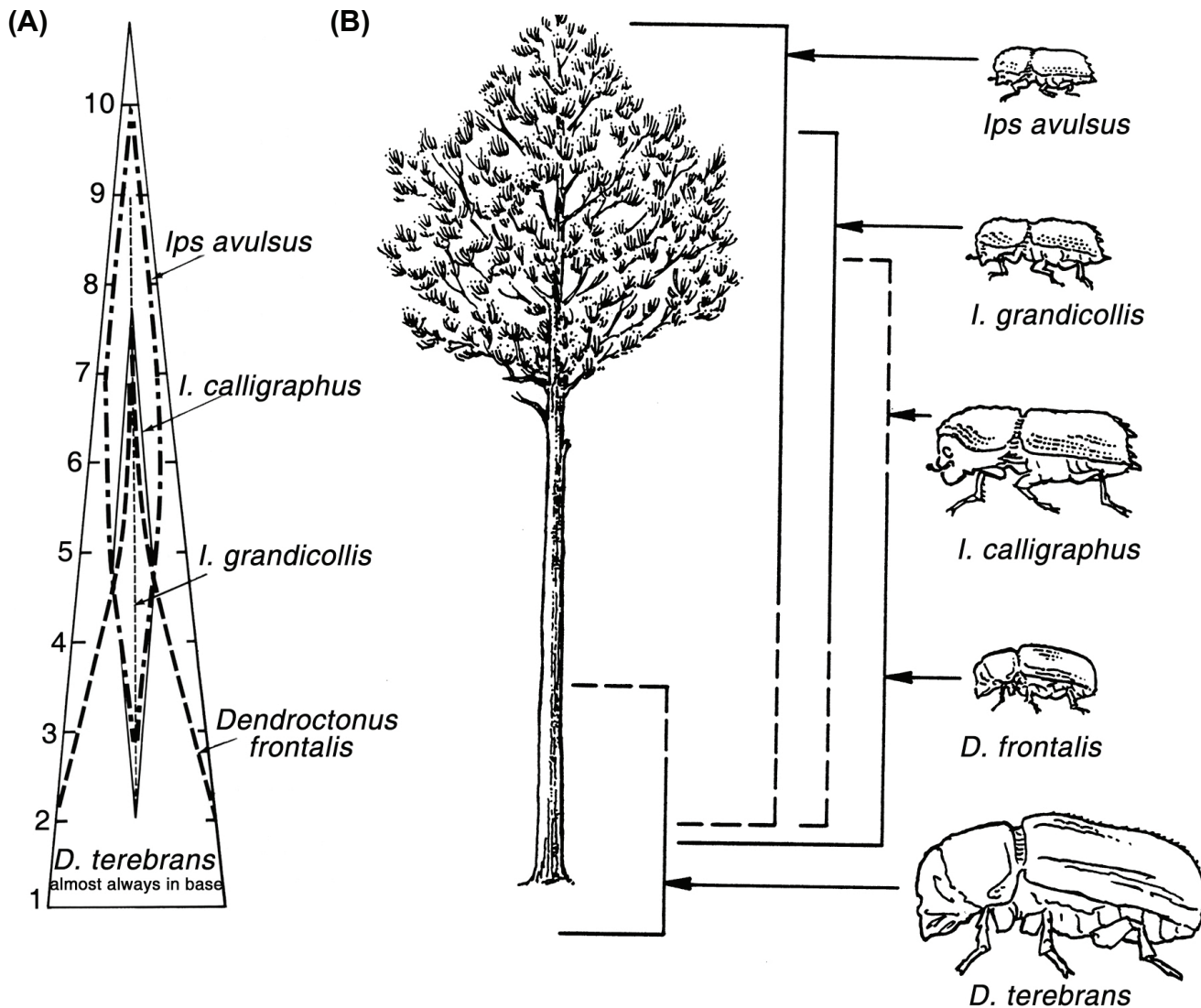


Figure 12.7—Two views of bark beetle guild spatial distribution within southern pines. (A) Diagram illustrating the approximate proportion of the tree bole occupied by the different species of the SPB guild. (adapted from Birch and Svihra 1979). (B) Different perspective of the same colonization patterns (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

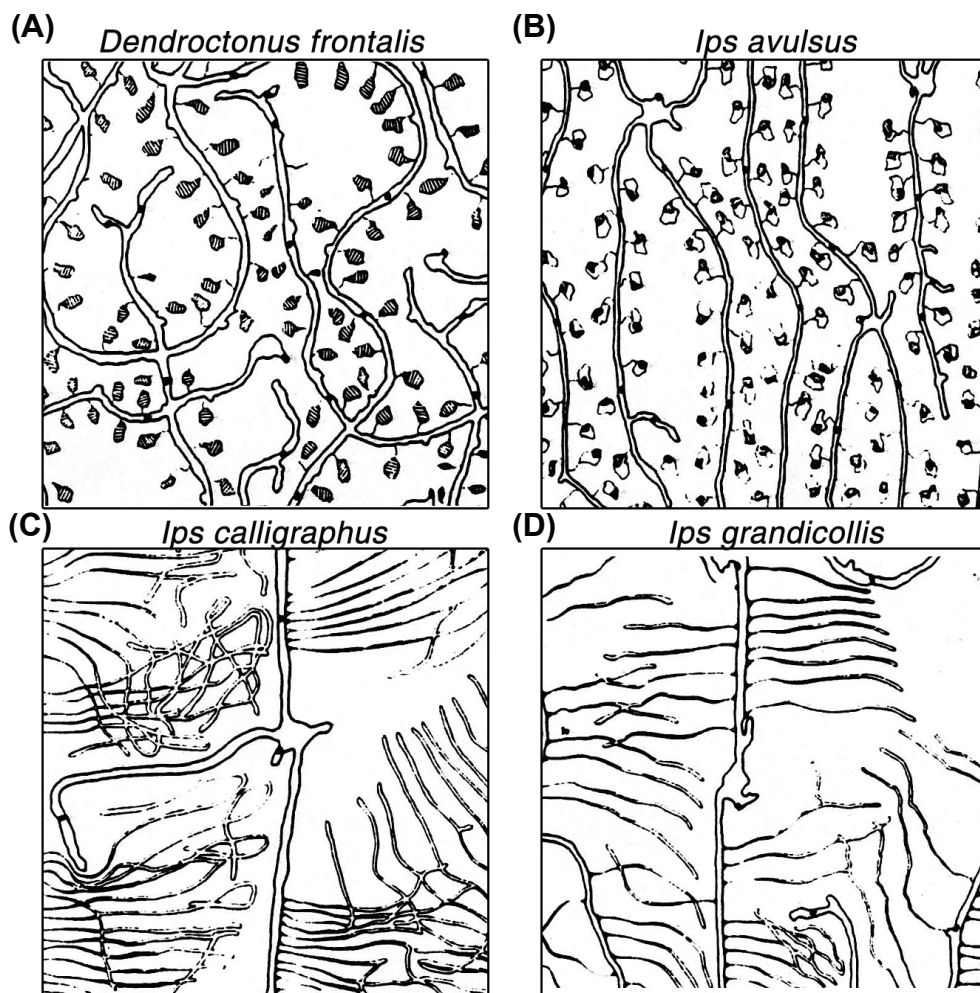


Figure 12.8—Typical southern pine bark beetle gallery patterns in subcortical pine phloem showing nuptial chambers, egg galleries, and larval mines arising from oviposition sites along the egg galleries. (adapted from Wagner and others 1985)

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)



brevicommin) 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*-brevicommin + *endo*-brevicommin) (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 °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 cm²/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/m² 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 cm²), 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

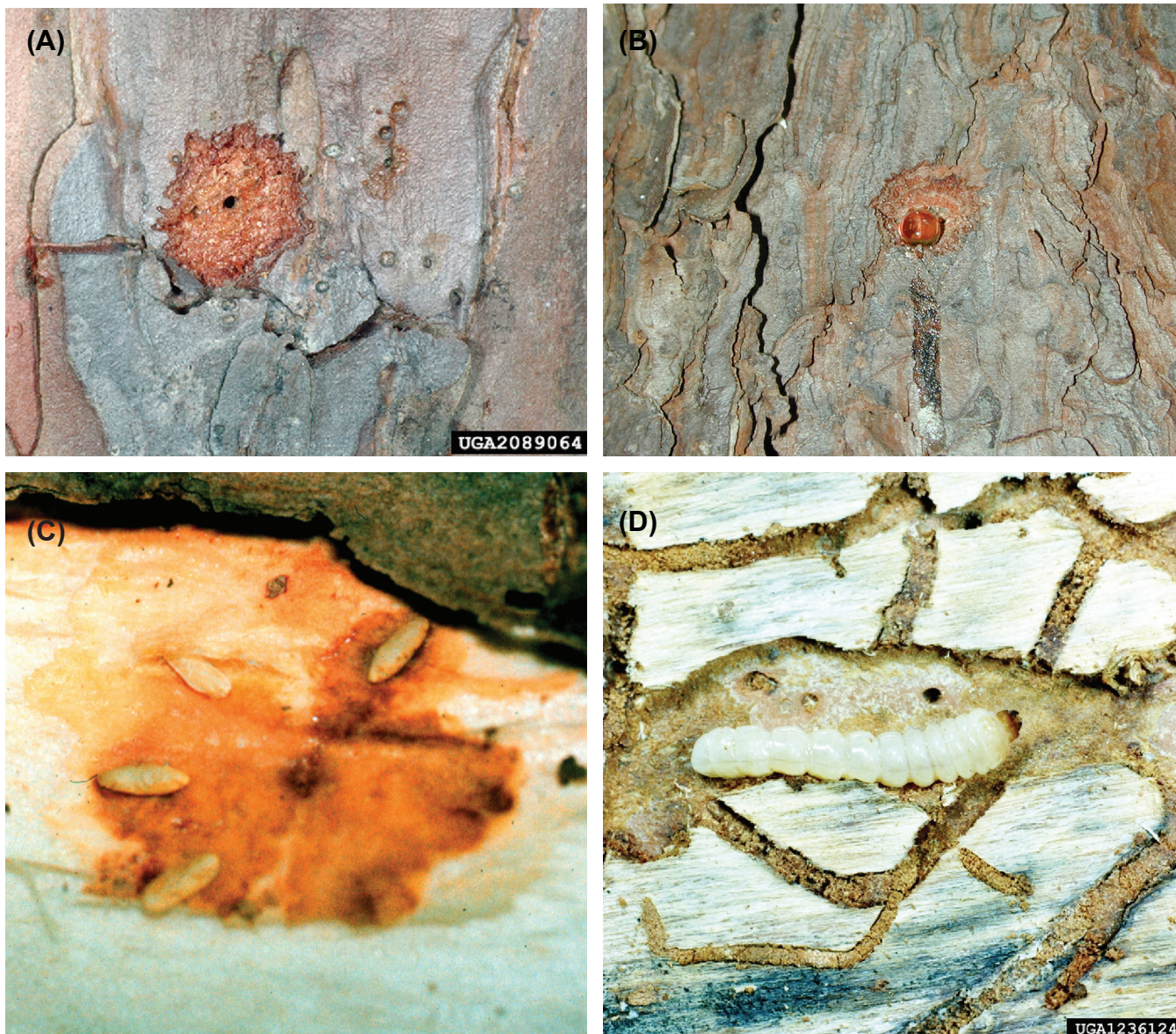


Figure 12.11—(A) *Monochamus titillator* (Fabricius) oviposition pit chewed in surface of pine bark (photograph by Lacy L. Hyche, www.forestryimages.org). (B) *M. titillator* oviposition pit on newly attacked pine showing fresh resin exuding from the oviposition hole (University of Arkansas, Forest Entomology 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.