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Southern Pine Bark Beetle Guild

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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.

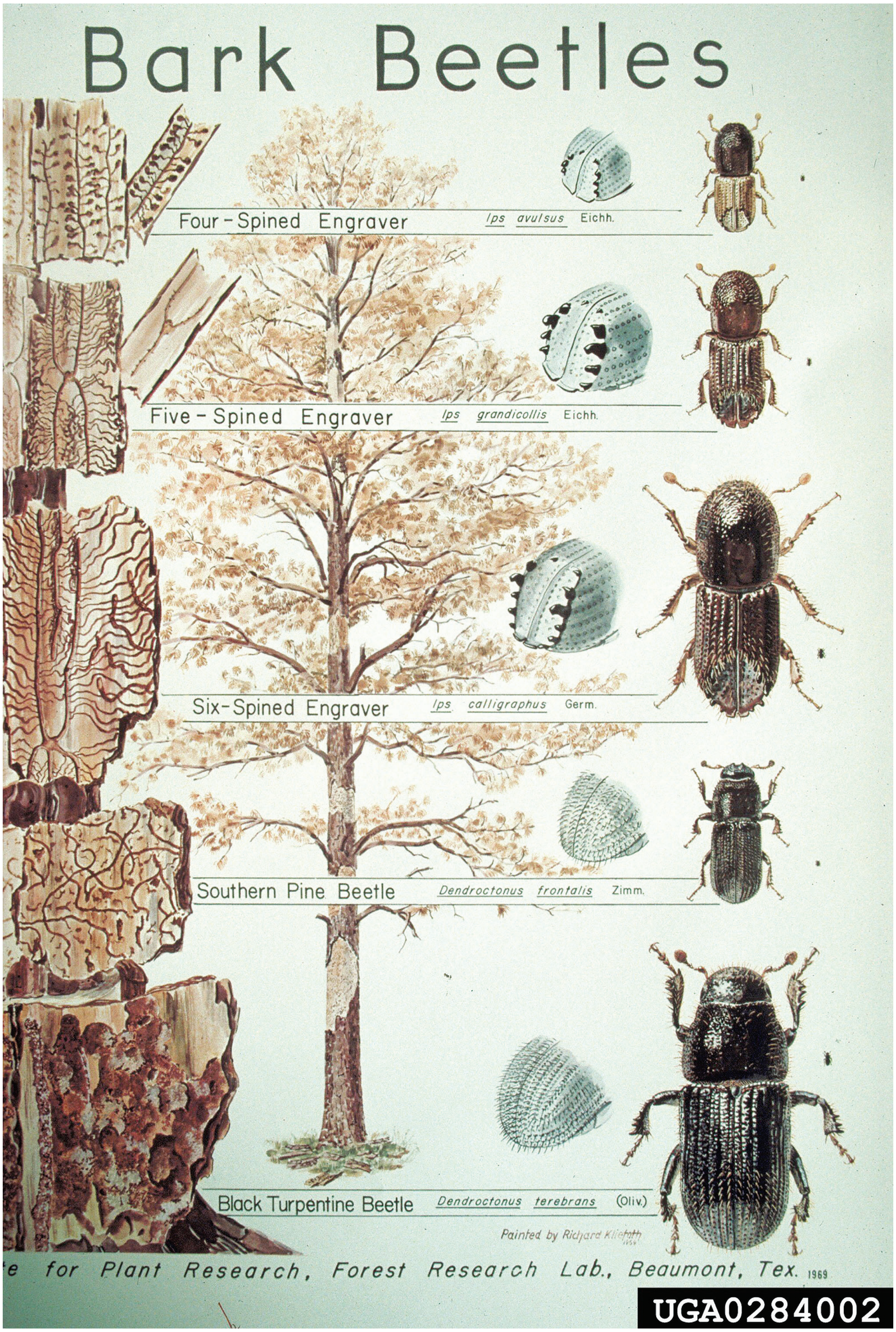

Figure 13.1—Southern pine beetle guild. (painting by Richard Kleifoth; Southern Forest Research Institute, photograph by Ron Billings, Texas Forest Service, www.forestryimages.org)

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.

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

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)

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).

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)

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 13.8—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)