



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 trees. 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 non-epidemic years.

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° to 10 °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)

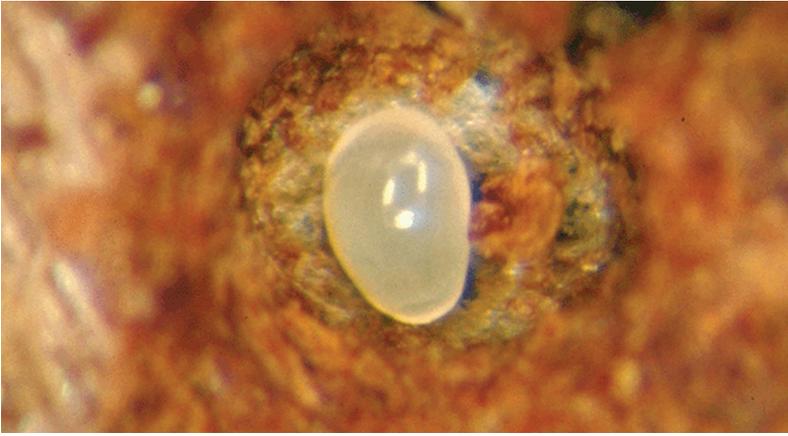


Figure 2.2—SPB egg. (reproduced from Payne 1980)

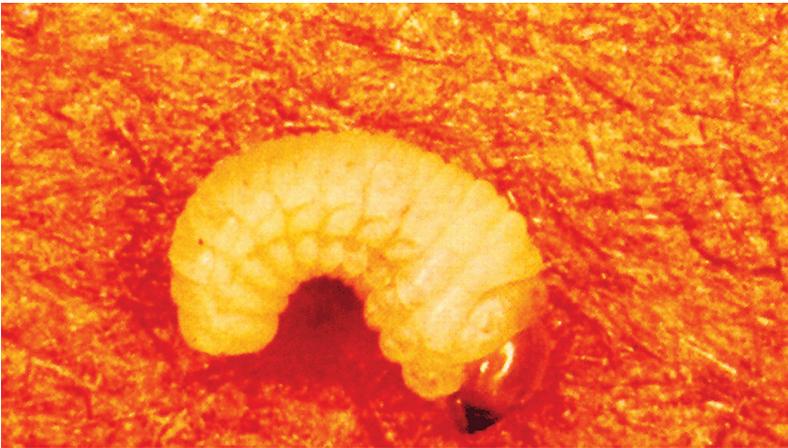


Figure 2.3—SPB larva. (reproduced from Payne 1980)



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 (sclerotized) 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 (Heikkinen 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



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)

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.

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).

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.



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

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 Taso 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/dm² 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/dm² 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

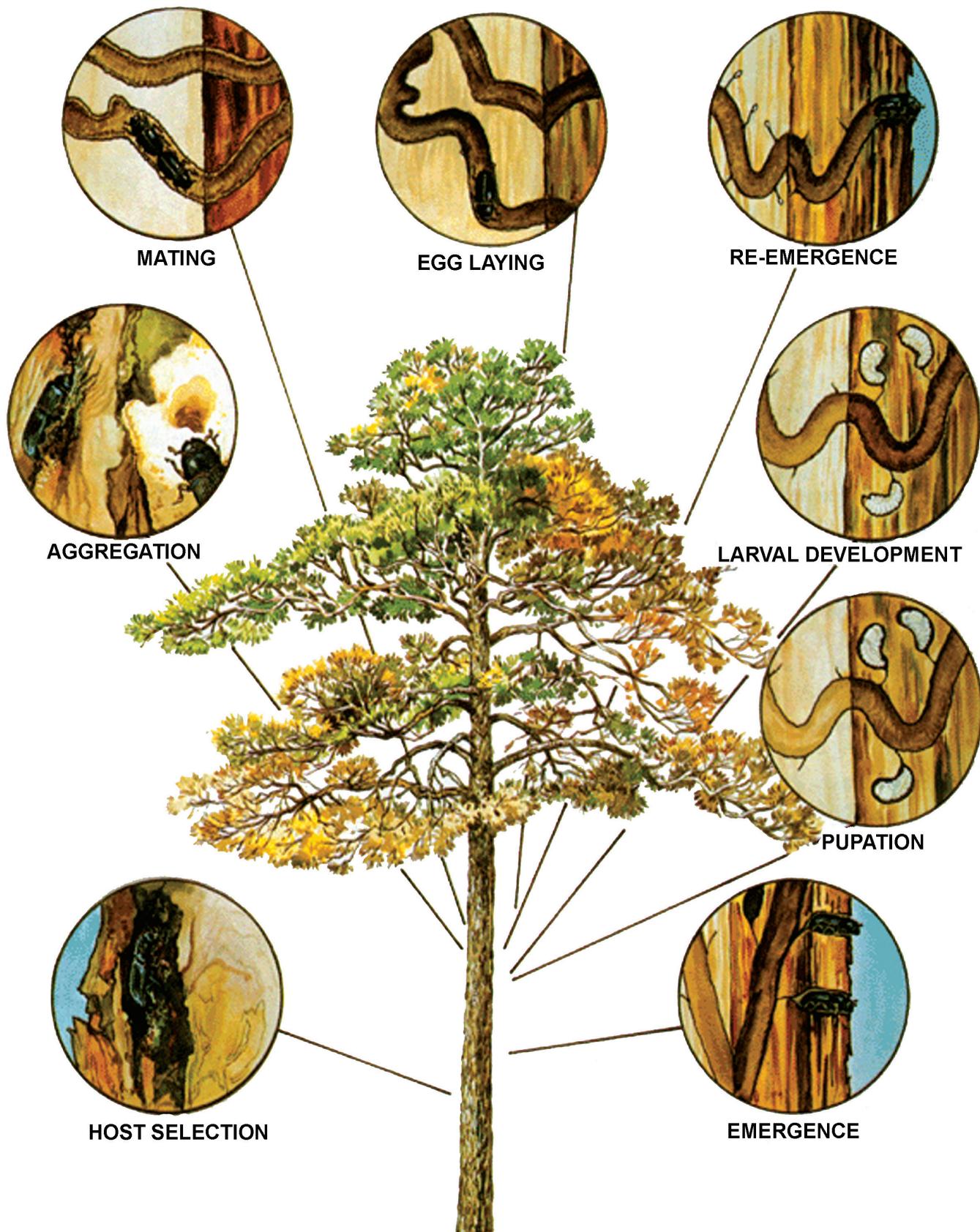


Figure 2.8—Stages of SPB colonization. (reproduced from Payne 1980)

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 mississippiensis* 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 *Roptrocercus eccoptogastris* (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 °C *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* Carrière) 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°C cause almost total mortality of overwintering SPB populations, and the isoclines corresponding to a probability of winter temperatures of -16°C 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.

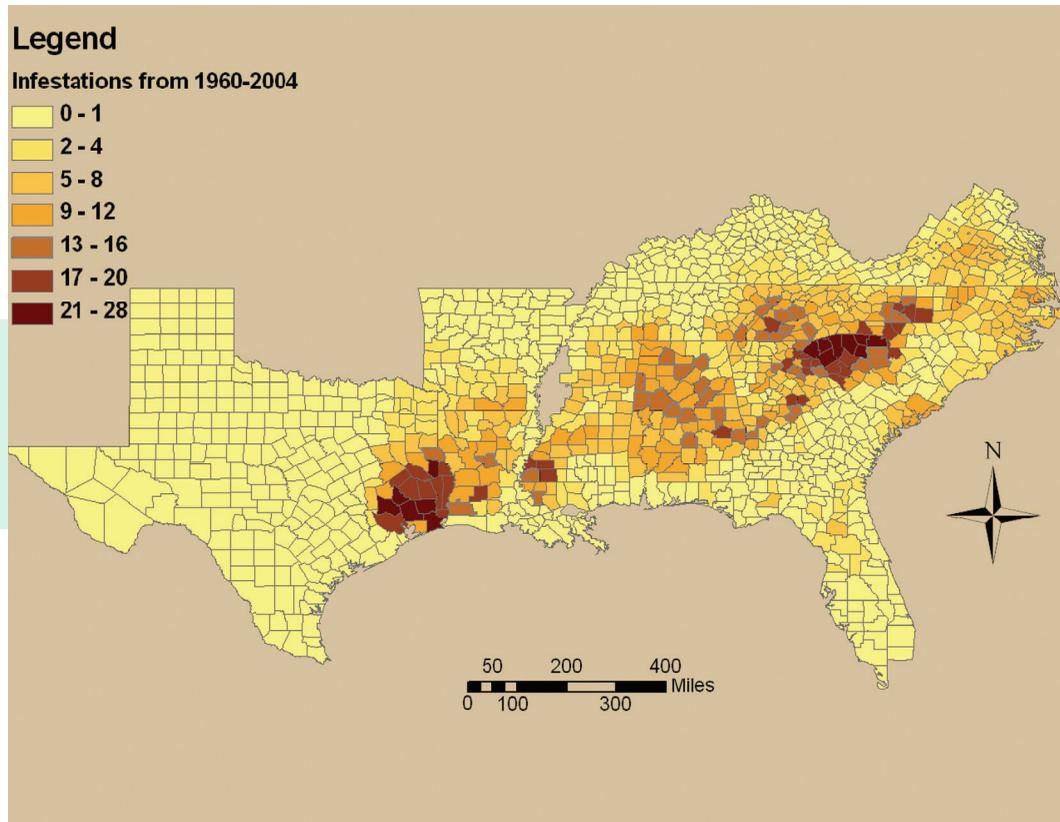


Figure 2.10—Frequency of SPB activity by county from 1960 to 2004. (data from Price and others 1998; updated by the USDA Forest Service through 2004)