Southern Pine Beetle, *Dendroctonus frontalis* (Coleoptera: Curculionidae: Scolytinae)¹

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Introduction

The southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, is the most destructive insect pest of pine in the southern United States. From 1960 through 1990, the bark beetle caused economic losses estimated at \$900 million (Price et al. 1992). From 1998 to 2002, a four-year outbreak in the southern Appalachian Mountains affected more than 1 million acres with an economic loss of more than \$1 billion (Clarke and Nowak 2009). In 2001, the Florida Forest Service accounted for 17,599 acres of damaged pines, causing an estimated \$38 million in damages. The pest has caused remarkably little damage in the last fifteen years, but its populations are once again increasing throughout the Southeast and along the Eastern Seaboard.

Southern pine beetle is a native insect that lives predominantly in the phloem and the inner bark of pine trees. Trees attacked by southern pine beetle often exhibit hundreds of resin masses (i.e., pitch tubes) that appear as “popcorn” on the outer tree bark. Southern pine beetle females colonize live or freshly dead phloem tissue, where they construct winding, S-shaped or serpentine galleries. The galleries can effectively girdle a tree, causing its death (Hain et al. 2011). Southern pine beetle females also possess mycangia, in which they carry their symbiotic fungi, most commonly an

Entomocorticium species and *Ceratocystiopsis ranaculosus* (Six and Bracewell 2015). These fungi are introduced into the phloem and serve as the predominant source of nutrition for the larvae. Hence, compared with most other bark beetles that colonize southern pines, the larval tunnels of *Dendroctonus frontalis* can be easily recognized as being very short, mostly consisting of a chamber with symbiotic fungi on the walls. The beetles also inadvertently mediate the transmission of blue-stain fungi such as *Ophiostoma minus*. The role of these fungi in the tree death is not completely settled, but the majority of evidence supports the scenario that these are associated with phoretic mites (Hofstetter et al., 2006a), that they compete with the *Dendroctonus* larvae, and that they have limited impact on the tree death compared with the actual beetle attack (Six and Wingfield 2011). Once the SPB has successfully colonized a tree, the tree cannot survive, regardless of control measures.

When beetle populations are low (endemic), attacks are generally restricted to damaged pines, typically trees injured by fire or lightning strike. However, epidemics periodically occur (Coulson and Klepzig 2011). The epidemics often originate in weakened or injured trees, but growing beetle populations begin to invade and overcome healthy, vigorous trees via mass attacks over a period of a few days or weeks (Coulson and Klepzig 2011). Widespread

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Figure 1. Pitch tubes of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, on the outer bark.
Credits: Jiri Hulcr, UF/IFAS

Figure 2. S-shaped galleries of southern pine beetle.
Credits: Jiri Hulcr, UF/IFAS

and severe tree mortality can occur during epidemics, as spots (groups of infested trees) may expand at rates up to 15 m (50 ft.)/day, and uncontrolled infestations may grow to cover thousands of acres, persisting for multiple beetle generations, until lack of hosts, extreme temperatures, direct control, or other factors intervene (Billings 2011). While SPB cause the greatest impact within conventional pine plantations, they also may kill large areas of pines in national, state, and private forests, as well as isolated or high-value trees in yards, parks, and various ornamental settings (Coulson and Klepzig 2011).

In the South, tree stressors including changes in climate and precipitation regimes induce numerous cases of tree mortality. While nearly all such stressed or dead pines display signs of colonization by various bark beetles, most of these are secondary. Typically only SPB infestations pose the risk of an epidemic. Therefore, to make informed management decisions, care should be taken not to confuse SPB with less aggressive but more common pine bark beetles of Florida, such as pine engravers (three *Ips* species) and black turpentine beetle (*Dendroctonus terebrans* (Olivier)) (Dixon 1984, 1986).

Distribution

Southern pine beetle has historically occurred in a generally continuous distribution across the southern, southeastern, and northeastern United States (AL, AR, FL, GA, KY, LA, MS, MO, NC, OK, SC, TN, TX, VA, and WV). Southern pine beetle also occurs in discontinuous fashion from AZ and NM south through Mexico and Central America into northern Nicaragua (Billings and Schmidtke 2002). The beetle is common in north Florida, but its abundance decreases southwards, and there is no known record of an SPB outbreak south of Osceola County. Southern pine beetle is unlikely to occur south of N 28° 15' latitude in Florida. The most likely hypothesis for this distribution is the scarcity and/or lack of loblolly pine in the southern half of the state. In the northeastern United States, SPB has recently (since 2014) expanded into Connecticut, New York, and Rhode Island, as a result of warmer winter temperatures (Lombardo et al. 2018).

Description

Eggs are 1.5 x 1.0 mm, oval in shape, shiny, opaque, and pearly white. Larvae range in size from 2 to 7 mm in length and are wrinkled, legless, and yellowish-white, with reddish-colored heads (Meeker et al. 2000). Pupae are the same general color as larvae and the same general form and size of adults. Adults are 2 to 4 mm long, short-legged, cylindrical, and brown to black. The broad and prominent head has a distinct notch or frontal groove on male beetles. Females possess a broad, elevated, transverse ridge along the anterior pronotum, which conceals the mycangium. The rear end or abdomen of adults is rounded, unlike some other pine beetles (*Ips*), in which the abdomen is impressed or hollowed out and surrounded with teeth. Callow (new) adults progressively change in color from yellowish-white to yellowish-brown to reddish-brown, and finally dark brown (Hain et al. 2011).

Figure 3. Dorsal view of southern pine beetles with female on the left and male on the right. Bar corresponds to 1.0 mm.

Credits: Demian Gomez, UF/IFAS

Figure 4. Lateral view of southern pine beetle.

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Diagnosis

The genus *Dendroctonus* can be distinguished from most other pine bark beetle genera by the head, which in this species is easily visible from above. In most other pine bark beetle genera, the head is hidden underneath the thorax when the beetle is viewed from above. Within the genus *Dendroctonus*, there is only one other species in the Southeast—the black turpentine beetle *D. terebrans*—and that is more than twice as large. Several species in the genera *Hylurgops* and *Hylastes* are also superficially similar, but they never attack healthy pines. For more information about bark beetle identification, we recommend Bateman and Hulcr (2017).

Attacks by SPB are easily distinguished from other pine bark beetle attacks by several features. First, pitch tubes are almost always in cracks, rather than on bark flakes. Pitch tubes are spread out along the main stem of the tree and less common at the base or in the crown. The color and consistency of pitch tubes are not diagnostic. The galleries of SPB are also unique in their zigzag to S shape, mostly vertical orientation, and the very short larval tunnels ending in feeding chambers.

Biology

Adult SPB females are responsible for host selection (Hain et al. 2011). After locating a suitable host tree, a female beetle bores through the bark to initiate gallery construction in the inner phloem. Soon after initial attack, females emit an aggregation pheromone (frontalin), which, in conjunction with host odors stemming from resin exudation at attack points, attracts other southern pine beetles, both males and females, to the tree. The aggregation of beetles results in a mass attack over a short period of time (Dixon and Payne 1979). Mass-attacking enables SPB to overcome the natural defense mechanisms of the tree, especially constitutive resin production. This resin under pressure can successfully “pitch out” beetles if there are only a few attacking beetles and the tree is relatively healthy. Mass-attacking SPB deplete the resin production capabilities of the tree and cause resin flow to cease, after which point the tree is easily overcome.

Mating soon takes place and females begin to construct long, winding, S-shaped galleries that cross over each other. These galleries are packed with frass and boring material. Parent adults may then reemerge from the tree 1 to 20 days after oviposition and proceed to attack the same tree or another (Hain et al. 2011).

Eggs hatch 3 to 34 days after oviposition depending on temperature (Hain et al. 2011). Larvae construct very short galleries (usually less than a few centimeters) in the phloem perpendicular to parent egg galleries. Each tunnel ends in a chamber where the larva develops and consumes almost exclusively the adjacent symbiotic fungus. As chambers are progressively expanded towards the outer bark, final instar larvae move to the outer bark and form a pupal cell. The pupal stage lasts 15 to 40 days, during which time the insects turn into callow adults. Callow adults remain under the bark for 6 to 14 days while their cuticle hardens and darkens. The young adults then bore an exit tunnel directly through the outer bark, leaving an exit hole behind. Generally, the emerging beetles fly off to attack another tree (Hain et al. 2011). Adult beetles are capable of flying ca. 2 miles (3

km), and it is estimated that during dispersal phases, half of the beetles travel more than 0.43 mile (0.69 km) (Turchin and Thoeny 1993). The duration from egg to adult ranges from 26 to 54 days (Hain et al. 2011). There may be as many as seven to nine generations per year in Florida.

In the South, emergence of overwintering beetles has been previously correlated with the blossoming of flowering dogwood (*Cornus florida* L.) or redbud (*Cercis canadensis*) in the spring (Coulson and Klepzig 2011). However, as winter temperatures continue to rise, the plant phenology is unreliable, the beetles fly increasingly year-round, and this correlation is reported as no longer sufficient (J. Eickwort, Florida Forest Service, pers. comm.). Spring emergence of SPB represents the primary dispersal phase, during which beetles often initiate multiple and widespread infestations. During summer months, beetle development is hastened, and infestations tend to proliferate and expand very rapidly. In the fall, southern pine beetle tends to produce scattered small infestations. These infestations typically remain small and dispersed during the winter months when beetle activity is slowest (Hain et al. 2011).

The SPB is associated with several fungi. Two, *Ceratocystiopsis ranaculosus* and *Entomocorticium* sp., are carried in the mycangia. The mycangial transmission and larval feeding on fungi such as *Ceratocystiopsis* satisfies the definition of ambrosial fungi. Larvae of this bark beetle feed predominantly on specific nutritional fungal symbionts (Hulcr and Stelinski 2017), possibly representing an intermediate step in the evolution from the bark beetle habit to the true ambrosia beetle symbiosis. Also commonly vectored is *Ophiostoma minus*, a plant pathogen, carried less consistently on the exoskeleton and via associated mites (Hofstetter et al. 2013). *Ophiostoma minus* has been historically considered a mutualist of *D. frontalis* (Craighead 1928; Bramble and Holst 1940). While *O. minus* is almost always present (see Bridges et al. 1985 for exceptions), larvae that feed on the fungus do not survive (Barras 1970). Moreover, the presence of *O. minus* in a tree colonized by SPB is heavily driven by the presence of mites (Hofstetter et al. 2006b, Lombardero et al. 2003), though spores of this and other fungi are also found in pits on the exoskeleton of adult SPB.

Hosts

Southern pine beetle will infest and kill all species of pine within its distribution (Birt 2011), but outbreaks are most common in loblolly pine stands. This may be a result of preference for this host as much as widespread availability of the host. In the southern United States, preferred hosts are loblolly pine, shortleaf pine (*Pinus echinata* Mill.),

pond pine (*Pinus serotina* Michx.), and Virginia pine (*Pinus virginiana* Mill.) (Coulson and Klepzig 2011). In Florida, SPB also readily attack and kill spruce pine (*Pinus glabra* Walter), and sand pine (*Pinus clausa* (Chapman ex Engelm.) Vasey ex Sarg.) (Chellman and Wilkinson 1975). Slash pine (*Pinus elliottii* Engelm.) and longleaf pine (*Pinus palustris* Mill.) are generally considered to be more resistant to southern pine beetle attacks, but during outbreaks even healthy individuals of these species can be successfully colonized (Belanger et al. 1993; Belanger and Malac 1980). Moreover, it has been recently shown that *P. palustris* and *P. taeda* are equally attacked and killed when they co-occur in a growing infestation (Martison et al. 2007). In the north-eastern United States, SPB mainly attacks pitch pine (*Pinus rigida* Mill.), shortleaf pine (*Pinus echinata*), and Virginia pine (*Pinus virginiana*), but it has also been observed infesting Norway spruce (*Picea abies* L.), red pine (*Pinus resinosa* Sol. ex Aiton), scots pine (*Pinus sylvestris* L.), and white pine (*Pinus strobus* L.) (Dodds et al. 2018).

Outbreaks

Outbreaks of SPB have traditionally been described as cyclical, but their occurrence is more accurately described as driven by host availability and previous population levels (Costanza et al. 2012). Outbreaks generally last for two to three years in areas where SPB has long been a problem (Meeker et al. 2000). Across the southeastern United States, the time between outbreaks has decreased while the intensity and distribution of each outbreak has increased since 1960 (Belanger et al. 1993; Price et al. 1992). Overall, however, SPB has shown a dramatic decline in outbreak activity over much of the South since the turn of the 21st century as compared to previous decades (Asaro et al. 2017). In Florida, infestations have been relatively few and small in the past (Chellman and Wilkinson 1975, 1980). Many factors are presumed to be involved in the development of outbreak conditions, such as the abundance and susceptibility of preferred hosts, and weather patterns and events (e.g., drought, storms).

Historically, Florida has not experienced many destructive SPB episodes, probably because of the lack of large contiguous areas of loblolly and shortleaf pine in susceptible stages. However, an epidemic in and around Gainesville in Alachua County during 1994 warranted a reconsideration of the serious threat SPB poses to Florida's pine forests. The last regionwide outbreak in the Southeast (1999–2002) impacted several pine species growing as natural stands, unmanaged plantations, or in mixed pine/hardwood stands (Nowak et al. 2016). In the South, most recent outbreaks have occurred in National Forests in higher-risk stands,

with very little spread beyond the national forest boundaries (Asaro et al. 2017). In Florida, low activity of the southern pine beetle has been registered between 2004 and 2015, with a resurgence in 2016 through 2018.

In the northeastern United States, the unprecedented expansion of SPB into New Jersey, New York, and Connecticut since 2014 due to warmer winters and poor growing conditions presents a risk for northern pine forests (Dodds et al. 2018). Temperature change models show that climate will be suitable for SPB expansion into previously unaffected forests throughout the northeastern United States and into southeastern Canada (Lesk et al. 2017). Because of short generation times, dispersal abilities, and host distribution, changes in minimum annual temperatures have almost immediate effects on regional patterns of SPB infestations (Ungerer et al. 1999).

Survey and Monitoring

Often the first noticed indication of SPB attack is foliage discoloration. Crowns of dying pines change color from green to yellow to red before turning brown and falling from the tree (Meeker et al. 2000). However, especially in Florida, by the time crowns are red SPB have already vacated the tree. The earliest sign of possible SPB attack is the presence of reddish-brown dust (from tunneling through outer bark layers), often combined with little white pitch specks. A more noticeable indication of SPB attack is the presence of multiple popcorn-sized lumps of pitch (i.e., pitch tubes) on the outer bark of pine stems (Meeker et al. 2000). These pitch tubes may occur from near ground level up to 60 ft. (18 m) high but may not develop at all on trees severely weakened before beetle attack. The most diagnostic sign of SPB activity is the presence of the winding S-shaped galleries that cross over each other and are packed with boring dust and frass. These can be found by exposing a portion of the inner bark beneath pitch tubes or by removing a section of bark. Another sign of possible SPB activity is the presence of clear exit holes (ca. 1 mm in dia.) on the exterior bark surfaces where second-generation beetles have emerged (Billings and Pase 1979). Southern pine beetle infestations typically kill groups of trees, the so-called “spots,” which allows for prioritizing investigations of suspect mortality.

Southern pine beetle monitoring takes advantage of the beetles’ chemical communication. Natural SPB attack is mediated by a complex of semiochemicals involving pheromones released by females (frontalin), kairomones produced by the host (α -pinene and many others), and male pheromones ((+)-endo-brevicomine) (Sullivan et al.

2007). For monitoring purposes, frontalin and α -pinene are deployed in intercept (funnel) traps while (+)-endo-brevicomine is placed several meters away from the trap. Horizontal displacement of the release point of the male pheromone (4–16 m away) significantly enhances its synergistic effect on SPB attraction to traps with frontalin (Sullivan and Mori 2009).

Prevention and Control

Preventative strategies for homeowners and forest managers include:

- Plant more resistant species such as longleaf pine and slash pine in place of loblolly pine. Plant loblolly pine only on appropriate sites (“the right tree for the right place”).
- Thin overstocked, dense, or stagnant stands to a basal area of 80 sq. ft. per ac. (18 sq. m per ha) or less, or use prescribed fire.
- Maintain at least 25 ft. (8 m) distance between mature pines in urban settings.
- Promote tree diversity in the landscape.
- Remove damaged pines rapidly, reducing stress on surrounding pines by heavy machinery as much as possible.
- Leave standing dead and dying trees from which SPB already left. This strategy promotes the emergence of natural enemies, which are critical in the natural regulation of the pest population. Trees that have been abandoned by SPB can be recognized by distinctly red or gray needles, by numerous exit holes on bark flakes, and by the absence of the young SPB generation inside the bark.
- Minimize construction and logging damage to pines and avoid soil compaction during operations.
- Minimize changes in soil and water levels around pines.
- Conduct logging or land-clearing operations during the coolest winter months.
- Shorten rotation ages to less than 30 years.
- Use only approved insecticides, such as bifenthrin or permethrin, and limit their use to high-value trees when the threat of southern pine beetle attack is imminent and the potential benefits outweigh the costs of chemical use and the damage to natural enemies
- Consider systemic injection of systemic pesticides, particularly emamectin benzoate in combination with propiconazole (Grosman et al. 2009).

In Florida, the Florida Forest Service offers the Southern Pine Beetle Assistance and Prevention Program, with the goal to minimize regional outbreaks by helping landowners with proactive management practices (Nowak et al. 2008). The program, limited to 44 northern Florida counties located within the range of SPB, offers reimbursements or incentives for thinning, prescribed burning, mechanical underbrush control, and planting longleaf or slash pine. Evidence suggests that a landscape-level preventative thinning is the most economical and sustainable approach to the mitigation of the southern pine beetle epidemics (Asaro et al. 2017).

Remedial control measures to suppress existing infestations are limited. The current strategy for suppression relies on identifying those spots capable of rapid and prolonged expansion and removing the “active” trees to prevent emergence of beetles and the loss of additional trees (Billings 2011). Generally, the most effective and desirable approach is to remove and process all southern pine beetle-infested pines as soon as possible (Meeker et al. 2000). Trees can be salvaged, and SPB will be destroyed in the milling process. If trees cannot be salvaged or transported away from the pine forest, bark should be destroyed, buried, or chipped and composted. In forested settings, it is recommended that a 50- to 100-ft. (15- to 30-m) buffer strip of green, uninfested trees also be removed to ensure that recently infested trees are not left behind and to disrupt the pheromone-mediated spread into nearby uninfested trees. On smaller infestations where none of the above approaches is practical, infested trees with a buffer strip may be simply felled toward the center of the spot. This cut-and-leave approach does not eliminate emerging beetles but it does decrease their abundance (Swain and Remion 1981; Coulson and Klepzig 2011). Trees from which SPB already emerged should be left at the site. Such trees no longer pose danger, and they produce large numbers of natural enemies that can significantly decrease bark beetle population density (Turchin et al. 1999).

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