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Southern Pine Beetle Population Dynamics in Trees

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Abstract

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

Keywords

bark beetles
competitors
parasitoids
population dynamics
predators
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4.1. INTRODUCTION

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

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

4.1.1. Southern Pine Beetle (SPB)

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

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

4.2. ATTACKING ADULTS

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

Research to investigate attacking populations of beetles has been conducted using a series of approaches designed to measure different components of the attack process. Bunt and others (1980) observed the behavior of individual arriving and attacking beetles on the bark surface of trees. Sticky traps or windowpane traps were used to intercept beetles at the bark surface (Coster and others 1977a, Dixon and Payne 1980, Hynum 1980). Counting numbers of attacking beetles within defined sample units, both through sample dissection or radiographs, is an important technique (Coulson and others 1975b, Pulley and others 1977). Collecting

bark samples and measuring evidence of attack sites on bark surface or within phloem tissues avoids problems with timing of sample collections (Linit and Stephen 1978) and is also used as an attack density estimation technique (McClelland and others 1979, Reeve and others 1998). All of these adult estimation procedures have been used to gather the information discussed below.

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

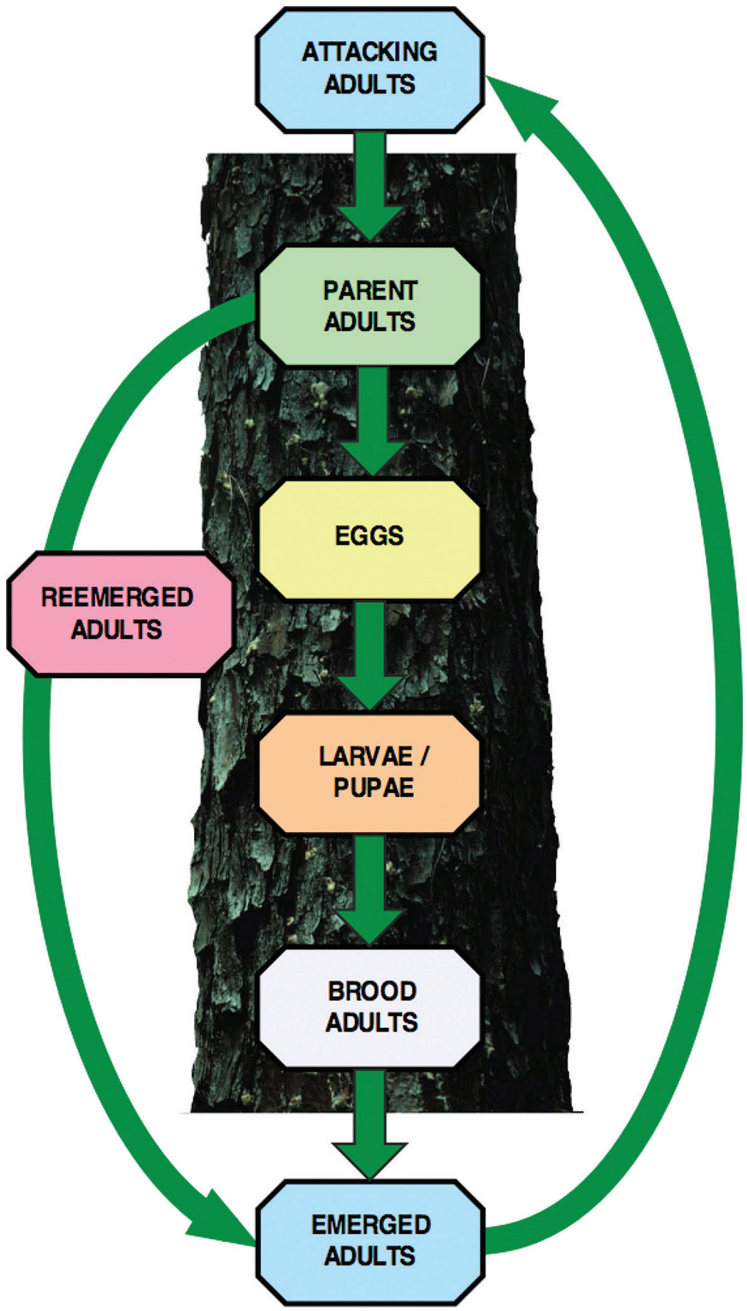

Figure 4.1—A diagram of the SPB life cycle illustrating measurable components of reproductive and developmental stages external to and within host trees. Adults attack trees and if successful, become parent adults, oviposit their eggs, and may then reemerge from that tree. Eggs within phloem develop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

distance to pheromones produced by the initial beetles attacking a potential host tree (Fares and others 1980).

Those species of insects that are able to detect trees being attacked and use as kairomones some aspect of the insect- or tree-produced semiochemicals may also influence the

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

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

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

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

Many different methods have been used to estimate density of attacking adults, including counting numbers of pitch tubes on the bark surface, removing bark with attached sapwood containing attacking adults and dissecting to

count attacking beetles (Coulson and others 1976c), making radiographs (x-rays) of bark with attached sapwood to estimate density of attacking beetles in samples (Pulley and others 1977), and removing bark after completion of attack (and sometimes after reemergence of parents) to search for evidence of attack sites (Linit and Stephen 1978, Stephen and Taha 1976).

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

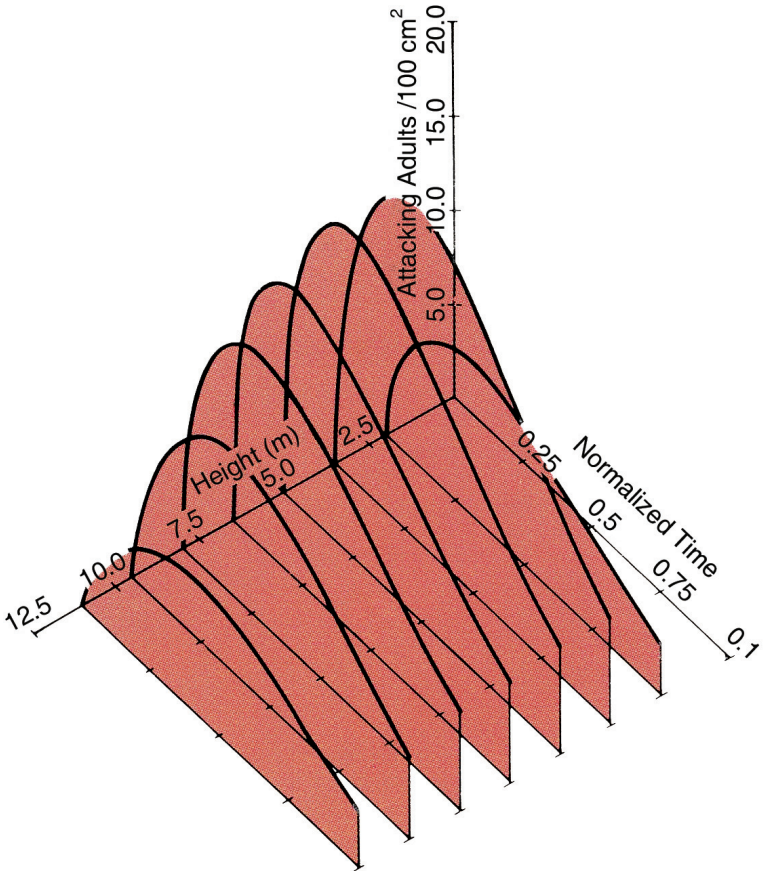

Figure 4.2—Summary of model projections representing the spatial and temporal patterns of SPB attack on an average host pine tree. Y axis = adult density, X axis = height on infested bole and Z axis = normalized time. Time is normalized from zero to one, with one representing 14 days. (illustration from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

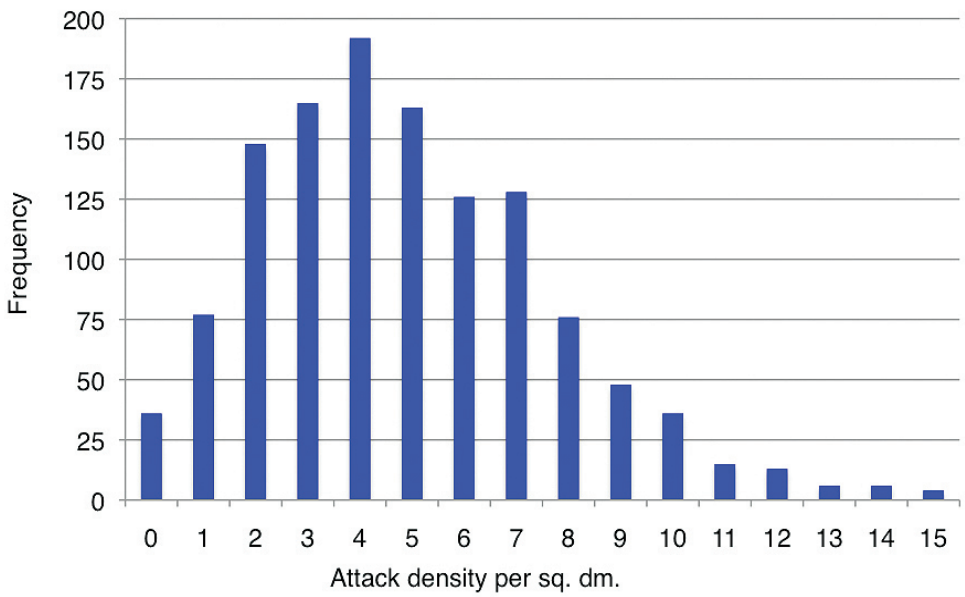

Figure 4.3—Distribution of numbers of successful SPB attacks per 1 dm^2 bark sample unit (= 100 cm^2). Mean attack density is 4.92 ± 0.27 (SE) and the mode is 4. Each attack is equivalent to a density of two beetles (one male and one female per attack). Data summaries from 181 trees sampled in 17 infestations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

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

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

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

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

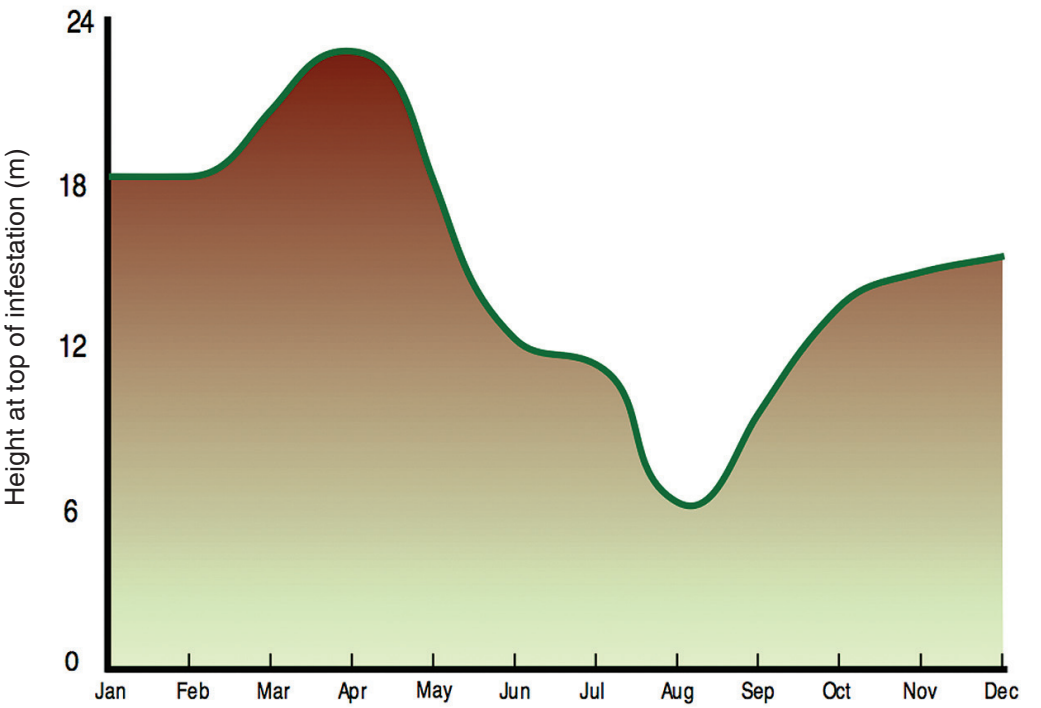

Figure 4.4 —Adaptation of data presented in Figure 2 of Thatcher and Pickard (1964) illustrating changes in height of attack and colonization of infested bole as a function of season. During cooler seasons the height at top of infestation is greater, and during hotter summer periods it may be much lower.

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

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

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

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

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

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

4.3. PARENT ADULTS

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

The sequence of mass attack is such that the midsection of the tree bole is normally attacked first, and colonization above and below that area lags in a somewhat predictable manner, resulting in a nonuniform beetle population age structure in infested trees (Coulson 1980, Fargo and others 1979). The abundance of available attacking adults (e.g., infestation size and age structure), coupled with seasonal effects (e.g., temperature) can greatly influence the rate of mass attack within individual trees (Coster and others 1977a). It is not uncommon to find attacking adults in the lower and upper margins of the infested bole at the same time that parent

adults, eggs, and sometimes larvae are found near mid-bole. This complicates within-tree sampling and estimation of within-tree SPB populations. A hypothetical model (Figure 4.11) was proposed that illustrates the actual proportion of different SPB life stages contained in an infested tree based on what observers noted as the predominant beetle life stage found at breast height (Hines and others 1980). Samples of different size, number, or timespecific to life stage sampled may be required to enable accurate estimation of different SPB life stage densities, thus requiring multiple visits through time to acquire the samples needed for all life stages (Coulson and others 1975b, 1979a; Stephen and Taha 1976).

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

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

Fecundity of parent adults ideally would be determined by examining entire, individual female galleries in naturally infested trees. SPB gallery structure is sinuate, and galleries

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

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

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

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

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

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

4.3.1. Gallery Construction

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

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

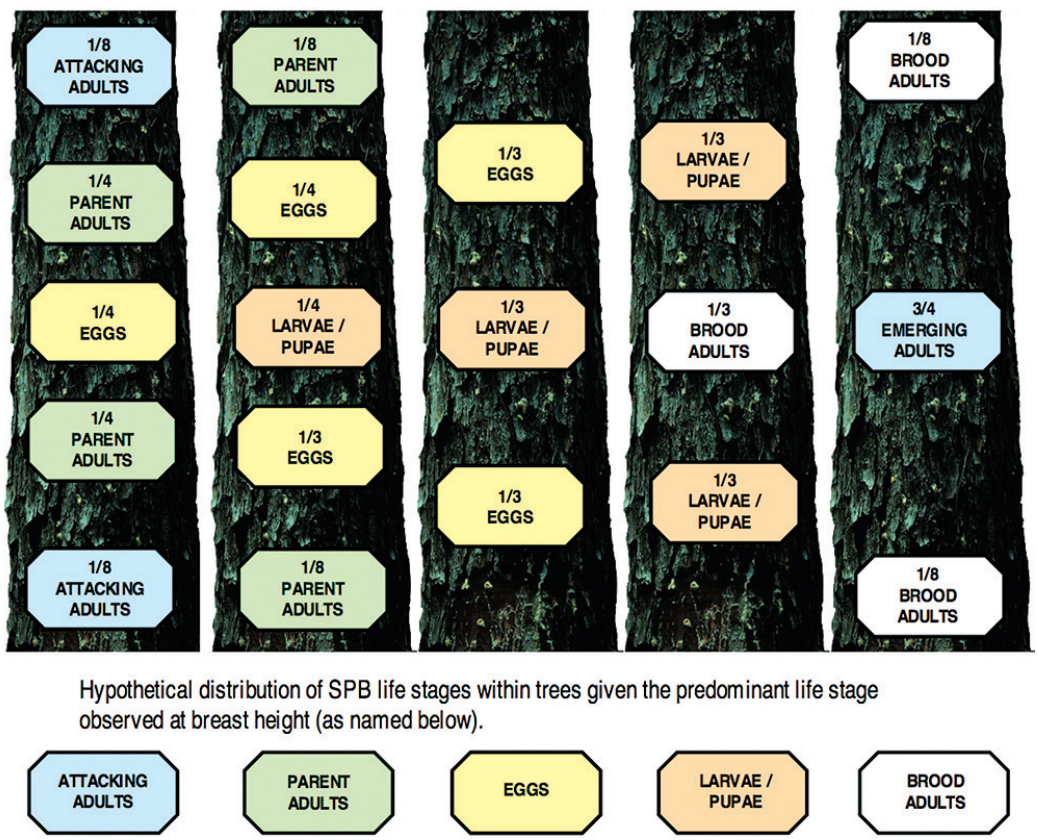

Figure 4.11—Figure adapted from data presented by Hines and others (1980), who proposed a hypothetical model of the actual proportions of different beetle life stages within infested trees given what observers report when the bark is cut away at breast height and the life stage present there is noted.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

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

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

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

4.4. EGGS

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

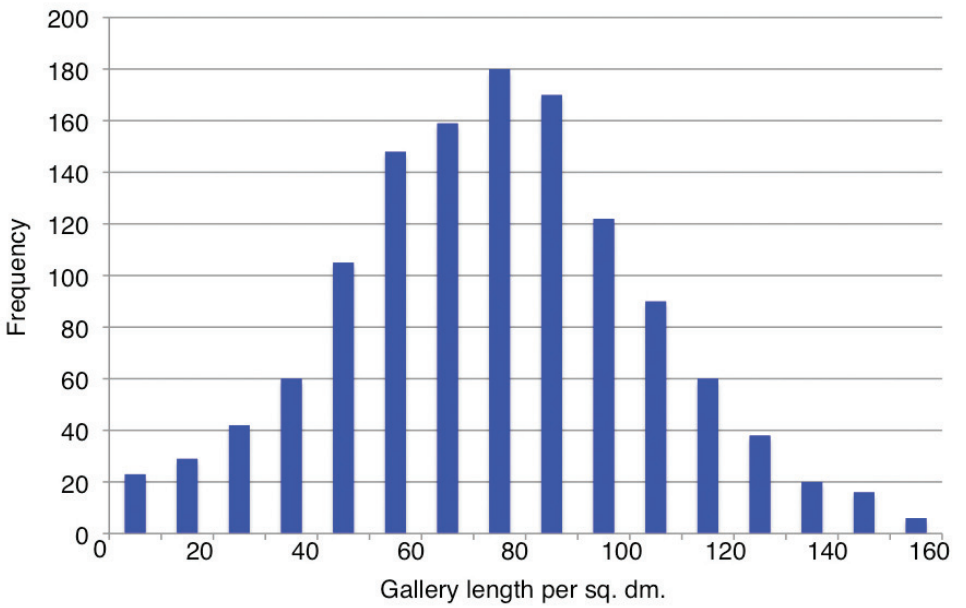

Figure 4.12—Distribution of total SPB gallery length recorded per 1 dm^2 bark sample unit. Mean gallery length is 85.01 ± 7.74 (SE). The gallery length density counts appear normally distributed with about 85 percent of counts ranging from 35 to 115 cm of gallery per dm^2. Data from 1268 samples on 181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

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

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

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

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

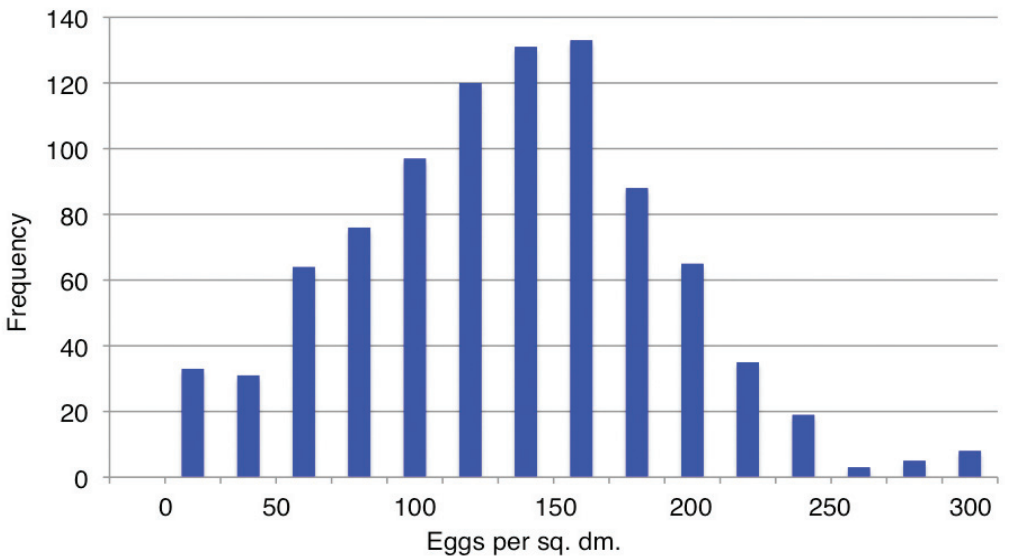

Figure 4.13—Distribution of total SPB egg density, determined by gallery dissection, per 1 dm^2 bark sample unit. Mean egg density is 135.66 ± 5.85 (SE). The egg density counts are slightly skewed to the right with a mode of 160, with about 85 percent of counts falling between 60 and 200 eggs/dm^2. Data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

4.5. REEMERGING ADULTS

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

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

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

of reemergence from a single tree has been estimated to take about 14 days (Coulson and others 1978).

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

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

4.6. LARVAE AND PUPAE

4.6.1. Development

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

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

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

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

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

4.6.2. Density

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

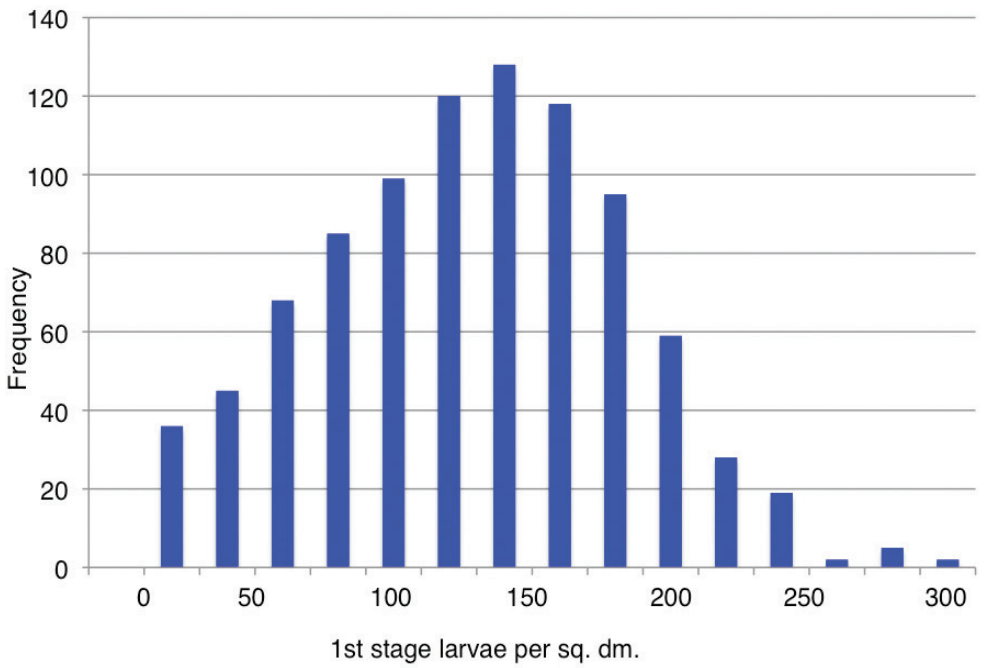

Figure 4.16—Distribution of SPB 1st instar larvae, determined by gallery dissection, per dm^2 bark sample unit. Mean 1st instar larval density is 129.88 ± 5.55 (SE). Data from 909 samples from 181 trees sampled in 17 infestations at six geographic locations in southern Arkansas between 1975 and 1977.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

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

4.6.3. Mortality Factors

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

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

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

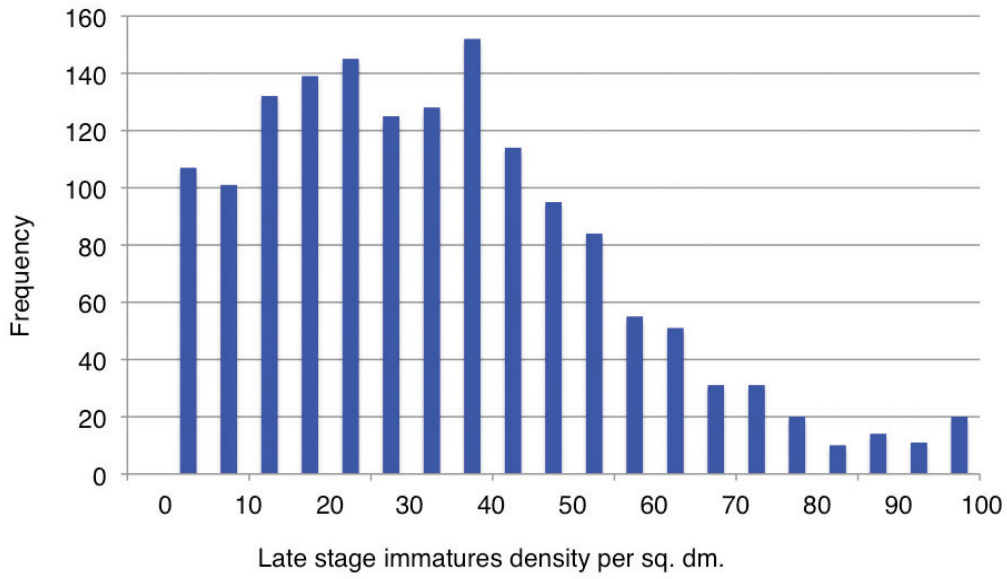

Figure 4.17—Distribution of SPB late stage immatures (larvae and pupae), determined by radiograph examination and bark sample dissection, per 1 dm^2 bark sample unit. Mean late stage immature density is 34.06 ± 1.25 (SE), and the data are skewed to the right. Data from 1,565 samples from 181 trees sampled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

Table 4.1—Average mortality table for within tree SPB based on data from Stephen and Taha (1979a). Average density (per dm²) and mortality are presented for SPB eggs, 1st stage larvae, late stage larvae/pupae, and emerging adults. Also shown are calculated apparent and real mortality for these stages and generation mortality. (see text for further explanation)

SPB life stage	No./dm² entering life stage	No./dm² dying during life stage	% apparent mortality	% real mortality
Eggs	135.7	5.8	4.30%	4.30%
1st stage larvae	129.9	95.8	73.70%	70.60%
Last stage larvae/pupae	34.1	14.5	42.50%	10.70%
Emerging adults	19.6			
Generation mortality				85.60%

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

Challenge of Estimating the Amount and Causes of Mortality

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

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

In addition to challenges of aggregation patterns changing during the beetles' life history and the dynamic colonization process occurring along the infested tree bole, a further obstacle to measuring beetle numbers and mortality is the difficulty of accurately seeing numbers of

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

Predators

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

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

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

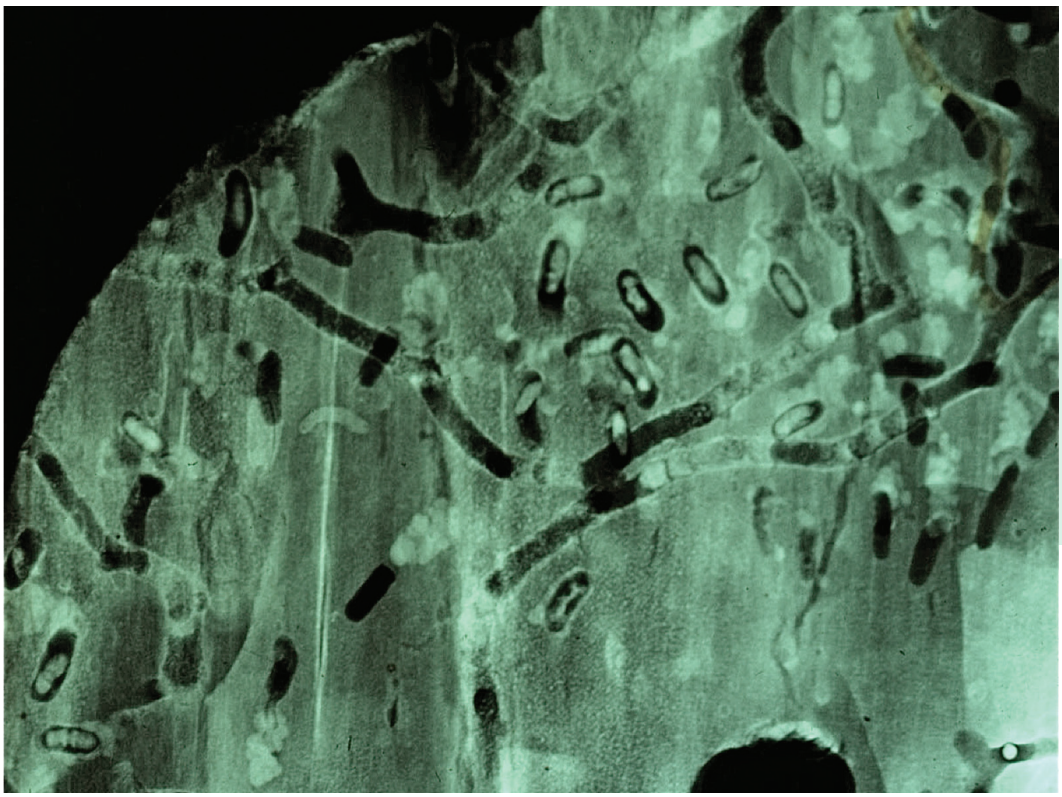

Figure 4.18— Radiograph (x-ray) of a partial bark sample containing late stage immature *D. frontalis*, parasitoids, and predators, plus dead beetles and empty pupal cells. (photograph by F.M. Stephen)

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

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

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

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

Parasitoids

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

Despite the abundance of collections of these species, little has been published that indicates parasitoids are able to regulate SPB

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

Competitors

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

Fungi

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

by blue stain fungi (Figure 4.14) graphically illustrates the effect of these different fungi on beetle development. Sorting out the complexity of interrelationships among coexisting fungi, mites, and SPB is an exciting area of research that has been the focus of much recent interest (see chapters 9 and 11).

Heat and Cold

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

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

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

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

4.7. EMERGING BROOD ADULTS

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

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

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

4.8. CONCLUSIONS

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

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

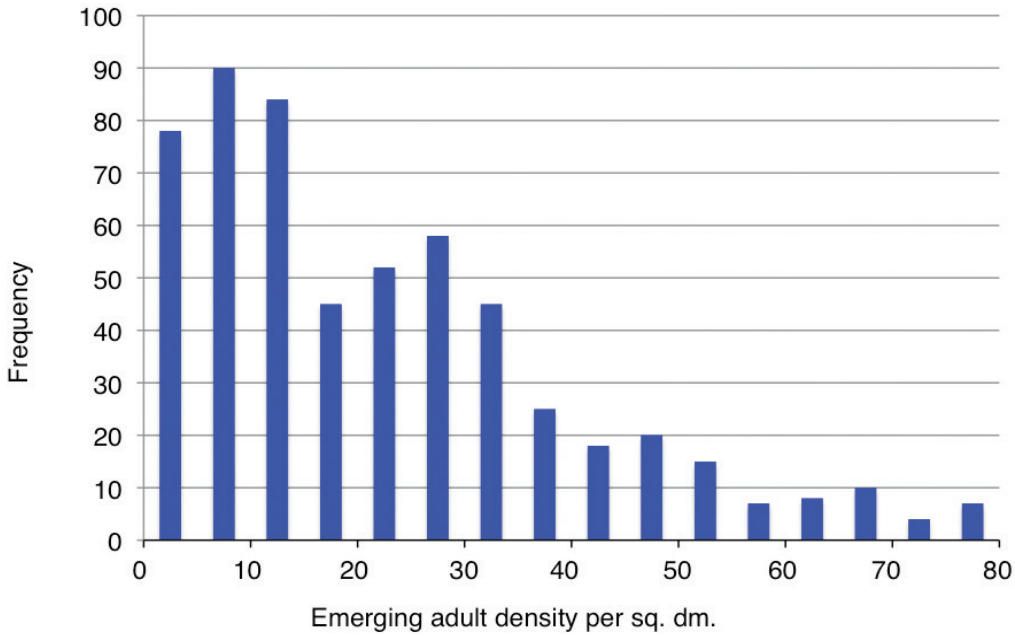

Figure 4.19—Distribution of emerging SPB adults, determined by collection of on-tree emergence traps, per 1 dm^2 bark sample unit. Mean emerging adult density is 22.82 ± 1.59 (SE) and count data are skewed to the right. Data from 566 samples from 181 trees sampled in 17 infestations at six geographic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

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

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

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