

## Host Suitability, Predation, and Bark Beetle Population Dynamics

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### I. Introduction

Many species of bark beetles (Coleoptera: Scolytidae) undergo dramatic population fluctuations that lead to extensive damage of coniferous forests. Considerable effort has been devoted to determining the causes of bark beetle outbreaks. The most common explanation is that outbreaks occur when there is an abundance of trees with low resistance to attacking adults, and which are suitable for beetle reproduction (Rudinsky, 1962; Stark, 1965; Berryman, 1973, 1976; Raffa and Berryman, 1983; Berryman and Ferrell, 1988; Christiansen and Bakke, 1988; Raffa, 1988). Outbreaks are often thought to occur as a result of stress on the trees that limits the effectiveness of the oleoresin system as a defense against attacking adult beetles (Berryman, 1972). Factors that have been implicated as agents of stress include drought, competition between trees, disease or defoliation by other insects, storms, and aging. The decline of outbreak populations to endemic levels is often attributed to an increase in the resistance of potential host trees, or simply to the depletion of trees suitable for beetle reproduction.

In this chapter, we examine the hypothesis that outbreaks in the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), are generated by environmental factors that affect host-tree suitability, especially water availability. There is a substantial literature linking climatic patterns to SPB outbreaks (Wyman, 1924; Craighead, 1925; Beal, 1927, 1933; St. George, 1930; King, 1972; Kroll and Reeves, 1978; Kalkstein, 1981; Michaels, 1984). Nonetheless, Turchin *et al.* (1991) found no relationship between the per capita rate of increase of SPB and any of three climatic variables (water deficits, winter temperatures, and summer temperatures). Here, we evaluate a physiological model for southern pine that predicts *decreased* suitability for SPB under moderate water stress, but increased suitability under severe water stress

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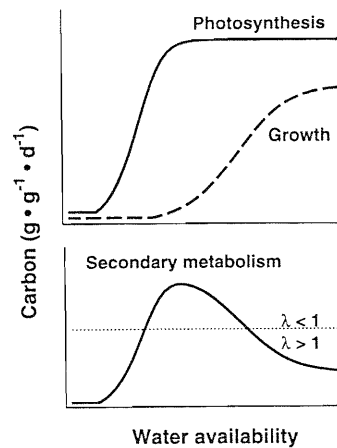


Figure 1. Hypothesized effects of water availability on the carbon budgets of pine. Moderate water deficits limit growth but not photosynthesis, thus as carbon availability for secondary metabolism increases, oleoresin production rises, and suitability for bark beetles is reduced. At very low water availability, trees constrict stomata to limit transpiration, causing photosynthesis and secondary metabolism to plummet, and suitability for bark beetles to increase. Thus attacking bark beetles are predicted to have high reproductive success ( $\lambda > 1$ ) under conditions of high water availability or extreme drought stress, but low reproductive success ( $\lambda < 1$ ) under moderate water stress.

(Fig. 1). Although this model is derived from simple physiological principles, it leads to more complex predictions than have usually been considered in judging the role of climatic effects on bark beetle population dynamics; it has the potential to reconcile some of the conflicting conclusions about the role of climatic patterns in driving the population dynamics of SPB and other bark beetle species.

In contrast with host resistance, natural enemies generally have been assigned a minor role in controlling bark beetle dynamics (Rudinsky, 1962; Christiansen and Bakke, 1988; Raffa, 1988), although they have sometimes been credited with accelerating the decline of outbreaks (Berryman, 1973; Berryman and Ferrell, 1988; Grégoire, 1988). However, a number of studies using exclusion cages around host trees have shown that natural enemies can inflict substantial mortality on immature bark beetles (Linit and Stephen, 1983; Miller, 1984, 1986; Riley and Goyer, 1986; Weslien, 1992). Furthermore, a 30-year-time-series analysis suggests that SPB outbreaks are driven by some population process acting in a delayed density-dependent manner (Turchin *et al.*, 1991), as might be expected if specialist natural enemies are influencing population dynamics. Among the potential natural enemies, clerid beetles (Coleoptera: Cleridae) are likely candidates in many systems for influencing bark beetle population

dynamics (Thatcher and Pickard, 1966; Berryman, 1967; Moore, 1972; Mills, 1985; Weslien and Regnander, 1992; Weslien, 1994). Typically, clerids are specialist predators of bark beetles that prey on both larval and adult life stages. *Thanasimus dubius* is the clerid species most abundant in the SPB system. It has long been recognized as a potentially important source of mortality for SPB (Fiske, 1908; Thatcher and Pickard, 1966; Moore, 1972), and its abundance relative to SPB has been used to predict future SPB activity (Billings, 1988). Here we report preliminary results from a research program designed to (1) quantify the potential effects of *T. dubius* on SPB populations, (2) compare the numeric effects of *T. dubius* relative to the effects of host suitability, and (3) evaluate the potential role of *T. dubius* in influencing SPB population dynamics.

## II. Moisture Stress and Host Suitability

### A. Models of Host Suitability Applied to Bark Beetle Populations

Several general models have been proposed to explain population variation in herbivorous insects based on the physiological condition of host plants. However, the various hypotheses can lead to different predictions, and the data are equivocal. The plant stress hypothesis (White, 1974) suggests that insect performance is favored in stressed plants (e.g., water limited) because of increased nitrogen availability in consumed tissue. This hypothesis is often linked to arguments that stressed plants synthesize less defensive chemicals (Rhoades, 1979), and that climatic effects can allow the release of endemic insect populations to epidemic levels (Greenbank, 1956; Mattson and Haack, 1987a,b). Larsson (1989) has discussed difficulties in rationalizing the plant stress hypothesis with many experimental results, although he concludes that performance of cambium feeders (e.g., bark beetles) is often enhanced on stressed hosts. The plant vigor hypothesis (Price, 1991), which may be viewed as in conflict with the plant stress hypothesis, is supported by observations that many herbivorous insects feed preferentially on vigorously growing plants. Waring and Cobb (1992) concluded from their review of over 450 studies that stress has strong effects on herbivore population dynamics—positive, negative, or nonlinear. Many studies lack the details of induced plant stress (e.g., level, timing, and duration of water deficit), which are essential for understanding the nature of plant as well as herbivore responses. Further, it seems to be generally unrecognized that physiological changes associated with ontogeny of plants, apart from stress effects, may alter host suitability for herbivorous insects (Kozlowski, 1969).

For the case of bark beetles, plant stress has long been a favored explanation for outbreaks. Wyman (1924), Craighead (1925), and St. George (1930) all implicated climatic effects, especially drought, in weakening host trees and permit-

ting increases in SPB populations. These early formulations of the stress hypothesis, like modern versions, assumed that tree "vigor" is positively correlated with the ability to resist attack by herbivores, perhaps because fast-growing trees were thought to have larger carbon budgets with which to produce defensive chemicals (Waring and Pitman, 1980; Waring, 1983; Raffa, 1988). Drought stress of trees remains one of the most commonly cited explanations for bark beetle outbreaks. In a volume devoted to the dynamics of forest insect populations (Berryman, 1988), four of five chapters dealing with injurious bark beetle species specifically invoke drought stress as a key factor in the release of beetle outbreaks (*Dendroctonus micans*, Grégoire 1988; *Dendroctonus ponderosae*, Raffa 1988; *Ips typographus*, Christiansen and Bakke 1988; *Scolytus ventralis*, Berryman and Ferrell 1988).

In spite of a long history in the literature, the linkage between drought stress and SPB population dynamics is only tenuously supported by the evidence. There have been few experimental tests, probably owing to the logistical problems of working with large trees. Manipulations of loblolly pine have shown that severe water deficits can enhance the success of attacking SPB (Lorio and Hodges, 1977), as predicted by the stress hypothesis, but these treatments may have exceeded normal climatic variation. Time-series analyses failed to detect any sign of climatic effects on SPB populations (Turchin *et al.*, 1991). Pine stands at highest risk for SPB infestations frequently appear to be those in which trees grow fastest, not slowest (Lorio *et al.*, 1982; Lorio and Sommers, 1986). In fact, the earliest scientific accounts suggest that SPB may prefer vigorously growing, "healthy" trees (Hopkins, 1892, 1921).

## B. An Alternative Model for the Effects of Water Availability on Pines

We have been testing an alternative physiological model for the effects of water availability on the suitability of southern pines for bark beetles (Lorio *et al.*, 1990). Our hypotheses are derived from principles of plant growth-differentiation balance (Loomis, 1932, 1953), and a conceptual model of loblolly pine suitability for SPB (Lorio *et al.*, 1990). Growth-differentiation balance allows two sets of predictions relevant to bark beetles: one dealing with static carbon budgets (Fig. 1) and another incorporating phenological patterns of tree growth (Lorio, 1986, 1988). Our static model predicts a curvilinear response of secondary metabolism to water availability, implying that drought may increase or decrease suitability for bark beetles depending on the initial water status of the trees and the severity of the drought (Fig. 1). Moderate water stress is predicted to limit growth more than photosynthesis, resulting in an increase in the proportion and total amount of carbon allocated to secondary metabolism. In contrast,

severe water deficits are predicted to limit carbon assimilation, thereby restricting secondary metabolism and increasing tree suitability for bark beetles.

Phenological considerations can be overlain on this static model. Pine trees in the southeastern United States grow very rapidly in the spring and early summer, but by midsummer tree growth typically becomes limited by soil water deficits. This change in environmental conditions corresponds to an ontogenetic transition in the cambium from the production of earlywood to latewood. The latewood is highly invested with vertical resin ducts that function in the synthesis and transport of oleoresin (a mixture of monoterpenes and resin acids that impedes attacking bark beetles, but also plays a role in secondary attraction of SPB). Annual variation in climatic conditions influences the timing of seasonal water deficits and, within the limits of endogenous controls, the ontogenetic transition from earlywood to latewood. Measurements of resin flow from standardized wounds to the face of the cambium indicate that spring and early summer is a time of relatively low resin flow in loblolly pine. The transition to latewood formation is accompanied by an increase in resin flow, presumably because there are more vertical resin ducts, and because growth limitations imposed by water deficits leave more carbon for secondary metabolism. The predictable increase in SPB infestations during spring and early summer (Billings, 1979) may occur because tree physiology tends to be growth-dominated at that time (Zahner, 1968; Lorio and Sommers, 1986). Climatic patterns that protract the period of earlywood production in southern pine (e.g., high precipitation in midsummer) are predicted to favor population growth in SPB by protracting the time when trees are suitable for beetle colonization.

## C. Experimental Results from 1990

In our first attempt at testing these predictions, Dunn and Lorio (1993) manipulated the water balance of 11-year-old loblolly pine using a combination of rain-exclusion shelters and irrigation. Compared to irrigated trees, trees treated with rain-exclusion shelters had lower xylem water potential, lower cambial growth, lower photosynthetic rates, and lower resin flow. Irrigated trees suffered 149–218% more SPB attacks than sheltered trees, but those SPB that attacked irrigated trees produced 32–52% fewer eggs per pair of attacking adults. This experiment did not provide an entirely satisfactory test of our growth-differentiation balance model because the summer in which it was conducted (1990) happened to be unusually hot and dry, and rain shelters that were designed to produce moderate deficits, limiting growth but not photosynthesis, actually produced such severe drought stress that photosynthetic rates were 30–60% lower than those of irrigated trees. Consequently, we were unable to evaluate whether the reduced resin flow in sheltered trees resulted from an increase,

decrease, or no change in the proportional commitment of carbon to secondary metabolism. Nonetheless, resin flow was very high in all trees, and attacking SPB averaged only 2.9–7.9 eggs per attacking pair, which indicates that even severe drought stress was insufficient to render the trees into high-quality hosts for attacking SPB.

#### D. Experimental Results from 1991

In 1991, we initiated a similar study with eight 22-year-old loblolly pine at each of three treatment levels: rain shelters to exclude precipitation, natural precipitation, and natural precipitation plus irrigation. Rain shelters were complete on 10 April and irrigation began on 5 June. SPB attack was induced on half of the trees on 22 July. The attacked trees were cut 10 days later. Bolts were removed from each tree at 1 and 3 m above ground, and two 500-cm<sup>2</sup> areas on opposite sides of each bolt were dissected to determine SPB performance.

Treatments were successful in producing a gradient of soil water availability. By 22 July, estimated soil water storage (Zahner and Stage, 1966) ranged from 2 to 12 to 17 cm in sheltered, control, and irrigated treatments, respectively. A calculated soil water deficit of >25 cm had accumulated in the sheltered treatment by the time of attack. Predawn water potential did not differ among treatments initially, but by mid-June, the sheltered trees began to show lowered water potentials, indicating development of moderate water deficits.

Water regime influenced tree height growth and cambial growth, but not photosynthesis (Fig. 2). Height growth was reduced at very modest water deficits (control versus irrigated), whereas cambial growth was reduced only at somewhat greater water deficits (sheltered versus control). The resin yield of sheltered trees rose dramatically in late June to nearly twice that of control and irrigated trees (Fig. 3). Because carbon assimilation was not affected by the water treatments (Fig. 2), sheltered trees were apparently committing a larger proportion of their carbon budgets to secondary metabolism and a lower proportion to growth (i.e., decreased growth : differentiation). There was a strong negative relationship between beetle attack success and tree resin production (Fig. 4). In the upper trunk, SPB attack densities did not differ across treatments (18–22 attacking pairs per 500 cm<sup>2</sup>). However, beetles attacking sheltered trees produced less gallery than those attacking control or irrigated trees (mean  $\pm$  SE = 145  $\pm$  3 versus 216  $\pm$  25 versus 348  $\pm$  48 cm per 500 cm<sup>2</sup>, respectively), and had much lower reproductive success (4.6  $\pm$  1.4 versus 7.1  $\pm$  1.3 versus 12.5  $\pm$  4.0 eggs per adult pair, respectively). In the lower trunk, SPB reproductive success was even more severely reduced in sheltered trees relative to irrigated trees (1.7  $\pm$  0.4 versus 3.1  $\pm$  1.0 versus 11.3  $\pm$  4.3 eggs per adult pair, respectively). Presumably beetles encountering high resin flow were forced to spend more time

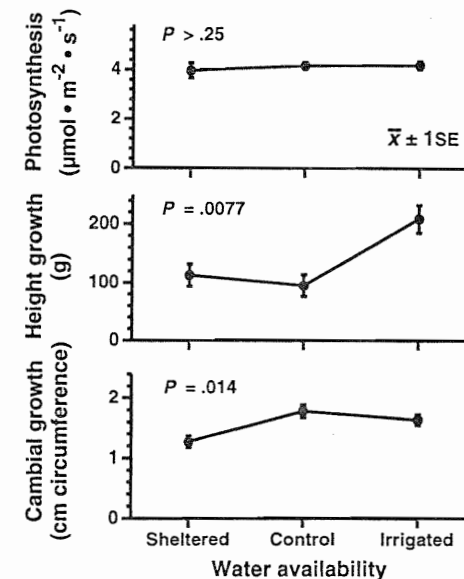


Figure 2. Effects of water availability on net photosynthesis, height growth, and cambial growth in 22-year-old loblolly pine. *P* values show results of tests for linear trend. Photosynthesis was measured at midmorning on nine dates during the summer. Height growth includes the second through the fourth flushes, with the first flush used as a covariate. Cambial growth is cumulative circumference growth at breast height (1.37 m) during the treatment year, with circumference growth in the previous year used as a covariate.

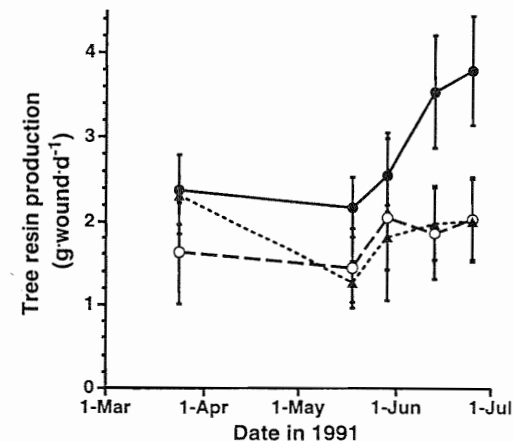


Figure 3. Resin production in 1991 as affected by sheltering (solid circles), control (open circles), and irrigation (solid triangles).

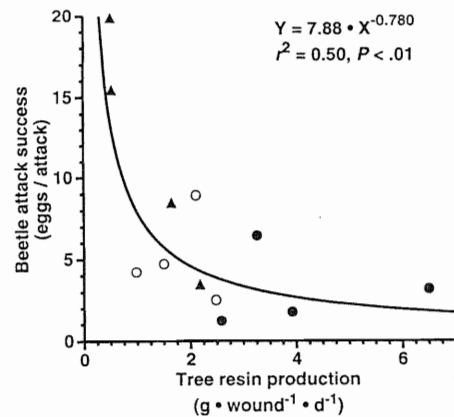


Figure 4. Beetle attack success (eggs per attacking adult) as a function of resin production in individual trees exposed to different water regimes: sheltering (solid circles), control (open circles), and irrigation (solid triangles). Attack success was determined by dissecting four 500-cm<sup>2</sup> sections of phloem from each tree just after oviposition was completed.

removing resin from their attack galleries and had less time for excavating oviposition galleries. SPB attacking irrigated trees left 2.7 to 6.6 times more progeny than their counterparts attacking sheltered trees.

These results seem counterintuitive if it is assumed that water deficits and growth limitations are inherently bad for trees and good for bark beetles. However, results strongly support hypotheses derived from plant growth-differentiation balance (Loomis, 1932, 1953). Trees do not partition carbon according to fixed ratios. Environmental effects can dramatically alter commitments of carbon to growth versus secondary metabolism. In the case of water deficits that limit growth but not photosynthesis, the accumulating carbon supports cellular differentiation (e.g., secondary wall thickening, the formation of vertical resin ducts) and can lead to increased secondary metabolism (e.g., oleoresin synthesis), resulting in a more resistant tree. Conversely, well-watered trees tend to sustain growth further into the summer, which limits carbon for cellular differentiation and secondary metabolism, and produces a less resistant tree.

### E. Future Studies

These results suggest new and largely untested predictions about the role of climatic patterns in bark beetle population dynamics. For example, years with high precipitation, especially if it prolongs the period of earlywood growth, are expected to favor SPB population increases. Similarly, productive sites with

relatively high water availability are expected to provide better habitat for SPB. This latter prediction is consistent with stand risk ratings for SPB in the Kisatchie National Forest of Louisiana (Lorio *et al.*, 1982; Lorio and Sommers, 1986). Future research will include the development of models that input precipitation patterns and soil attributes to predict patterns of secondary metabolism in loblolly pine and rates of population increase in SPB. One of the key unknowns is the level of water deficits at which tree secondary metabolism begins to drop and bark beetle success increases (Fig. 1).

## III. Predation and SPB Dynamics

### A. Background on Interactions between *Thanasimus dubius* and SPB

Once attack of the host tree by SPB is under way, a large assemblage of natural enemies prey upon or parasitize various stages of SPB, both inside and outside the tree. One of the first enemies to appear is adult *Thanasimus dubius* (F.) (Coleoptera: Cleridae), which are attracted by SPB pheromones and volatiles emitted by the damaged host tree (Vité and Williamson, 1970; Dixon and Payne, 1979, 1980). Adult *T. dubius* catch and consume the adult SPB arriving on the host tree. At the same time, *T. dubius* mate and oviposit on the bark surface (Thatcher and Pickard, 1966). After hatching, *T. dubius* larvae enter the phloem, where they feed on the larval progeny of those SPB that successfully entered the tree.

A number of studies suggest that *T. dubius* is the most important natural enemy of SPB, although its role in SPB dynamics still remains uncertain. Moore (1972) estimated that 24% of SPB larvae were killed by insect predators and parasitoids, and attributed half of this mortality to *T. dubius* larvae. Linit and Stephen (1983) estimated that 26% of the mortality of SPB larvae was due to natural enemies, especially *T. dubius*. These results must underestimate the total impacts of *T. dubius* on SPB because they do not include adult predation. As early as 1908, Fiske noted that on trees where *T. dubius* was numerous, the fragmentary remains of adult SPB could be found in quantity within crevices in the bark. Thatcher and Pickard (1966) released SPB and *T. dubius* adults into a room containing a freshly cut pine log, and found that *T. dubius* reduced by about 50% the number of SPB successfully attacking the log. Studies of *T. dubius* in laboratory arenas provide further indications that *T. dubius* can capture and consume large numbers of SPB (Turnbow *et al.*, 1978; Nebeker and Mizell, 1980; Turnbow and Franklin, 1980; Frazier *et al.*, 1981).

Clearly, *T. dubius* can inflict considerable mortality on SPB, but additional information is required to define its role in SPB population dynamics. For example, we need more detailed estimates of the mortality inflicted on SPB by

*T. dubius* (both adults and larvae) across a natural range of predator and prey densities. We also need information on the numerical response of *T. dubius* to fluctuations in SPB density. In addition, theory has emphasized the importance of both predator and prey movement in population dynamics (Kareiva and Odell, 1987; Murdoch and Stewart-Oaten, 1989; Hassell *et al.*, 1991; Ives, 1992a,b; Murdoch *et al.*, 1992), but at present we have information only for SPB (Turchin and Thoeny, 1993). Finally, developments in age-structured population models suggest that the relative durations of the predator and prey life cycles can have important effects on dynamics (Nisbet and Gurney, 1982; Hastings, 1984; Nune, 1985; Murdoch *et al.*, 1987; Godfray and Hassell, 1989), but until now we had little information on the development of *T. dubius* under field conditions.

### B. Functional Response of *Thanasimus dubius*

To estimate the mortality inflicted by adult *T. dubius* on SPB, we conducted laboratory experiments in which SPB were exposed to different predator densities. The experimental arenas were bolts (80 cm long) cut from mature loblolly pines, with 50 cm enclosed by a spherical cage. Predator densities were set to 0, 10, 20, and 40 adult *T. dubius* per bolt, which encompasses the range of predator densities we have observed in the field (0 to 1.25 predators per dm<sup>2</sup> of bark surface area). The predator treatments were crossed with prey densities of 100, 200, and 400 SPB per bolt, to create a range of attack densities representative of what might occur over one day in nature. At the end of the experiment, we counted the number of SPB elytra in the cage to estimate the number of SPB eaten by *T. dubius* prior to entering the bolt. Then bolts were dissected to count the number of SPB that had successfully entered the phloem. Each treatment combination was replicated three times.

Predation by adult *T. dubius* substantially reduced the proportion of SPB successfully attacking the bolt (Fig. 5). As predator density increased from 0 to 40 adults per bolt, the proportion of SPB entering the bolt fell from about 60 to 20%. Moreover, there appeared to be an impact on attack success even at the lowest predator density (10 adults per bolt). Adult *T. dubius* consumed 17–53% of the attacking SPB, with the proportion eaten increasing with predator density (Fig. 5). However, the proportion eaten declined with increasing prey density, implying some saturation of the predator's functional response at high SPB densities. These results suggest that predation by adult *T. dubius* in the field could cause substantial mortality of SPB and slow colonization of individual host trees, and reduce the total number of trees that are attacked.

### C. Numerical Response of *Thanasimus dubius*

To examine numerical responses of *T. dubius*, we initiated a long-term sampling program to monitor adult densities of SPB and *T. dubius* in the

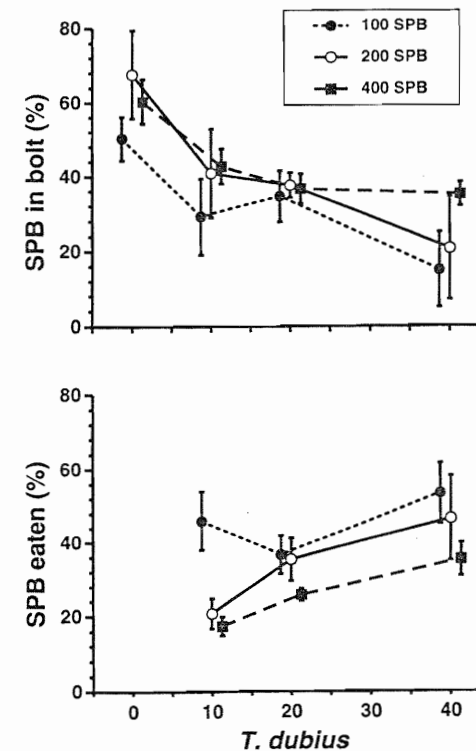


Figure 5. Proportion of SPB ( $\pm 1$  SE) successfully entering the bolt by the end of the experiment, and the proportion eaten by *T. dubius* ( $\pm 1$  SE) as a function of SPB and *T. dubius* density. *Thanasimus dubius* density had a significant negative effect on the proportion entering the bolt ( $P < 0.001$ ), whereas SPB density had a significant positive effect ( $P < 0.015$ ). Conversely, *T. dubius* density had a significant positive effect on the proportion eaten ( $P < 0.001$ ), whereas SPB density had a significant negative effect ( $P < 0.001$ ).

Kisatchie National Forest in central Louisiana. Since 1989, we have maintained three to nine baited multiple funnel traps (Lindgren, 1983) deployed in transects across each of four Ranger Districts. The traps are baited with frontalin (the aggregation pheromone of SPB) and turpentine; this combination of chemicals is highly attractive to both SPB and *T. dubius* (Vité and Williamson, 1970; Payne *et al.*, 1978; Dixon and Payne, 1979). The bulk of insect captures typically occur during the first 6 months of each year. Consequently, we estimated the relative abundance of SPB and *T. dubius* as individuals caught per trap per day for each district, during the first 6 months of each year. The four districts showed similar temporal patterns of SPB and *T. dubius* abundance, so we averaged the trap catches across them to yield a mean value for each year of the survey. Graphical

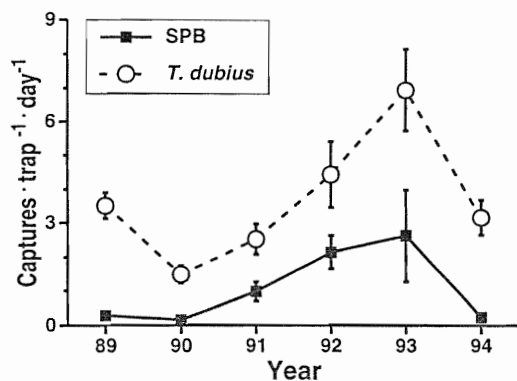


Figure 6. Trap catch per day of SPB (solid squares) and *T. dubius* (open circles) within the Kisatchie National Forest, for the period 1989–1994.

analysis suggests a numerical response by *T. dubius* to changes in the density of SPB (Fig. 6). As SPB populations changed from endemic levels in 1989–1990 to a mild outbreak in 1993, followed by a collapse in 1994, captures of *T. dubius* paralleled these changes in prey density (Fig. 6). This pattern of numerical response is consistent with the hypothesis that *T. dubius* predation could impact SPB population dynamics, suppressing or at least moderating outbreaks. Although *T. dubius* abundance varied over time, adults were always present, even when SPB densities were very low (Fig. 6). We now know that some *T. dubius* enter a prolonged diapause (see the following), so some of the *T. dubius* trapped during low SPB density could have been individuals emerging from trees attacked by SPB one or more years previously.

#### D. Life History of *Thanasimus dubius*

Laboratory studies of *T. dubius* have indicated a development time from egg to adult of about 110–240 days, depending on temperature (Nebeker and Purser, 1980; Lawson and Morgan, 1992). However, recent results indicate that in nature many *T. dubius* individuals undergo an extended period of development inside the host tree. Figure 7 shows the emergence of *T. dubius* adults from a tree attacked by SPB in October 1992. Thirty-two *T. dubius* adults emerged in the spring of 1993, which is about the time that would be expected based on previous laboratory studies. However, another 57 *T. dubius* emerged during the following autumn and winter, and another 15 emerged this past autumn, approximately 2 years after the time of SPB attack and *T. dubius* oviposition. Apparently, this prolonged development is not unusual. Bark samples taken from trees long va-

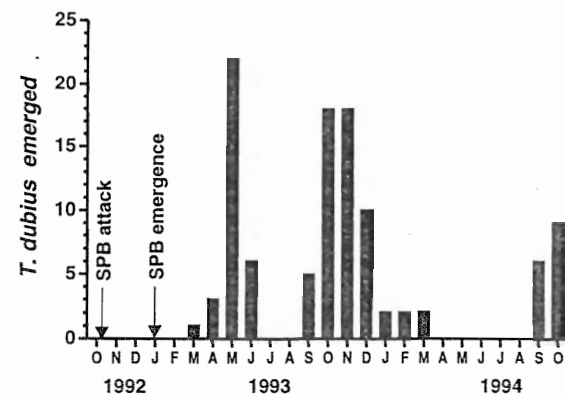


Figure 7. Pattern of *T. dubius* emergence from a tree attacked by SPB in October 1992. A large emergence trap, covering a 150-cm length of the tree, was used to collect the emerging adults. Also shown is the time at which SPB emergence occurred.

cated by SPB frequently contain large numbers of immature *T. dubius* that are apparently in a state of diapause. At a site in East Texas, 49% of 307 pupation chambers still contained live *T. dubius* immatures almost 2 years after SPB attack, and at a site in central Louisiana of similar age, 36% of 181 chambers still contained living *T. dubius*. By comparison, we estimate that SPB may complete about six generations per year in central Louisiana (based on climatic records and the temperature sensitivity of developmental processes; Gagne *et al.*, 1982; Wagner *et al.*, 1984; M. P. Ayres, unpublished analyses).

These revisions in our understanding of the *T. dubius* life cycle have two important implications for the population dynamics of *T. dubius* and SPB. First, the protracted life history of *T. dubius* makes it a viable candidate for the delayed density dependence thought responsible for generating population cycles in SPB, which operates with a 1-year time lag (Turchin *et al.*, 1991). If the generation time of *T. dubius* were only 6 months in the field, as we had previously thought, then we would have rejected *T. dubius* as the force driving SPB population cycles. Second, theoretical studies suggest that a long development time in the predator, relative to that of the prey, has a strong destabilizing effect on predator-prey dynamics (Nunney, 1985; Murdoch *et al.*, 1987; Godfray and Hassell, 1989). On these grounds we would expect a *T. dubius*–SPB system to exhibit long-term oscillations in predator and prey abundance, unless some rapidly acting factor compensates for the destabilizing effect of this delay in *T. dubius* development (Nunney, 1985).



## IV. Conclusions

SPB population dynamics, like those of many other bark beetles, are characterized by extreme fluctuations (up to four orders of magnitude within 5 years; Turchin *et al.*, 1991). Historically, explanations of bark beetle population dynamics have recognized the potential role of natural enemies, but have usually emphasized variation in host suitability. Our ongoing work with SPB is aimed at (1) elucidating and testing physiologically explicit models of environmental effects on tree suitability for bark beetles, (2) assessing the numerical impacts of natural enemies on SPB population dynamics, and (3) evaluating the relative contributions of host suitability and natural enemies in producing observed population dynamics.

SPB population fluctuations show pattern in both time and space. Time-series analyses indicate a cyclical pattern to SPB outbreaks (Turchin *et al.*, 1991). The periodicity of these outbreaks is difficult to explain with any climatic mechanisms (e.g., effects of precipitation patterns on suitability of host trees) unless there is some periodicity to the climatic patterns; none has yet been discovered (Turchin *et al.*, 1991), although our revised understanding of moisture effects on tree physiology suggests that linear models may be an inadequate test (Fig. 1). It seems more likely that the cyclic tendencies of SPB populations are due to some biological agent(s) that act in a delayed density-dependent fashion (e.g., natural enemies or competitors). SPB population fluctuations are also characterized by large-scale spatial synchrony. For example, severe SPB outbreaks occurred in 1985–1986 from East Texas through Louisiana, Mississippi, and Alabama (Price *et al.*, 1992). This spatial synchrony is difficult to explain if population dynamics are primarily driven by natural enemies, because most natural enemies of SPB are other arthropods that seem unlikely to move more than a few kilometers per generation. It seems more likely that the spatial synchrony is driven by forces that act on a regional scale, such as climatic variation. Even infrequent climatic events may be adequate to synchronize population cycles across broad geographic areas (Royama, 1984).

Our research supports the hypothesis that SPB population dynamics are influenced by both density-dependent interactions with *T. dubius* and environmental effects on host trees. *Thanasimus dubius* adults at natural densities can kill up to 53% of the SPB adults attempting to colonize a tree (Fig. 5). By comparison, moderate drought stress can increase resin flow in trees and reduce SPB reproductive success by 63–85% relative to that in irrigated trees (Figs. 3 and 4). In both cases, these are probably underestimates of the potential effects on SPB population dynamics. The *T. dubius* larvae feed on SPB larvae beneath the bark, but we presently can only estimate effects of adult predation. Similarly, tree water balance and physiological status probably influence the growth and survival of SPB larvae, but we presently can only estimate effects on attacking

adults. The expected effects of these two forces on SPB population dynamics are quite different. *Thanasimus dubius* has a long development time, which makes it a good candidate for producing outbreak cycles, whereas climatic effects on host-tree suitability may influence the amplitude of outbreaks and synchronize population cycles on a regional scale.

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