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High-resolution analysis of stem increment and sap flow for loblolly pine trees attacked by southern pine beetle

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Abstract: Manual and automated dendrometers, and thermal dissipation probes were used to measure stem increment and sap flow for loblolly pine (*Pinus taeda* L.) trees attacked by southern pine beetle (*Dendroctonus frontalis* Zimm.) in east Tennessee, USA. Seasonal-long measurements with manual dendrometers indicated linear increases in stem circumference from April through June. Changes in stem circumference slowed after this time, and further increases were either modest or not observed. These effects coincided with a massive midsummer infestation of trees with southern pine beetles. High-resolution measurements with automated dendrometers confirmed that, while early-season increases in radial increment were positive, daily rates of radial increment for slow- and fast-growing trees were largely negative in early to late July. Sap velocity also declined despite favorable weather conditions, but these reductions were not observed until mid-August. Thus, effects on radial increment and stem circumference preceded those on sap velocity by several weeks. The timing of these events, combined with the known developmental rate of southern pine beetles, suggest that disruption of whole-tree water balance is not a prerequisite for the success of attacking beetles or for oviposition by colonizing females and larval development, all of which were completed by early August. Additional field experiments that use high-resolution techniques to measure stem increment and sap flow are needed to more rigorously characterize temporal changes in host physiology during initial invasion and colonization of trees by southern pine beetle.

Résumé : Des dendromètres manuels et automatiques ainsi que des capteurs de dissipation de chaleur ont été utilisés pour mesurer l'accroissement de la tige et l'écoulement de la sève chez des pins à encens (*Pinus taeda* L.) attaqués par le dendroctone méridional du pin (*Dendroctonus frontalis* Zimm.) dans l'est du Tennessee, aux États-unis. Des mesures prises tout au long de la saison avec des dendromètres manuels ont montré une augmentation linéaire de la circonférence de la tige du mois d'avril au mois de juin. Par la suite, les changements dans la circonférence de la tige ont ralenti et les augmentations subséquentes ont été modestes ou n'ont pas été détectées. Ces effets coïncident avec une infestation massive des arbres par le dendroctone méridional du pin au milieu de l'été. Des mesures à haute résolution avec des dendromètres automatiques confirment que tandis que les augmentations de croissance radiale observées en début de saison étaient positives, le taux quotidien de croissance radiale chez les arbres à croissance lente et chez les arbres à croissance rapide était fortement négatif du début à la fin juillet. La vitesse d'écoulement de la sève a également diminué malgré des conditions météorologiques favorables mais cette diminution n'a pas été observée avant le milieu du mois d'août. Par conséquent, les effets sur l'accroissement radial et en circonférence ont précédé ceux sur la vitesse d'écoulement de la sève de plusieurs semaines. La séquence de ces événements dans le temps, combinée au taux de développement connu du dendroctone méridional du pin, laisse croire que la perturbation du bilan hydrique global d'un arbre n'est pas une condition préalable pour le succès d'une attaque par les insectes, de l'oviposition par les femelles ni du développement des larves qui était complété vers le début du mois d'août. D'autres expériences sur le terrain avec des techniques à haute résolution pour mesurer l'accroissement de la tige et la vitesse d'écoulement de la sève sont requises pour caractériser de façon plus rigoureuse les changements temporels dans la physiologie de l'hôte pendant l'invasion initiale et la colonisation des arbres par le dendroctone méridional du pin.

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Introduction

The southern pine beetle (*Dendroctonus frontalis* Zimm., Coleoptera: Scolytidae) is arguably the most destructive forest insect in the southeastern United States (Ayers and Lombardero 2000). This native pest commonly increases to epidemic proportions causing widespread mortality of trees in natural and managed forest ecosystems, with direct economic losses that can exceed $350 million per year (USDA Forest Service 1995; Price et al. 1997).

Adult southern pine beetles mostly attack southern yellow pines, including loblolly pine (*Pinus taeda* L.), Virginia pine (*Pinus virginiana* Mill.), shortleaf pine (*Pinus echinata* Mill.), slash pine (*Pinus elliottii* Engelm.), and longleaf pine (*Pinus palustris* Mill.), although Eastern white pine (*Pinus strobus* L.) may be attacked in large outbreaks (Payne 1980). Beetles employ aggregation pheromones to organize synchronous mass attacks of individual trees (Renwick and Vité 1969; Grosman et al. 1997). Adult beetles gain entry into a suitable host by boring through the outer bark and into the phloem, where they excavate oviposition galleries and lay eggs (Payne 1980). In the process of excavation, which has the effect of girdling the tree, host trees release oleoresin that acts as a physical impediment to gallery construction and can limit beetle reproduction (Lorio 1986; Dunn and Lorio 1992; Nebeker et al. 1992; Reeve et al. 1995; Strom et al. 2002; Tisdale et al. 2003). Mass colonization by large numbers of beetles can quickly deplete resin supplies. Although beetle reproduction varies greatly depending upon resin dynamics, it is rare that trees survive beetle attacks once gallery construction and oviposition have taken place (Wood 1982).

During beetle attack, the host tree may be infected with one or more fungi carried by the beetles, especially *Entomocorticium* sp. A (formerly SJB 122), *Ceratocystiopsis ranaculosus*, and *Ophiostoma minus* (formerly *Ceratocystis minor*) (Klepzig et al. 2001). The role that these fungi play in facilitating colonization of host trees or in determining the ultimate fate of trees attacked by southern pine beetles is largely unknown. *Ophiostoma minus*, the causal agent of bluestain in southern pines, has been hypothesized to assist in killing the tree by growing into the sapwood, releasing toxins into the xylem stream, and disrupting tree water balance through aspiration of tracheid tori or vascular plugging with resin (Caird 1935; Bramble and Holst 1940; Mathre 1964; Basham 1970; DeAngelis et al. 1986; Miller et al. 1986). Such physical disruption of the xylem could elicit negative effects on whole-plant water relations or otherwise predispose trees to stress during periods of limited soil water availability. However, the long-held belief that bluestain fungi are directly responsible or required for tree mortality is widely debated (Paine et al. 1997). Resolution of this debate will require an improved understanding of how host trees respond to initial attack and subsequent effects of infestation on growth and tree water balance.

Here we report temporal patterns of stem increment and sap flow for loblolly pine trees attacked by southern pine beetles in east Tennessee, USA. This study was originally designed to explore individual and interactive effects of climate, soil water availability, and ozone on stand growth and water use. Interactive effects of ozone and soil water availability on changes in stem circumference for trees measured with manual dendrometers at this site had been indicated in previous studies (McLaughlin and Downing 1995, 1996). In an attempt to further improve our understanding of these processes, automated dendrometers and thermal dissipation probes were installed in 1999 to examine radial increment and whole-tree water use in more detail. Midway through the season, however, southern bark beetles invaded the stand, resulting in widespread infestation of instrumented trees. Thus, although data could no longer be used to address our original objectives, a unique opportunity emerged to examine the effects of southern pine beetle on growth and whole-tree water use. This permitted us to (*i*) identify temporal trends in stem increment and sap velocity following infestation, (*ii*) characterize the relative sensitivity of these two processes to southern pine beetle attack, and (*iii*) interpret observed effects on growth and sap velocity given the known developmental biology of this insect. This latter objective was accomplished using a biophysical model of insect development parameterized for *D. frontalis* (Ungerer et al. 1999).

Materials and methods

Description of study site and measurements of stem growth and sap velocity

Observations of stem growth and sap flow in large loblolly pine trees were made during 1999 at the National Environmental Research Park, Oak Ridge, Tennessee (35°55′N, 84°22′W). The study site was in agricultural use prior to 1942 and was planted with loblolly pine around 1960. Study trees were 40–45 years old and averaged 23 m in height. Basal area ranged from 22.1 $m^2 \cdot ha^{-1}$ at the stand edge to 32.9 $m^2 \cdot ha^{-1}$ in the stand interior (McLaughlin et al. 2003). Soils are a sandy loam and characterized as alluvial, deep, and fertile. Long-term mean annual temperature is 14.2 °C, and precipitation averages 1352 mm.

Automated dendrometers (Agricultural Electronics, Tucson, Arizona) were installed 22 June on six loblolly pine trees for the purpose of measuring rates of radial increment. Each dendrometer was equipped with a linear-variable differential transducer and a spring-loaded inner core that pressed against the stem. Sample trees averaged 49.4 ± 10.3 cm (±SD) in diameter, and ranged from 37.9 to 67.5 cm. Dendrometers were installed at breast height on stainless steel rods inserted through the bark and into the sapwood (McLaughlin et al. 2003). Data were collected at 15-min intervals. Stem circumference was also measured bi-weekly with spring-tensioned manual dendrometers. Changes in stem circumference were measured with electronic calipers. Manual measurements had a precision of ±0.02 mm.

Sap velocity rates for each tree were determined at 15-min intervals with thermal dissipation probes (Dynamax, Houston, Texas). These devices operate on the constant power principle (Granier 1987) and consist of two cylindrical probes, each 1.3 mm in diameter and 3 cm in length. The two probes were inserted into the outer sapwood of each tree and were separated vertically along the stem by 4 cm. Probes were installed 12 July. Five-millimetre cores were

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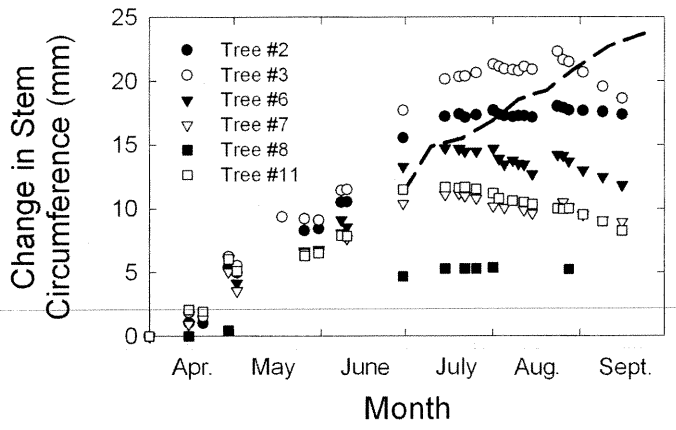
Fig. 1. Seasonal changes in stem circumference for six loblolly pine trees monitored with manual dendrometer bands during a southern pine beetle epidemic in eastern Tennessee. The broken line represents the expected end-of-season pattern for stem circumference based on earlier analyses of McLaughlin and Downing (1996).



taken near the point of installation with an increment borer to determine sapwood thickness. All dissipation probes were insulated with Styrofoam and shielded with aluminum foil to minimize temperature fluctuations in the sapwood.

Instruments for measuring air temperature, relative humidity, radiation, precipitation, and wind speed were located nearby (500 m) at the Oak Ridge National Laboratory free-air CO_2 enrichment facility (Norby et al. 2001). Soil water content (%, *v/v*) was measured at the study site with a time domain reflectometer (Soil Moisture Equipment Corp., Santa Barbara, California) following the procedures of Topp and Davis (1985). Replicated (n = 4) measurements were made weekly at each of two depth increments; 0–15 cm and 0–30 cm. Volumetric soil water content was converted to soil water potential based on methodology described by Saxton et al. (1986). Radiation, vapor pressure deficit, air temperature, and wind speed were used to calculate rates of potential evapotranspiration (PET) for the site using the Penman–Monteith equation (Stewart 1988; Wullschleger et al. 2000).

Data analysis

Site-specific information on southern pine beetle population size and stage of infestation associated with measurements of stem growth and sap flow as made in this study are not available. Anecdotal observations, however, taken during the season indicate that stands of loblolly pine adjacent to our site began to show changes in canopy coloration in May and early June. Typical symptoms included yellowing and then reddening of foliage. These symptoms progressed towards our site throughout June. Frass from pine beetle excavations was first observed on data loggers and instruments in late June, and pitch exudation was observed along the stems of most individuals in early July. Given this sequence of events, we speculate that all study trees were infested with pine beetles by 30 June. This date was used as the baseline from which the time between initial infestation and beetle-induced effects on stem increment and sap velocity were determined.

Manual dendrometers were used to characterize seasonal changes in stem circumference and to identify periods of growth cessation (if there were any) associated with southern pine beetle infestation. Such periods were determined by comparing data collected here against repeated measurements of stem circumference for loblolly pine published earlier for this same site by McLaughlin and Downing (1996).

Diurnal changes in stem radius as measured with point dendrometers are characterized by three phases: shrinkage, recovery, and increment (Downes et al. 1999; McLaughlin et al. 2003). In this study, we used the amplitude of the diurnal cycle, inflection points in rate of daily increments, and the relationship of concurrent diurnal patterns of stem increment and sap velocity to identify temporal patterns of response for trees attacked by southern pine beetle. Depending on the diurnal relationships among shrinkage, recovery, and increment, daily rates of radial growth may be positive or negative.

To identify significant reductions in sap velocity, we used linear regression techniques to establish relations between mean daily sap velocity and PET for each tree in the study. Data used in this step of the analysis were restricted to measurements of sap velocity taken between 23 July and 07 August. Coefficients of determination (R^2) were 0.95 or higher. These regression models provided a baseline against which subsequent estimates of sap velocity and PET were compared on a tree-by-tree basis. Reductions in sap velocity were deemed significant when data fell outside the 95% confidence interval.

Results

Season-long measurements of stem circumference with manual dendrometers showed wide variation among trees (Fig. 1). Stem circumference for the fastest growing tree increased 22.3 mm over the season compared with only 5.3 mm for the slowest growing tree. Early-season measurements indicated linear increases in stem circumference for all trees. From April through June, daily rates of change in stem circumference ranged from 0.06 to 0.20 $mm \cdot d^{-1}$ across the 90-d period. Stem circumference slowed considerably over the next 30 days (i.e., throughout July) and, despite expectations that changes in circumference would continue to increase in a linear manner, further increases were either modest or not observed.

Observed changes in stem circumference varied among fast- and slow-growing trees in the stand, with reductions occurring first in trees with low growth rates (Fig. 1). The slowest-growing tree (No. 8) was noticeably infested with beetles on 30 June and displayed little change in stem circumference after that date. In contrast, the two fastest-growing trees (Nos. 2 and 3) were among the last trees to be attacked by pine beetles and continued to show increases in stem circumference through mid- to late-July (Fig. 1).

Soil water content varied throughout the season (Fig. 2A). Values for the 0- to 30-cm depth increment ranged from 21.6% to 31.5%, with slightly lower (i.e., drier) values in the upper 0- to 15-cm soil layer. Seasonal variation in soil water potential was also observed for each of the two depth increments, approaching –0.30 and –0.13 MPa for the 0- to 15-cm and 0- to 30-cm soil layers, respectively, (Fig. 2B).

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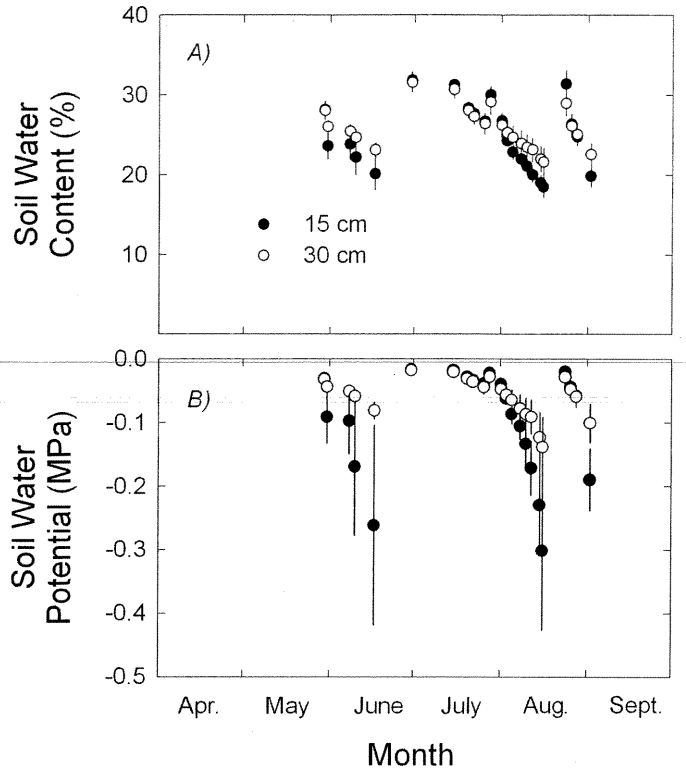
Fig. 2. Seasonal trends in (A) soil water content and (B) soil water potential for each of two depth increments (i.e., 0–15 cm and 0–30 cm). Soil water potential was calculated from measurements of soil water content. Data are means ± 1 SD (n = 4).

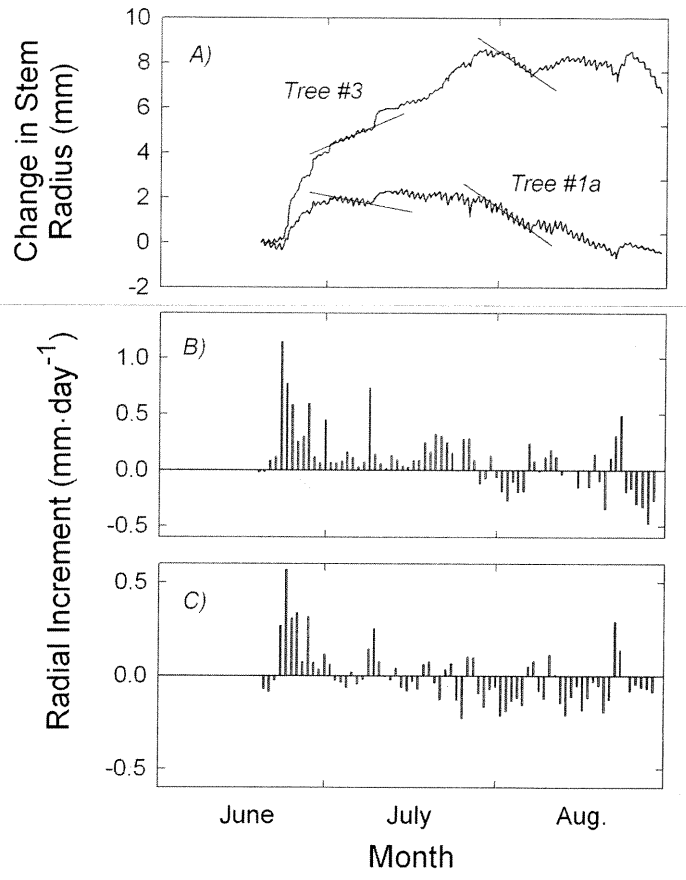


Soil water potentials were most negative during mid-June and mid-August. Soil water availability, however, remained high throughout the season. Plant available water in the 0- to 30-cm soil layer was estimated to be 75% on June 17 and 65% on August 16.

High-resolution measurements of stem radius with point dendrometers, albeit restricted to a portion of the total growing season, showed patterns similar to those obtained with manual dendrometers (Fig. 3A). Daily rates of radial increment for fast- and slow-growing trees varied throughout the measurement period, with rates in June averaging 0.33 and 0.15 mm·d^{-1}, respectively. Although day-to-day variation was high, increments in stem radius for this period were largely positive. Fast- and slow-growing trees, however, both exhibited slight to marked reductions in stem increment during early July (Fig. 3A). This effect was less pronounced in fast-growing trees, which continued to display positive increments in stem radius until 28 July (Fig. 3B). In contrast, stem increment for slow-growing trees (No. 1a) declined and remained low throughout July (Fig. 3C). Trees exhibited a second period of growth decline in early August, but unlike the earlier period, all trees independent of growth rate exhibited similar reductions in stem increment.

Midday rates of sap velocity measured between 23 July and 6 August varied little among the trees sampled in this study (Fig. 4). Average maximum rates of sap velocity ranged from 0.054 for tree No. 6 to 0.066 mm·s^{-1} for tree No. 3. This consistency in sap velocity mirrored rates of calculated

Fig. 3. Temporal changes in (A) stem radius and (B, C) daily radial increment for two loblolly pine trees (No. 3 and No. 1a, respectively) that differ in their relative growth rates. Periods during which stem increment declined in early July and again in early August are delineated for fast- and slow-growing trees with solid lines.



PET (Fig. 4A), reflecting the favorable weather conditions during this period.

Throughout the period between 23 July and 07 August, mean daily sap velocity and PET were highly correlated for all trees (data not shown). However, beginning on 13 August for tree No. 6 and 17 August for trees No. 2 and No. 3, the relationship between mean daily rates of sap velocity and PET began to fall below the lower 95% confidence limit. Sap velocity rates at these times ranged from 0.020 to 0.029 mm·s^{-1} and thereafter progressively declined despite PET remaining high (Fig. 4). Within 4 days, mean daily sap velocity rates had declined by 21%–45%, and, within an additional 4–5 d, rates of sap velocity were zero.

Discussion

Because our measurements were confined to trees naturally colonized by southern pine beetles under field conditions, controls against which to compare temporal patterns of stem increment are not available. Stem increment for loblolly pine in this region, while it may be significantly impacted by soil water availability and elevated ozone levels during the season, tends to reestablish linear growth rates

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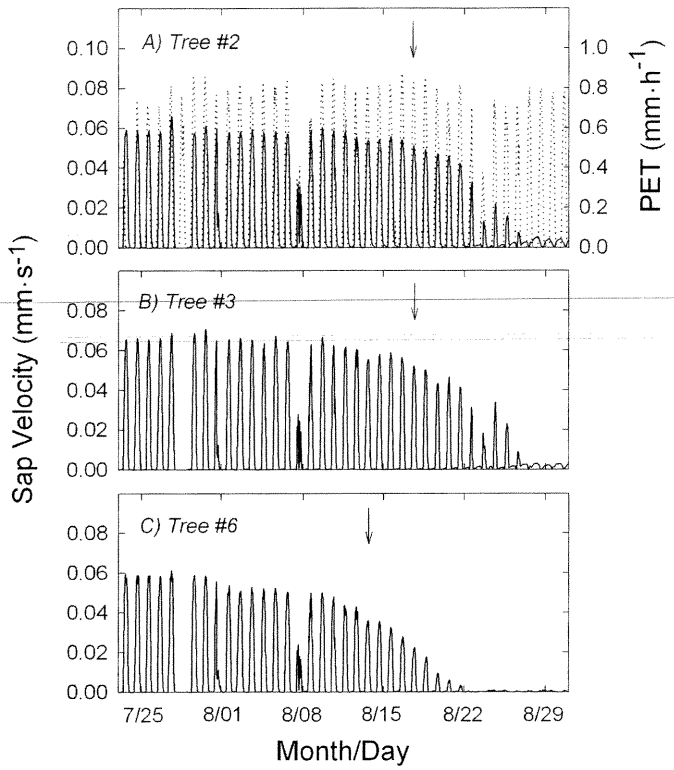
Fig. 4. Sap velocity rates (solid lines) as measured for three loblolly pine trees infested with southern pine beetle. Panel A also shows calculated rates of potential evapotranspiration (PET) (dotted line) based on weather data collected at the site and the Penman–Monteith equation. Arrows indicate when beetle-induced reductions in sap velocity were significant.



late in the season as observed by McLaughlin and Downing (1996). It was our expectation that barring infestation of trees with southern pine beetles, linear patterns of growth would be observed in our study throughout September and October. Stem increment in all trees did not increase, however, past mid-August. Rates of stem increment for yellow poplar saplings in the understory at our site were, by comparison, fairly uniform throughout the 1999 season, showing few, if any signs of growth reduction due to limited soil water availability or weather. Soil water potential did decline during the season, although these events were not of the duration or severity to alone cause reductions in rates of stem increment or sap flow of the magnitude observed in this study. Therefore, while we cannot rule out the possibility that perturbations in stem increment in loblolly pine as measured with manual and automated dendrometers were due to temporal changes in climatic and (or) edaphic conditions, we believe that a plausible explanation for observed changes in stem increment lies in the fact that trees were responding directly to heavy infestation by pine beetles. Shifts in carbon allocation from growth to synthesis of oleoresin (Lombardero et al. 2000) and physical disruption of cells in the cambial zone by southern pine beetles during gallery excavation likely contributed to observed patterns.

Although our measurements allow us to closely associate temporal changes in stem increment and sap velocity, field observations are inadequate to assess the developmental biology of southern pine beetles per se during the year. Using temperature data collected at this site, and biophysical development models parameterized for *D. frontalis* (Ungerer et al. 1999), it was possible to compare the timing of changes in growth and tree water use to the general timing of beetle development within a tree. For beetles attacking study trees from 26 June to 4 July 1999, oviposition by colonizing adult females would have occurred from day of attack until ~16 July, larval development of progeny would have occurred from 4 July to 6 August, and emergence of adult progeny from their pupation sites in the outer bark would have been from 28 July to 19 August. Since declines in sap velocity did not occur until mid-August, disruption of tree water balance was apparently irrelevant to the success of attacking adult beetles (departed by mid-July) or developing progeny (pupating in the inert outer bark by early August). This result is contrary to the long-standing hypothesis (Paine et al. 1997) that fungal-mediated disruptions of tree water balance are critical to the attack success of southern pine beetles (but see Klepzig et al. 2001). Fungi did presumably contribute to the disruption of water balance in our study, but at the time when xylem function began to fail, the progeny of attacking beetles would have already departed the trees, and the phloem and cambium would have been so thoroughly girdled that mortality was assured long before effects on sap velocity were observed. This interpretation is consistent with that of Lorio et al. (1995), who indicated that trees may be irreversibly stressed because of attack by southern pine beetle and destined to die, yet continue to transpire for many weeks.

Because our measurements were restricted to a few trees at one site, it is dangerous to generalize from these data alone. However, the timing of declines in sap flow that we measured was consistent with the observation that tree canopies do not change color until many weeks after southern pine beetle attack (Billings and Ward 1984). Photographs taken at our site show that trees displayed little change in canopy coloration until September 13, at least 1 month after reductions in sap velocity were first observed. Our results are consistent, therefore, with those of Ballard et al. (1982) who reported that water stress was not observed in lodgepole pine (*P. contorta* Dougl.) until 8 weeks after pine beetle attack. Presumably the color change of foliage, which is critical for aerial detection of beetle infestations, is a physiological result of failures in xylem function and is a symptom that does not arise until many weeks after effects on growth are observed.

Finally, instruments such as automated dendrometers and sap-flow probes are increasingly being used in combination to better understand how processes of stem increment and whole-plant water relations are coordinated in trees (Downes et al. 1999; McLaughlin et al. 2003; Sevanto et al. 2002; Zweifel et al. 2001). Together, these techniques hold promise as forest scientists move to better document and understand the mechanisms whereby insects like southern pine beetles promote widespread forest mortality. Field experiments that use high-resolution techniques to measure stem increment and sap flow are needed to more rigorously compare the temporal progression of beetle attacks and loss of physiological function in host trees. Such measurements will

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provide much-needed data and mechanistic insights for developing models that better depict the dynamic interactions that undoubtedly exist among pine beetles, host tree physiology, and environmental regulation of defense mechanisms (McNulty et al. 1998; Wilkens et al. 1998).

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