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PHYSIOLOGICAL AND CHEMICAL ECOLOGY

Modified Water Regimes Affect Photosynthesis, Xylem Water Potential, Cambial Growth, and Resistance of Juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae)

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ABSTRACT We modified soil water supply to two groups of juvenile loblolly pines, *Pinus taeda* L., by sheltering or irrigating root systems in early summer or in late summer and measured oleoresin flow (primary defense), net photosynthesis, xylem water potential, and cambial growth throughout the growing season. When consistent significant differences in oleoresin flow and water potentials were detected between treatments, we induced attack by the southern pine beetle, *Dendroctonus frontalis* Zimmermann. Compared with irrigated trees, sheltered trees had lower xylem water potentials, reduced cambial growth, reduced photosynthesis, and reduced resin flow. In terms of response to beetle attack, sheltered trees had fewer attacks and less total gallery constructed, but those beetles that did attack sheltered trees were more successful (50–100% more eggs per attacking pair). However, the success of attacking beetles was generally very low, even in sheltered trees (only three to eight eggs per attacking pair). This performance, along with water deficits that strongly affected tree physiology, growth, and development, indicates that juvenile loblolly pine can make internal adjustments that limit the success of southern pine beetle attack.

KEY WORDS *Dendroctonus frontalis*, drought, plant defense

ENVIRONMENTAL CONDITIONS CAN affect the resistance of plants to herbivores by increasing or decreasing the amount of carbon that is partitioned to defensive functions (Mooney & Chu 1974, Lorio 1986, Bryant et al. 1987). Adverse conditions such as severe drought can reduce plant defense by decreasing the assimilation of carbon needed to synthesize allelochemicals (Christiansen et al. 1987). Severe water deficits, created by trenching and sheltering root systems greatly reduced resistance of mature loblolly pines, *Pinus taeda* L., to attack by southern pine beetle, *Dendroctonus frontalis* Zimmermann (Lorio & Hodges 1968, 1977), but little evidence exists to indicate that the southern pine beetle is dependent on severe drought conditions for successful attack. Although drought may be a precursor for other phytophagous insects (Mattson & Haack 1987), drought conditions are not clearly associated with southern pine beetle outbreaks (Turchin et al. 1991).

Favorable conditions for growth, such as abundant water supply, can also reduce plant defense because growth processes may utilize available energy to the extent that secondary metabolism is minimized (Loomis 1932, Lorio & Hodges 1985, Lorio & Sommers 1986). Recent evidence suggests that moderate water deficits may increase plant resistance to herbivory (Conner 1988, McQuate & Conner 1990a, b; English-Loeb 1989, Ross & Berisford 1990). Mechanisms that explain this increased resistance are not understood. Under moderate water deficits, plants maintain relatively high rates of photosynthesis (Brix 1962, Luxmoore 1991) but experience substantial reduction in vegetative growth (Hsiao 1973). This reduction in plant growth leads to a surplus of available carbon that may be shunted into increased allelochemical synthesis (Loomis 1932, Lorio 1986, Reddy & Das 1988, Charles et al. 1990, Horner 1990, Ross & Berisford 1990, Rhizopoulou & Diamantoglou 1991).

Lorio (1986) proposed a plant physiological concept called growth-differentiation balance (Loomis 1932) as a basis for understanding changes in loblolly pine resistance to colonization by the southern pine beetle. The concept proposes that energy is preferentially distributed

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to growth processes when environmental conditions favor growth (e.g., adequate light, water, and nutrients), and that proportionately more energy is partitioned among differentiation processes (e.g., oleoresin synthesis) when conditions such as moderate water deficits limit growth processes without adversely affecting photosynthesis and translocation.

Initial studies with loblolly pine showed that oleoresin flow from bark wounds, a major resistance factor to attacking southern pine beetles, was highest during late summer when calculated soil water storage was at moderate levels, whereas oleoresin flow was lowest in late spring through early summer when soil water was plentiful and trees were growing rapidly (Lorio & Sommers 1986). Subsequently, a conceptual model of the seasonal change in pine resistance (based on resin flow from bark wounds) to southern pine beetle attack was proposed and tested, but tests did not include inducing beetle attacks (Lorio et al. 1990).

Juvenile pines may not be considered ideal food and habitat for the southern pine beetle, but infestation incidence in young plantations is common during outbreaks. With an increase in the proportion of pine forests comprising plantations, the frequency of infestations may increase generally in such stands. Our objectives in this study were to manipulate water regimes of juvenile loblolly pine and determine the effects on the interrelations of tree physiological responses, primary defense (oleoresin flow), and induced attack by the southern pine beetle. We modified water supply by sheltering and irrigating root systems, and measured the following tree responses: net photosynthesis, xylem water potential, radial growth, and resin flow from bark wounds throughout the 1990 growing season. When consistent differences in xylem water potential and oleoresin flow were detected between treatments in early August, and then again in late October, we induced southern pine beetle attack and measured tree responses and beetle performance.

Materials and Methods

Study Site and Tree Selection. Investigations were conducted in Grant Parish LA., USA (31° 25′ N, 92° 17′ W), in an 11-yr-old plantation of loblolly pine planted at a spacing of 2.4 by 2.4 m (≈1,682 trees per ha). The predominant soil was similar to Glenmora silt loam, a moderately well-drained, slowly permeable soil, with slow to medium runoff, and with a seasonally perched water table 60–90 cm below the soil surface. Selected trees were of similar above-ground characteristics with an average diameter of 15 cm, 10 m in height, and a live-crown ratio of approximately 50%. Stand basal area averaged 32 m^2 per ha.

Environmental Conditions. Weather conditions were recorded daily 1 km from the study site. Daily maximum and minimum temperatures were measured with a Vaisala ES-120 temperature probe equipped with an Omnidata Easy Logger recording system. Daily precipitation was measured with a Fisher-Porter recording rain gauge.

A two-level soil water balance equation was used to estimate daily soil water storage, daily deficits, and cumulative water deficits, assuming an initial 20 cm of available soil water in sheltered, irrigated, and nontreated soils (Zahner & Stage 1966). Soil water depletion was allowed to equal potential evapotranspiration minus precipitation plus irrigation until soil water was reduced to 67% of storage capacity. Subsequently, depletion was determined by multiplying the ratio of current storage to storage capacity times the excess of potential evapotranspiration over precipitation plus irrigation. This procedure allows for linear depletion over the first 33% of storage capacity, followed by a curvilinear depletion over the remainder of the storage capacity, a reasonable model for the soils at this study site, that have fine sandy loam surface soils and sandy clay loam subsoils (Zahner & Stage 1966).

Treatments. Two groups of 16 loblolly pines were selected, one for an early summer experiment, and the other for a late summer experiment. Eight trees in each group were irrigated and the remaining eight trees had shelters constructed over much of their root systems to impede infiltration of rainfall. Shelters were constructed of wooden frameworks covered with plywood and tarpaper. Labor and costs were minimized by sheltering and irrigating two adjacent trees. Total area covered by each shelter was 4.3 by 7.3 m, which extended ≈1 m past the driplines of the two trees. Shelters were built above the ground (75 cm at their peaks, and 25 cm at their edges). Irrigated trees received water over the same area from a portable tank and soaker hose. Applications averaged 2.5 cm of water/wk.

Shelters for the early-summer experiment were completed on 13 February. Irrigation of nonsheltered trees began on 25 June when soils were at 46% of field capacity (≈10 cm). Late-summer experimental shelters were completed on 13 June and irrigation of non-sheltered trees began on 29 August. Trees in the late-summer group experienced ≈2 mo of drought before irrigation.

Physiological and Defensive Measurements of Trees. At ≈2-wk intervals on relatively cloud-free days, we measured xylem water potentials, net photosynthesis, and resin flow. To measure xylem water potential, branch samples were excised from the upper midcrown by pole pruner, placed in a plastic bag, and measurements were completed within 3 min. Ginn et al. (1991) reported photosynthetic rates of needles were not affected by removal from the tree for up to 30 min. Extreme care was taken to sample branches from the same general position within each tree's canopy. Xylem water potential was measured at predawn (0500–0600 hours), midmorning (1000–1100 hours), and at solar noon (1230–1330 hours) with a pressure chamber (PMS Instruments, Corvallis, OR) and expressed as megapascals (MPa). Tree damage was minimized by sampling alternate trees at 2-wk intervals (four trees per treatment per sampling date).

Net photosynthesis was measured at midmorning from two fascicles of fully expanded secondary needles excised from the same branch used to measure xylem water potential. Measurements were made with a portable infrared gas analyzer using a closed system and a quarter-liter chamber (model LI-6200; LICOR, Lincoln, NE). For the early-summer experiment, 1-yr-old needles were used; for the late-summer experiment, current-year needles were used. Net photosynthesis was expressed per unit leaf area (Johnson 1984).

Beginning at 0800 hours on each sampling date, oleoresin yield was measured over 24 h by making a wound with a 1.3-cm-diameter arch punch down to the face of the xylem and collecting resin in plastic vials for 24 h (Lorio et al. 1990). Samples were collected at points 1 and 3 m above the ground on opposite sides of the tree ($n = 4$ per tree) and yield was determined to the nearest 0.1 ml. Wounding effects were minimized by offsetting each new collection site ≈5 cm horizontally to the right and 2.5 cm vertically up the bole.

Tree Radial Growth. Tree radial growth was measured with aluminum dendrometer bands equipped with steel springs, which were installed around the circumference of each tree at 2 m above ground (Liming 1957). Growth increment was recorded at weekly intervals to the nearest 0.25 mm.

Attack and Colonization Assessment. When measurements of xylem water potential and photosynthesis were significantly different between treatments for 30 consecutive d, southern pine beetle attacks were induced. For the early-summer experiment, beetle attacks were induced on 11 August (day 222), and for the late summer experiment, on 27 October (day 298). Trees were baited with frontalin (aggregation pheromone) and commercial grade turpentine. To ensure an adequate population of beetles, logs of loblolly pine with emerging adult beetles and late-stage pupae were placed on the site. Attack progress was assessed daily by visually counting the number of pitch tubes. We allowed trees to be colonized for 13 d in August and 25 d in October and November, primarily because of differences in air temperature.

Trees were felled, and the 2.5-m section of the main stem extending from 1 to 3.5 m above the ground was taken to the laboratory and stored at 5°C. Beetle colonization success was determined from four areas (10 by 50 cm) of inner bark. Samples were from opposite sides of the bolt taken at center points of 1 and 2 m from the base of the cut bolt. Pitch tubes and entrance holes without resin were counted (number of attacks) by careful dissection of the outer bark, then the living bark was carefully cut away with a filet knife to expose the galleries. Number's of live and dead beetles (usually embedded in dried resin) were counted. Egg niches were counted with the aid of a magnifying lens and marked individually by pen. Galleries were traced onto sheets of mylar and their total lengths (cm) were measured with an electronic planimeter (Dunn & Lorio 1992).

Statistical Analysis. All southern pine beetle colonization data were evaluated using analysis of variance (ANOVA). Tree physiological measurements and resin data were analyzed by t tests. Duplicate measurements of physiology and southern pine beetle colonization taken from each tree were averaged before analysis so that trees rather than measurements were replicates. Repeated measures ANOVA was not considered appropriate, given that different subsets of trees were sampled sequentially.

Results

Environmental Conditions and Xylem Water Potentials. *Early Summer Experiment.* Rainfall during the late winter and spring was extremely high (102 cm from January through May) (Fig. 1). By 25 June (day 176), when irrigation began, calculated soil water storage was reduced to 2.3 cm for sheltered and 9.2 cm for nonsheltered trees. Significant treatment differences in xylem water potentials were first observed on 19 July (day 200) and were evident throughout the remainder of the experiment (Fig. 2). At the time of induced southern pine beetle attack (day 222), soil water storage was 0.7 cm for sheltered trees and 9.1 cm for irrigated trees. With the onset of drought in mid-June and the start of irrigation, consistent differences in xylem water potential were established between treatments (Fig. 2). Mean differences in xylem water potential between treatments ranged from 0.2 to 0.4 MPa ($P < 0.01$) for ≈30 d before beetle attacks were induced. Predawn xylem water potential remained at −0.4 and −0.5 MPa in irrigated trees throughout the sampling period (April–August). In contrast, predawn xylem water potential values of the sheltered trees decreased from −0.4 MPa early in the season to <−0.8 Mpa on day 226. These responses closely follow changes in calculate soil water balance (Fig. 1).

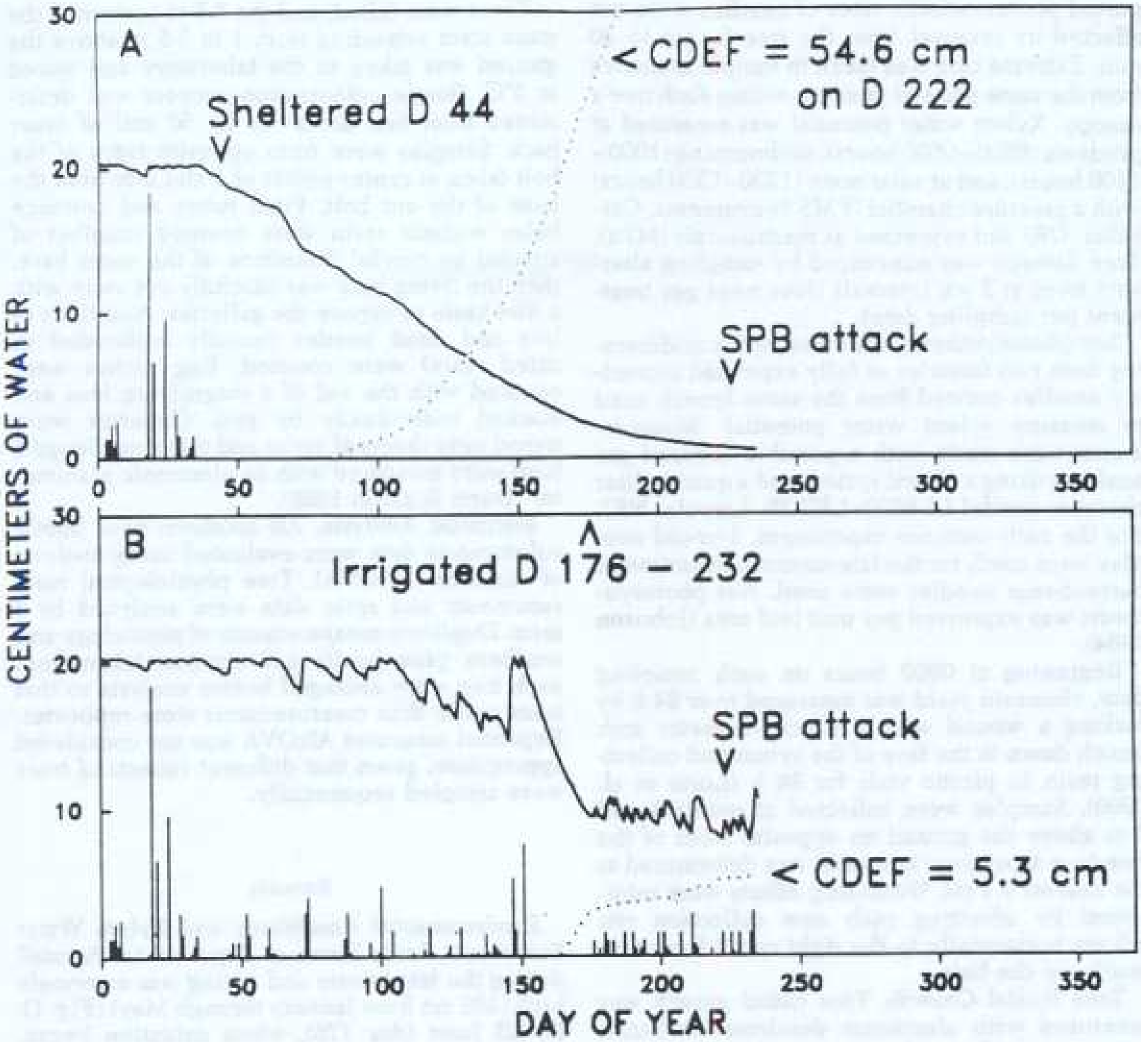

Fig. 1. Calculated water balance for the early-summer experiment through day 235, when all trees were cut and sampled for success of southern pine beetle (SPB) attack in 1990 near Alexandria, LA. Field capacity for the top 1.5 m of soil is estimated to be 20.3 cm (8 in). (A) For the sheltered treatment, daily precipitation (vertical bars) is shown until day 44, when shelters were completed, cumulative daily deficits (CDEF) until day 222, when southern pine beetle attack was induced, and soil water storage until day 235. (B) For the irrigated treatment, daily precipitation is shown until day 176, after which irrigation is also shown. CDEF and soil water storage are shown until day 235. See text for a description of the procedure for calculations (Zahner & Stage 1966).

Late-Summer Experiment. Trees in both treatments experienced ≈60 d of severe soil water deficit before irrigation of nonsheltered trees (Fig. 3). Results from a single sampling date (day 192) before irrigation failed to detect any statistical differences in xylem water potential, radial growth, or net photosynthesis between treatments (data not shown). Irrigation plus late-season rainfall quickly increased the amount of soil water under nonsheltered trees. Subsequently, xylem water potential became significantly lower in sheltered trees with average differences of 0.2 MPa for ≈40 d before beetle attack (Fig. 4). At the time of attack (day 298), there was an extremely large difference in soil water storage between sheltered and irrigated trees (Fig. 3).

Photosynthesis. *Early-Summer Experiment.* No differences in rates of net photosynthesis were detected between treatments during the wet spring. However, beginning in early July (day 183) photosynthetic rates were significantly higher in irrigated than in sheltered trees (Fig. 5A). Throughout the remainder of the sampling period photosynthetic rates were 30–60% lower in sheltered than in irrigated trees.

Highest rates of net photosynthesis were measured early in the season when soil water was plentiful, temperatures were warm, and evapora-

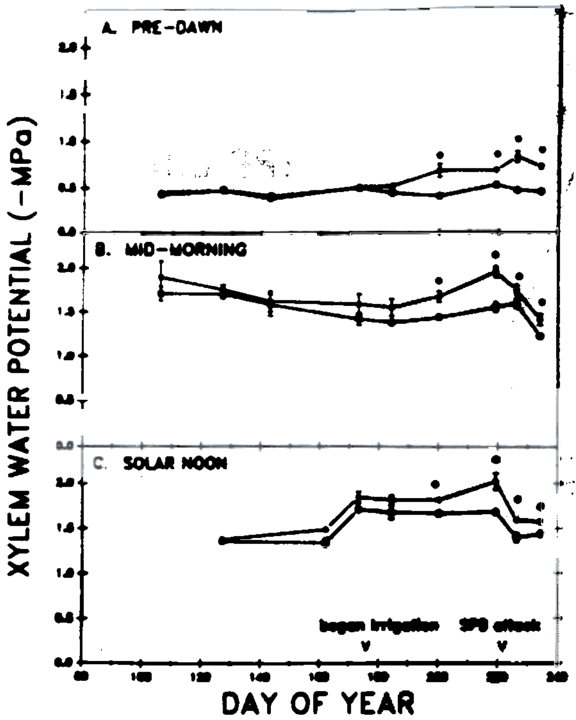

Fig. 2. Seasonal course of xylem water potentials of sheltered (filled circles) and irrigated (open circles) loblolly pines in the early-summer experiment expressed as megapascals (MPa). (A) Predawn; *, $P < 0.01$. (B) Midmorning; *, $P < 0.01$. (C) Solarnoon; *, $P < 0.02$

tive demands were low. Rates were lowest when soils were very dry, temperatures were hot, and evaporative demands were high. Both irrigated and sheltered trees showed a seasonal reduction in net photosynthesis, but irrigated trees declined only about 20% from their early-season rates compared with a 50% decline in sheltered trees.

Late-Summer Experiment. Net photosynthetic rates were significantly lower in sheltered trees compared with irrigated trees (Fig. 6A), but rates in sheltered trees were relatively high compared with trees in the early-summer experiment. At the time of beetle attacks, sheltered trees were experiencing less stress than that experienced by sheltered trees in the early-summer group. However, all trees in the late-summer experiment experienced a long period of accumulating water deficits (Fig. 3).

Tree Radial Growth. *Early-Summer Experiment.* Radial growth was significantly greater in irrigated trees compared with sheltered trees, but only after the onset of irrigation; however, after the early response to irrigation there was a negative trend in growth (Fig. 5B). During the early wet season, sheltered trees actually grew faster than the nonsheltered trees, but differences were not significant.

Late-Summer Experiment. Radial growth was significantly lower in the sheltered trees during five of seven weekly sampling dates following irrigation and before southern pine beetle colonization (Fig. 6B).

Resin Flow. *Early-Summer Experiment.* Flow of oleoresin from sheltered trees was lower than from irrigated trees throughout the study, but the differences became significant only after the start of irrigation on day 184 (Fig. 5C). At the time of initial beetle attack (day 222), resin flow averaged 4.1 ml for the irrigated and only 1.5 for the sheltered trees. During beetle colonization, resin flow increased by 66% in the irrigated trees, and by 76% in the sheltered trees. This indicated that all trees, regardless of their soil water status, rates of photosynthesis, and xylem water potential, were resisting beetle attack strongly.

Late-Summer Experiment. Before southern pine beetle attack, resin flow from irrigated trees was slightly higher than from sheltered trees, but differences were not significant (Fig. 6C). Resin flow rates increased dramatically upon beetle attack, but in contrast to the early summer experiment, the increase was mostly in irrigated trees. Resin flow did not increase in three nontreated, nonattacked trees that were sampled for resin flow during this period (data not shown).

Beetle Attack and Colonization Assessment. *Early-Summer Experiment.* There were twice as many beetle attacks in irrigated compared with sheltered trees, and twice as many dead adults were found in irrigated trees, thus the proportion of dead beetles to number of attacks was almost identical for both treatments (Table 1). There was a strong significant relationship, however, between mean resin flow and number of dead beetles for both treatments ($r^2 = 0.84$; df = 1, 14; $P < 0.01$). Number of live beetles (successful colonizers) and number of eggs did not differ significantly between treatments, but there were 48% more eggs per attack in sheltered than in irrigated trees (4.3 versus 2.9).

Late-Summer Experiment. Significantly more southern pine beetles (≈30%) attacked irrigated than sheltered trees (Table 2). There were no differences in the number of live beetles between treatments, but there were twice as many dead adults in irrigated trees as in sheltered trees. Consequently, irrigated trees had a higher proportion of dead beetles to number of attacks than did sheltered, but proportions for both treatments were much less than in the early-summer experiment. As in the early-summer test, there was no significant difference between treatments in the number of eggs oviposited, but the number of eggs per beetle attack was 108% higher in sheltered trees (7.9 versus 3.8).

Resinous gallery length comprised 21% of total gallery length in sheltered trees and 36% in irrigated trees, considerably less than the 71% and

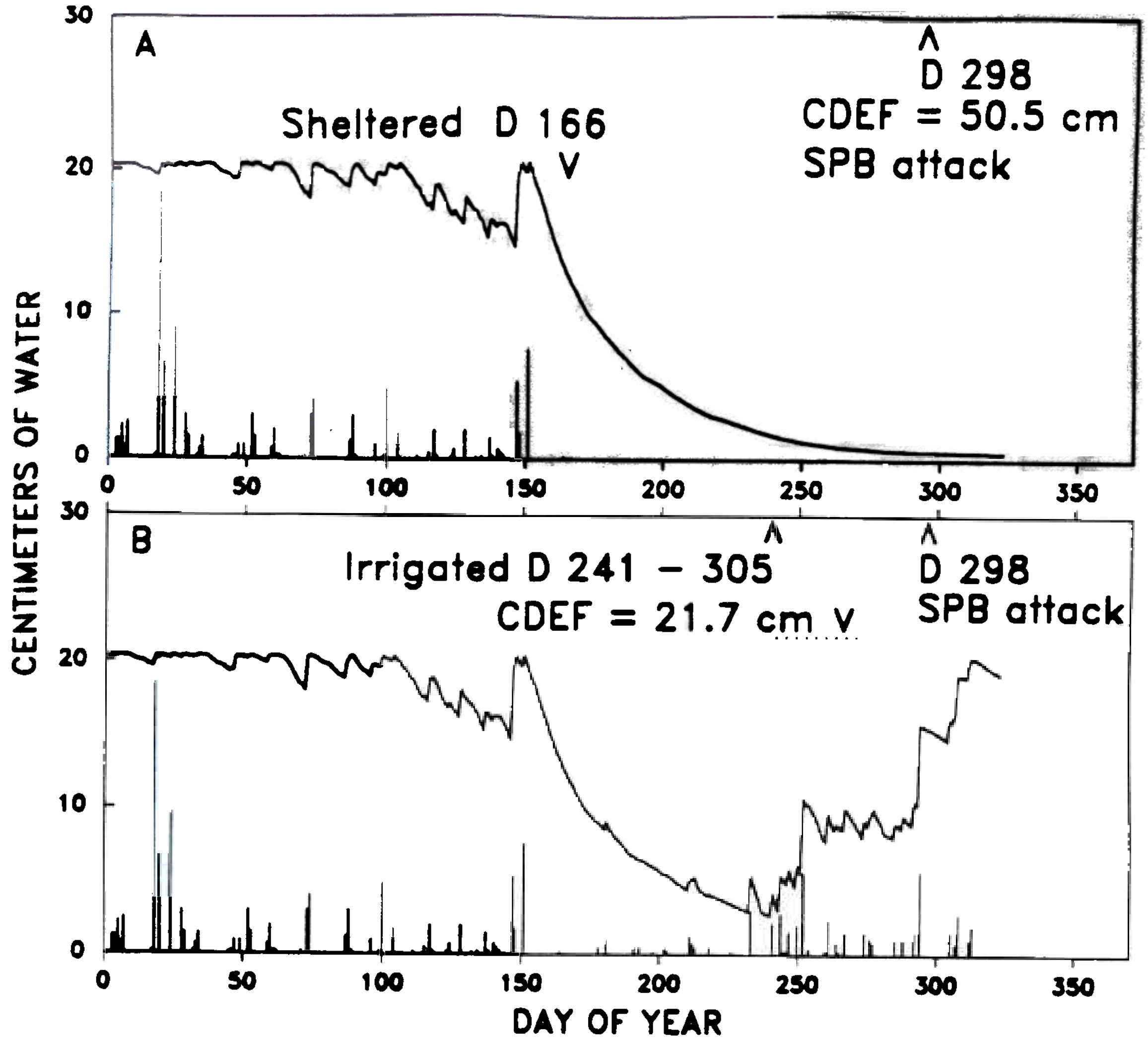

Fig. 3. Calculated water balance for the late-summer experiment through day 323, when all trees were cut and sampled for success of southern pine beetle (SPB) attack in 1990 near Alexandria, LA. Field capacity for the top 1.5 m of soil is estimated to be 20.3 cm (8 in). (A) For the sheltered treatment, daily precipitation (vertical bars) is shown until day 166, when shelters were completed, cumulative daily deficits (CDEF) until day 298, when southern pine beetle attack was induced, and soil water storage until day 323. (B) For the irrigated treatment, daily precipitation is shown until day 241, after which irrigation is also shown. CDEF and soil water storage are shown until day 323. See text for a description of the procedure for calculations (Zahner & Stage 1966).

78% measured for the sheltered and irrigated trees in the early summer experiment.

Discussion

The most impressive results of the study were those from the sheltered trees in the early-summer experiment; these trees sustained severe soil water deficits for >100 d but strongly resisted southern pine beetle colonization. Compared with irrigated trees, sheltered trees had lower xylem water potentials, reduced cambial growth, reduced photosynthesis, and reduced resin flow. In terms of response to beetle attack, sheltered trees had fewer attacks and less total constructed gallery, but those beetles that did attack sheltered trees were more successful (50–100% more eggs per attacking pair). However, the success of attacking beetles was generally very low, even in sheltered trees (only three to eight eggs per attacking pair). This performance, along with the severe water deficits that greatly affected tree physiology, growth, and development, indicates that juvenile loblolly pines can make internal adjustments that limit southern pine beetle attack success.

In the early-summer experiment, sheltering of tree root systems to prevent recharge of soil wa-

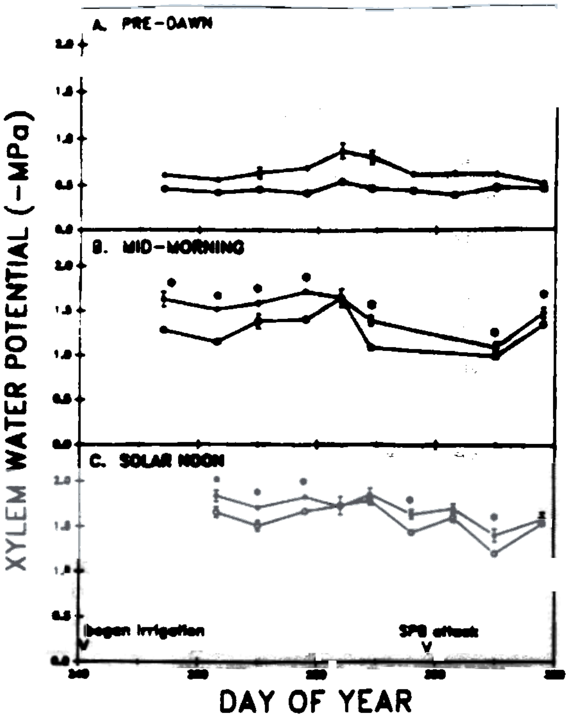

Fig. 4. Seasonal course of xylem water potentials of sheltered (filled circles) and irrigated (open circles) loblolly pines in the late-summer experiment, expressed as megapascals (MPa). (A) Predawn; $P < 0.01$ (all points). (B) Midmorning; *, $P < 0.05$. (C) Solar-noon; *, $P < 0.05$.

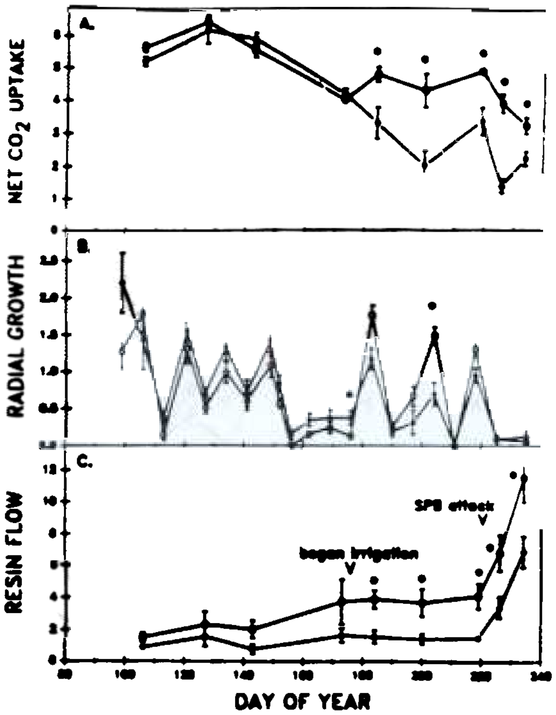

Fig. 5. Seasonal course of three responses of sheltered (filled circles) and irrigated (open circles) loblolly pines in the early-summer experiment. (A) Net photosynthesis, $\mu mol/m^2/s$. (B) Radial growth, mm/wk. (C) Resin flow, ml/24 h. *, $P < 0.05$ in all graphs.

ter resulted in calculated cumulative daily soil water deficits amounting to ≈55 cm just before beetle attack, whereas irrigation to supplement rainfall resulted in only ≈5 cm of cumulative deficits (Fig. 1). Effects of sheltering relative to irrigating were demonstrated by negative effects on water potential, cambial growth, photosynthesis, resin yield, and lower resistance to beetle attack. However, all trees showed a high degree of resistance, indicated by the large proportion of egg galleries filled with resin in trees from both treatments (sheltered, 72% versus irrigated, 78%) (see Table 1). Moreover, when the trees were dissected, the phloem tissues surrounding the galleries were heavily impregnated with resin and oxidized products. Copious amounts of resin flowed from the severed stumps of felled trees. These results indicate that, under the conditions of this study, the water deficits established by sheltering to prevent recharge of soil water did not greatly reduce tree resistance to southern pine beetle attack. However, the clear negative effects of sheltering on net photosynthesis indicate reduced energy levels available for either growth or secondary metabolism (e.g., resin synthesis).

This study does not provide a very satisfactory basis for testing growth-differentiation balance principles. Shelters were designed to induce moderate water deficits, but because of the drought, severe water deficits developed. As a consequence, photosynthesis (carbon) was greatly reduced in the sheltered trees relative to the irrigated trees. The growth-differentiation hypothesis predicts changes in the ratio of secondary metabolism to available carbon (Loomis 1932, Lorio 1986, Herms & Mattson 1992), and in this study, total carbon differed significantly between treatments, confounding any simple evaluation of the prediction. For example, sheltered trees had lower secondary metabolism (lower resin flow), but the ratio of secondary metabolism to total carbon may have been less, more, or the same because total carbon was also less.

In our irrigated treatments we were unable to supply enough water to maintain fully saturated soils; therefore, moderate soil water deficits developed. Based on calculated daily water deficits, the lack of a major impact on net photosynthesis, and a less pronounced decline in cambial growth rate, we judge that the irrigation treatment resulted in proportionately more energy available for both growth and secondary metabolism than with sheltering. We have no treatment results with irrigation adequate to recharge soil water to field capacity (≈20 cm) to compare with our treatment that partially supplemented

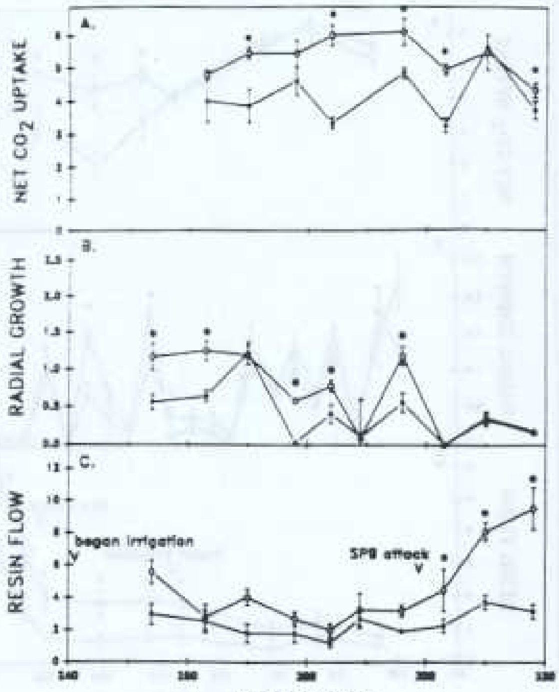

Fig. 6. Seasonal course of three responses of sheltered (filled circles) and irrigated (open circles) loblolly pines in the late-summer experiment. (A) Net photosynthesis, μmol/m^2/s. (B) Radial growth, mm/wk. (C) Resin flow, ml/24 h. *, $P < 0.05$ in all graphs.

rainfall. However, it appears to us that tree responses to treatment and induced beetle attack indicate water deficits were considerably less severe (e.g., little or no effect on photosynthesis) than with sheltering and more severe than would occur with an abundant water supply. Granting this, results agree with expectations based on growth-differentiation balance principles (Loomis 1932) and literature supporting the idea that moderate water deficits increase plant resistance to insect attack (Lorio & Hodges 1985; Lorio and Sommers 1986; Conner 1988; McQuate & Conner 1990a, b; English-Loeb 1989; Ross & Berisford 1990; and others).

In the late-summer experiment, sheltering resulted in calculated cumulative daily soil water deficits amounting to ≈51 cm just before beetle attack, whereas irrigation resulted in ≈22 cm of cumulative deficits, 4 times that of the early summer trial. Sheltering relative to irrigating affected water potential, cambial growth, photosynthesis, and resin yield similar to the earlier trial, the principal differences being that sheltered trees had generally higher net photosynthesis rates and little increase in resin yield following beetle attack. Percentage of resin-filled gallery was low for both treatments (sheltered, 21%; irrigated 36%), and number of eggs per attack was higher (sheltered, 7.9; irrigated, 3.8) than in the earlier test. Results are more equivocal than those of the early-summer test, possibly because of considerable differences in environmental conditions, such that with irrigation, no calculated daily deficits occurred after day 233 (Fig. 3). However, irrigated trees exhibited responses indicating somewhat higher resistance to attack than did sheltered trees.

In this study, juvenile pines demonstrated a great capacity to adjust internal water status. Even after several months of no rainfall (sheltered trees) and extreme heat, mean xylem water potentials were only −0.8 MPa before dawn and 2.0 MPa at solar noon (Fig. 2). A drop in calculated soil water storage from 20 cm in the wet spring to ≈1 cm later in the summer caused only a minor decrease in xylem water potential of twigs (Figs. 1A and 2). This may indicate osmotic adjustment of living tissue in needles and twigs, as well as a decrease in stomatal conductance. The significant drop in photosynthesis of sheltered trees indicates stomatal closure in response to high evaporative demand and low water supply; such a response would lead to reduced transpiration and conservation of water. These results also suggest that photosynthesis is a more sensitive indicator of soil moisture depletion than is xylem water potential in juvenile loblolly pine.

Table 1. Southern pine beetle colonization measurements of sheltered and irrigated loblolly pine after 13 d of attacks induced in August (mean ± SD, n = 8 trees per treatment)

Beetle measurements[a]	Sheltered	Irrigated	*F*	*P*
Attack	6.1 ± 4.5	13.3 ± 5.7	30.9	0.0001
Live beetles	2.6 ± 3.9	3.9 ± 4.4	1.5	0.22
Dead beetles	5.5 ± 4.1	12.2 ± 6.0	27.3	0.0001
Resinous gallery, cm	30.6 ± 20.6	72.2 ± 39.3	28.0	0.0001
Clear gallery, cm	12.2 ± 20.8	20.9 ± 25.8	2.2	0.14
Total galleries, cm	42.8 ± 34.3	93.0 ± 55.0	19.3	0.0001
No. eggs	26.4 ± 28.1	38.0 ± 52.4	1.2	0.27

[a] Data per 500 cm^2 bark surface area.

Table 2. Southern pine beetle colonization measurements of sheltered and irrigated loblolly pine after 25 d of attacks induced in October (mean ± SD, n = 8 trees per treatment)

Beetle measurements[a]	Sheltered	Irrigated	*F*	*P*
Attack	10.0 ± 5.4	14.9 ± 8.1	8.0	0.0006
Live beetles	11.4 ± 7.7	13.3 ± 10.7	0.67	0.42
Dead beetles	3.2 ± 4.7	10.2 ± 7.3	10.7	0.0002
Resinous gallery, cm	14.4 ± 14.8	29.0 ± 23.0	9.1	0.0004
Clear gallery, cm	53.8 ± 49.9	52.5 ± 62.6	0.1	0.93
Total galleries, cm	68.3 ± 58.9	81.5 ± 69.6	0.7	0.42
No. eggs	78.6 ± 96.6	57.2 ± 59.3	1.1	0.29

[a] Data per 500 cm^2 bark surface area.

Dramatic increases in resin flow during beetle attack were unexpected. Because there was no pronounced increase in resin flow before attack, the increased flow during attack may have been caused partially by an induced response to beetle colonization (Dunn & Lorio 1992). Short-term, rapid depletion of soil water has been reported to cause increased resin flow from bark wounds (Lorio & Sommers 1986), but that did not occur in this particular study (Figs. 1 and 3). Further, control trees not attacked by beetles showed no increase in resin flow. Although resin flow often decreases rapidly following mass attack by the southern pine beetle, attack densities in our study were relatively low and may not have been sufficient to rapidly deplete the preformed resin supply and resin synthesized in response to invading beetles or associated microorganisms.

Although attack densities were relatively low, many more beetles were attracted to the higher resin-yielding trees than to trees with lower resin flow in both experiments. It has been suggested that bark beetles are capable of adjusting their population densities and attack rates (Raffa & Berryman 1983), assuming that population levels permit, to overcome increasing tree resistance. The mass-attack phenomenon of the southern pine beetle is particularly well known and documented (Payne 1980). Given that adequate populations of beetles are available, any tree can be overwhelmed, perhaps with considerable mortality of the earliest attacking beetles. However, beetles did not attack our study trees in great numbers and it seems likely that some of them would have survived (47 of 50 neighboring nonstudy trees survived southern pine beetle attacks). In this case the southern pine beetle populations seem to have behaved anomalously by not aggregating in large numbers on the study trees, but because of the copious flow of resin from all attacked trees, early attacks may not have produced the expected secondary attraction. Raffa & Berryman (1983) suggested that conifers are capable of interfering with bark beetle communication by engulfing beetles in resin, but that the effect is inversely related to the number of beetles initiating attacks. It has been reported, however, that pheromone production is prolonged in trees that resist attacking bark beetles with abundant resin flow (Vité & Pitman 1968, Coster & Vité 1972).

The most striking outcome of this study with juvenile loblolly pines was the high level of resistance exhibited by sheltered trees with the imposed soil water deficits. Only four to eight eggs per attacking beetle pair were produced. More moderate water deficits, such as were developed with irrigation to partially supplement rainfall, may have caused increased partitioning of carbon to resin synthesis relative to growth. If so, this would increase resistance relative to conditions of either limited water supply that reduces photosynthesis or abundant water supply that favors carbon partitioning to growth (Loomis 1932). Results also indicate that tree and beetle responses vary considerably through the year, an important consideration in studies of bark beetle tree interactions.

Results with mature trees would likely be different. Aside from the absence of a strong sink (reproductive growth) known to suppress both apical and cambial growth, and the distribution of carbon (Kozlowski 1971), patterns of secondary metabolism and resistance to herbivory may be dramatically different in mature trees compared with juvenile trees (Reichardt et al. 1984). Current studies are investigating the effects of controlled soil-water regimes on the physiology of mature loblolly pines and their resistance to southern pine beetle attack.

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