

Environment and ontogeny modify loblolly pine response to induced acute water deficits and bark beetle attack

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Abstract

We evaluated the impact of tree resistance on within-tree population dynamics of southern pine beetle, *Dendroctonus frontalis* Zimm. (Coleoptera: Scolytidae) in loblolly pine, *Pinus taeda* L., as affected by prevailing water regimes, acute water deficits imposed by applying dry-ice (solid CO₂) collars to tree boles, and by the seasonal ontogeny of pines. We conducted the study in the spring of 1986, when bole cambial growth had not yet shifted from earlywood to latewood formation, and in the summer of 1987, when latewood formation was well advanced. In each year there were five treated and five control trees. In 1986, under relatively well-watered conditions, results did not support the hypothesis that induced acute water deficit will enhance success of southern pine beetle attack and brood production. All trees were readily attacked and overcome with no apparent beneficial effects of the dry-ice treatment on within-tree population dynamics. In 1987, under drier conditions, results supported the hypothesis. Treated trees again were readily colonized, but three of the five control trees resisted attack to the extent that all attacks eventually failed. In 1986, all study trees maintained relatively high water potentials for more than 3 weeks following beetle attack. However, resin yields from bark wounds decreased rapidly. In contrast, water potentials of controls decreased gradually in 1987 and resin yields increased as controls resisted beetle attacks. Water potential of treated trees dropped rapidly 2 weeks after initial beetle attack, and resin yields decreased rapidly, as they did in 1986. Consideration of environmental conditions and ontogenetic stage of host trees is extremely important in attempts to assess the effects of manipulative treatments on tree susceptibility to beetle attacks. Further, they illustrate the dynamic nature of tree resistance to beetle attack in the absence of abnormal stresses. Simultaneous study of environmental conditions, as well as physiological changes associated with ontogeny of trees, can effectively support research on interactions between bark beetles and host trees.

Keywords: *Dendroctonus frontalis*; *Pinus taeda*; Water potential; Growth; Differentiation

1. Introduction

A wide array of abiotic and biotic factors, such as weather (King, 1972; Kalkstein, 1976; Gagne et al., 1980), lightning (Hodges and Pickard, 1971; Coulson et al., 1983, 1986), natural enemies (Linit and Stephen,

1983; Stephen et al., 1988; Turchin et al., 1991), site and stand conditions (Hicks, 1980; Paine and Stephen, 1987a), and host condition (Blanche et al., 1983; Paine and Stephen, 1987b) have long been recognized as important to southern pine beetle (SPB) (*Dendroctonus frontalis* Zimmermann) population dynamics. In recent years the potential effect of host condition on susceptibility to SPB, as affected by environment and

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stage of seasonal growth and development, has received serious consideration (Lorio and Hodges, 1985; Stephen and Paine, 1985; Lorio, 1986, 1988; Lorio and Sommers, 1986; Blanche et al., 1992; Dunn and Lorio, 1992, 1993). The role that mutualistic fungi associated with SPB may play in beetle attack and death of the tree has been re-examined (Bridges et al., 1985; Hodges et al., 1985; DeAngelis et al., 1986; Parmeter et al., 1992). However, detailed studies of tree conditions provide few data to link host conditions to population dynamics of colonizing bark beetles.

The objective of the research reported here was to evaluate the impact of tree resistance on within-tree SPB population dynamics as affected by environment, artificially imposed acute water deficits, and the seasonal ontogenetic growth stage of the trees (e.g. earlywood versus latewood formation). We induced acute stress in trees at a study site where loblolly pine (*Pinus taeda* L.) seasonal growth and development was being studied independently (Lorio et al., 1990). Results from that study in 1984 and 1985 indicated important changes in resin yields from bark wounds through seasons of the year and from year-to-year depending on prevailing environmental conditions. The study continued through 1986 and 1987, and descriptions of the seasonal course of precipitation and characterization of the environmental conditions by use of a soil water balance program (Zahner and Stage, 1966) were available for the study reported here.

Our intent was to determine the extent to which treatment affected the impact of host resistance on specific parameters of within-tree SPB populations. Our general hypothesis was that a treatment to cause acute water deficit within the tree bole would enhance SPB attack success and brood production relative to control trees. A secondary hypothesis was that control trees subjected to SPB attack well after transition to latewood formation, and development of much of the current year's complement of vertical resin ducts, would resist attack more strongly than control trees attacked during earlywood formation.

2. Materials and methods

2.1. Trees and environment

The study was conducted during the late spring of 1986 and the midsummer of 1987 in a 35- to 45-year-

old loblolly pine stand in the Kisatchie National Forest in central Louisiana (latitude 31°25'N, longitude 92°17'W). Trees were similar in mean ($\pm$ SE) diameter at 1.4 m above ground, 39.7 ($\pm$ 0.47) cm, total height, 25.0 ($\pm$ 0.45) m, and live-crown ratio, 37.3 ($\pm$ 1.37)%. The principal soils are Malbis fine sandy loam, a plinthic paleudult, and Ruston fine sandy loam, a typic paleudult, with slopes of 1 to 5% and site index (height at age 50 years) of 27 m for loblolly pine. Available water-holding capacity in the top 1.5 m is estimated to be approximately 20 cm.

Temperature and precipitation data from a USA National Oceanic and Atmospheric Administration station about 11 km from the study site were used to calculate Thornthwaite monthly soil water balance for long-term (1951–1980) average conditions, and for the two study years (Thornthwaite and Mather, 1957). Zahner and Stage's (1966) two-level soil water balance program was used to calculate daily soil water storage, daily deficits, and cumulative daily deficits, using temperature from the same weather station and precipitation from a recording rain gauge located about 1 km from the study site. Soil water depletion was allowed to equal potential evapotranspiration (PE) minus precipitation (P) until soil water was reduced to 67% of storage capacity, followed by a curvilinear depletion over the remainder of storage capacity $[(PE - P)(\text{soil water storage})/(\text{storage capacity})]$, which is a reasonable model of the depletion pattern for loam soils.

2.2. Treatments

Following an approach used by Moeck et al. (1981), we reduced water potential in five trees by installing cardboard collars filled with solid pellets of CO₂ (dry ice) and sealed around the lower boles as described in detail in Stephen et al. (1988). Another five trees were used as controls. In 1986 the treatment was applied on 27 May and dry ice was replenished each morning through 2 June. In 1987 dry ice was first applied on 29 July and replenished daily through 5 August. Xylem temperatures were measured only in 1987. Thermocouples placed about 5 cm into the xylem reached 0°C and below on 31 July and remained so through the last day of treatment. In 1987, to improve heat conduction from the interior of tree boles to dry-ice collars, four 19-mm diameter, solid aluminum rods were inserted in pre-

drilled 20-mm holes, to the center of each treated tree within the zone to be collared with dry ice. Rods were spaced at 90° horizontally around the tree bole and extended about 8 cm beyond the outer bark, and were covered by the collar.

2.3. Inducing SPB attacks

One packet of synthetic pheromone, a frontalure attractant mix (Copony and Morris, 1972), was stapled on each study tree at 4–5 m above ground on 29 May 1986 and on 30 July 1987. A window trap (Southwood, 1978), equipped with a funnel attached to a jar containing ethylene glycol, was placed on each tree in the vicinity of the pheromone packet and monitored daily to determine the number of SPB responding to the pheromone and to natural attraction produced as SPB attacked the trees. Pheromone baits were removed at the end of the freezing treatments.

SPB-infested tree sections (bolts), containing brood adults ready to emerge, were transported to the study site from remotely located infestations to ensure an adequate population to challenge study trees. In some cases only the bark, containing pupal and callow adult stages of SPB brood, was placed near the study trees. In 1987 additional infested material was imported into the study area because it appeared that insufficient SPB were attacking study trees to allow assessment of treatment effects.

2.4. Tree measurements

Tree water potentials were assessed by use of a Plant Moisture Stress^a pressure chamber (Ritchie and Hinckley, 1975). Twigs were obtained from the upper portion of tree crowns by shooting them from the canopy with a 22-caliber rifle equipped with a telescopic sight. Twigs were placed in plastic bags immediately after retrieval and were prepared and placed in the pressure chamber for measurement of water potential within 2–3 min. The pressure required to force water within the vascular tissue to the surface of the cut stem was measured to the nearest 0.01 Mpa (0.1 bar).

Oleoresin yields from bark wounds were determined for study trees over short time intervals in both 1986

and 1987 as described by Lorio et al. (1990). In addition, data from another study being conducted in the same area were used to compare resin yields between years in relation to precipitation patterns and soil water balance calculations.

2.5. SPB population sampling and data analysis

All treated and control trees were intensively sampled to estimate densities of SPB attacks, eggs, immature brood, and emerging brood. The sampling process also permitted estimation of stage-specific mortality, parent adult re-emergence, natural enemy density, parent adult gallery length, and the number of eggs and amount of gallery produced per female beetle (Stephen and Taha, 1976). The basic sample unit was a 100-cm² bark disk, and all density estimates are expressed in those units.

Samples to estimate density of attacking SPB beetle adults and amount of parent adult gallery were taken after mass attack was complete, eggs had been deposited, and first stage larvae had eclosed. Ten samples were collected on each tree between 6 and 8 m above ground level. SPB egg density was estimated from the same samples collected for estimation of attack densities.

After mass attack was completed, density of re-emerging parent adults was estimated from ten, 100-cm² emergence traps (McClelland et al., 1978) placed on tree boles between 6 and 8 m above ground. Sampling the density of SPB late-stage brood was accomplished by cutting and removing ten, 100-cm² bark disks from the sampling region of the tree when brood were in the late larval to callow adult stages of development. These samples were also used for estimation of SPB natural enemy densities.

In 1986, the density of emerging brood adults was estimated from ten, 100-cm² emergence traps (McClelland et al., 1978) which were placed at a height of 6–8 m at the time of sampling for late stage brood. In 1987, the trees were felled when beetles had reached a late stage of brood development, and bolts approximately 30 cm long were cut and returned to the lab for rearing of brood adults. Only two control trees were sampled because detailed examination in the field confirmed that no brood was produced in three of the controls.

^aTrade names and company names are included to identify equipment and materials used and do not constitute endorsement by the USDA.

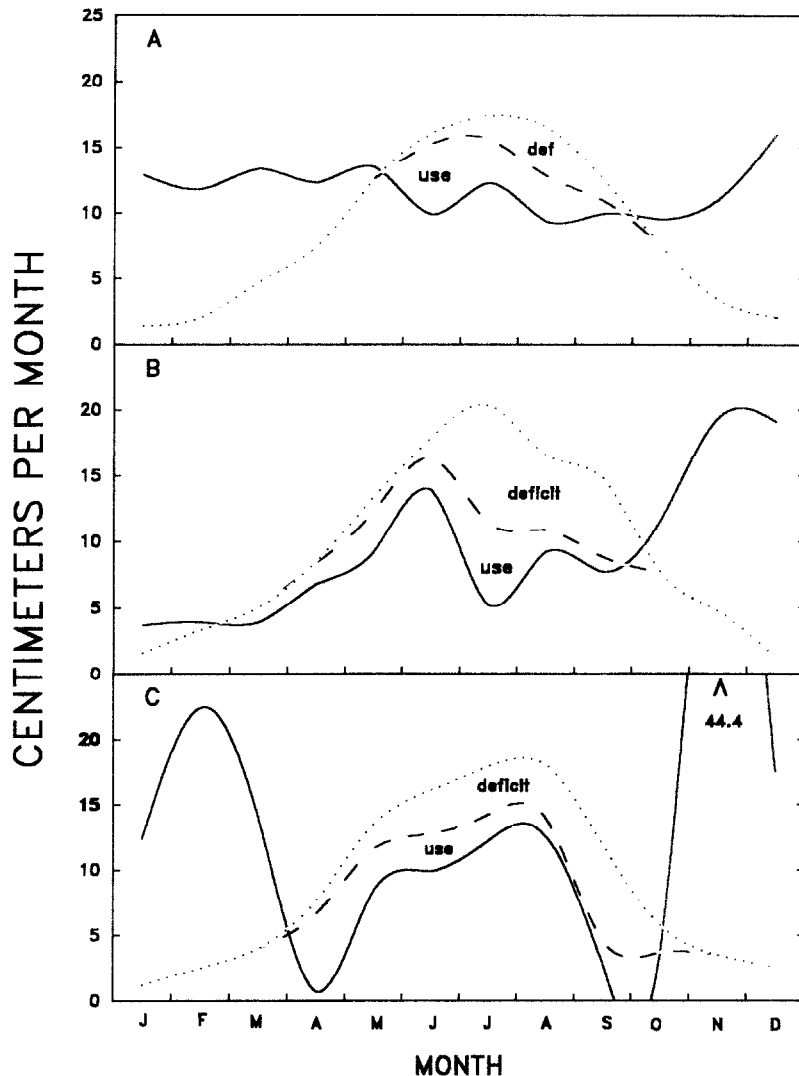


Fig. 1. Calculated monthly soil water balance (Thornthwaite and Mather, 1957) based on precipitation (solid line), and potential evapotranspiration (dotted line). When precipitation is less than potential evapotranspiration, actual evapotranspiration (dashed line) is calculated as the sum of precipitation and the amount of water supplied by the soil. The difference between potential and actual is shown as a deficit. (A) Average for 1951 through 1980 at Alexandria, La.; (B) average for 1986; (C) average for 1987.

2.6. Sample analysis

Parent adult galleries were measured on all ten bark disks from each tree. The length of gallery containing crystallized resin was recorded. On a randomly chosen half of the sample disks galleries were dissected with the aid of a dissecting microscope, and all egg niches, dead eggs, and first stage larvae were counted. The same ratio of eggs to gallery length was assumed for

the half of the sample disk that was not dissected, and totals for the entire disk were calculated by doubling the measured value. Attacks (successful and unsuccessful) were located and identified on the entire sample using the techniques described in Linit and Stephen (1978). Density of attacking adults was estimated as the density of successful attacks times two (assumes one female and one male per attack). Samples collected to estimate density of immature brood and natural ene-

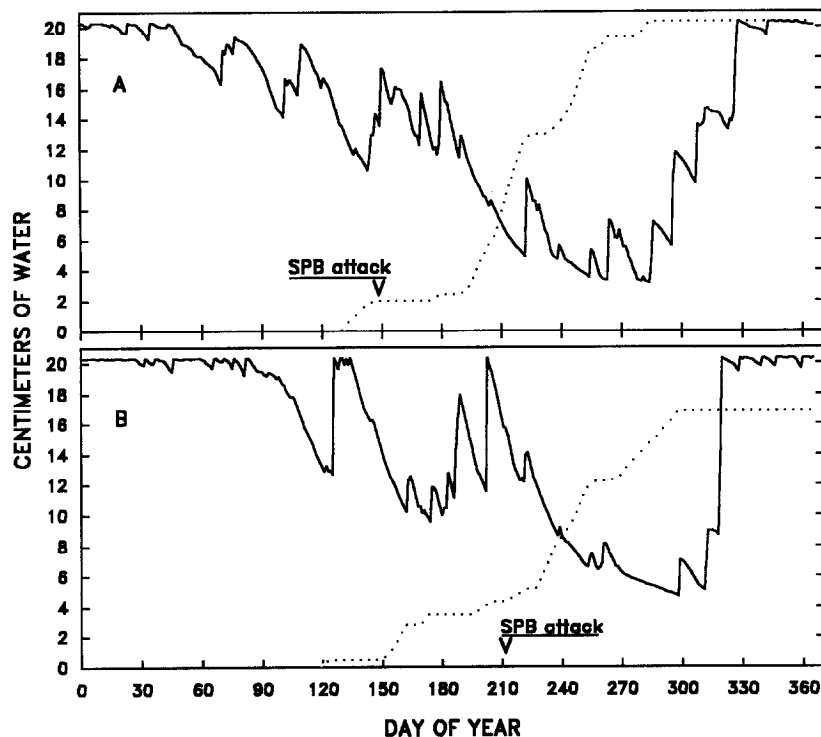


Fig. 2. Daily calculated soil water storage (solid line) and cumulative daily water deficits (dotted line) for (A) 1986 and (B) 1987. Times of treatment and induced SPB attack are indicated for each year. Note that in 1986 little deficit accumulated before or for more than a month after beetle attack, and that in 1987 soil water depletion was rapid and daily deficits accumulated regularly during the study. See text for more on calculation of daily soil water balance (Zahner and Stage, 1966).

mies were radiographed and interpreted by experienced personnel.

In 1986, estimates of SPB brood emergence were made from field-collected trap data; however, problems with trap installation and stability led us to change rearing methods. In 1987, rearing of adults was conducted in the lab using field-collected bolts (see above). Sections of the bolts with a mean of 2734 cm² of infested bark were isolated and individually screened for rearing of brood adults (Goldhammer et al., 1990). This rearing technique insured good survival of brood and complete trapping of all emerging beetles.

2.7. Data analysis

All statistical analyses were conducted using SAS (SAS Institute Inc., 1985). Seventeen count or calculated variables resulted from interpretation of the samples collected. Tests for normality indicated a need for transformations, so count data were subjected to square

root transformation, ratios to log transformation, and rates to logit transformation prior to statistical analysis.

A two-way analysis of variance (PROC GLM) was conducted to evaluate the effects of year, treatment, and year $\times$ treatment interaction. The error term incorporated only the tree-to-tree variation rather than including sample-to-sample variation along with tree-to-tree variation. The effect of year with treatment was not significant, so the two-way ANOVA was repeated with the interaction term deleted. Additionally, all variables demonstrating no significance for any effect were deleted from this analysis, and variance associated with them was not pooled in the error term. With one exception, there appeared to be no treatment effect in this step of the analysis (i.e. the year effect overwhelmed any treatment effect). The data were then partitioned by year because year was highly significant, and a one-way ANOVA was conducted for all variables for each year to determine treatment effect within a single year.

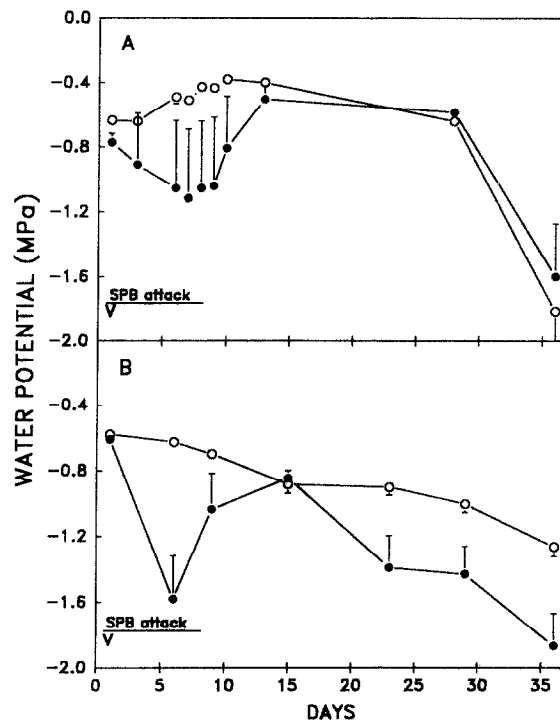


Fig. 3. Average morning xylem water potentials in megapascals (1 Mpa = 10 bars) for (A) 1986 and (B) 1987. Treated trees (filled circles) lost water potential rapidly during dry-ice application, (days 0 through 6 in 1986, and days 0 through 7 in 1987). Control trees (open circles) maintained relatively high water potentials for nearly 1 month after beetle attack. Beetle attacks were induced on day 1 in both years. In some cases symbols hide standard error bars.

Analyses of data from pheromone traps were primarily graphical with mean values and standard errors for dates plotted. Environmental data are presented graphically. Water potential, and resin yield data are also presented graphically with date means and standard errors plotted.

3. Results

Calculated monthly soil water balances (Thornthwaite and Mather, 1957) for long-term average conditions at Alexandria, LA (1951–1980), and for 1986 and 1987 are presented in Fig. 1. Long-term average rainfall is uniformly distributed throughout the year, with December having the highest average (Fig. 1(A)). Potential evapotranspiration reaches a maximum in July, but the largest calculated deficit of soil water supply occurs in August. Neither of the study years was similar to long-term average conditions, and

the water balance for both years differed considerably from each other (Figs. 1(B) and 1(C)). Very little water deficit occurred before and immediately following initiation of the study in late May 1986, whereas considerable water deficits accumulated prior to and immediately following initiation of the study in late July 1987.

Daily soil water storage and cumulative soil water deficits, calculated with a soil water balance program (Zahner and Stage, 1966), provide more detailed information (Fig. 2), and indicate that wet conditions prevailed during the course of the study in 1986 (Fig. 2(A)), whereas drying conditions prevailed in 1987 (Fig. 2(B)).

Xylem water potentials for 1986 and 1987 are presented in Figs. 3(A) and 3(B), respectively. In both years the treatment decreased water potentials dramatically compared with control trees through about the first 10 days. All trees were being attacked by SPB during this period. In 1986 water potentials of control

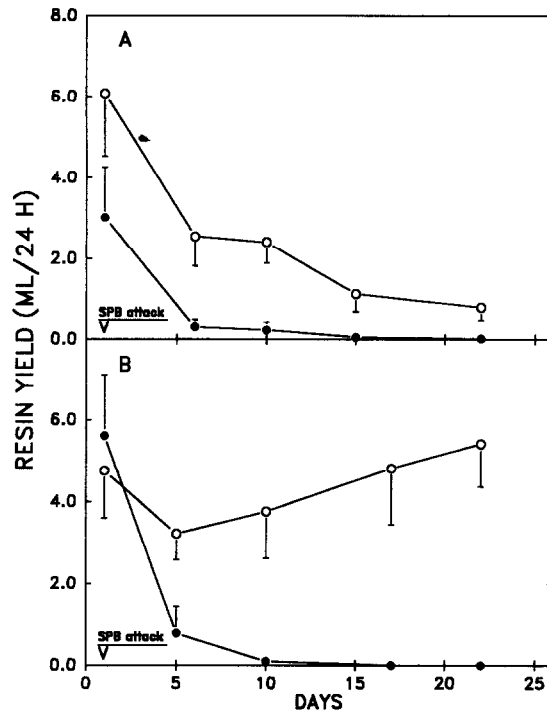


Fig. 4. Average resin yields for (A) 1986 and (B) 1987. Resin yields of treated trees (filled circles) dropped rapidly following dry-ice treatment and beetle attack in both years; however, note that resin yields of controls (open circles) in 1987 increased steadily following a decrease from day 1 to day 5. In some cases symbols hide standard error bars.

trees actually increased for 14 days following initiation of SPB attack. In 1987 water potentials of control trees gradually decreased following SPB attack, suggesting

a drying trend as indicated by the daily soil water balance calculations (Fig. 2(B)). In the absence of the freezing treatment, no dramatic changes occurred in tree water potentials up to 30 days following SPB attack.

Resin yields in 1986 and 1987 for treated and control trees from just before treatment and following induced SPB attack are shown in Figs. 4(A) and 4(B), respectively. In 1986 both treated and control trees responded to SPB attacks similarly, with resin yields decreasing rapidly following SPB attack, even though water potentials of control trees remained high (Fig. 3(A)). In contrast to 1986, resin yields in 1987 decreased temporarily in control trees, but then increased steadily up to 22 days (duration of measurements) after induced attack (Fig. 4(B)) while water potentials steadily decreased (Fig. 3(B)). In both 1986 and 1987 treated trees yielded little resin following treatment and induced SPB attack.

Results of window-trap catches of females and males for individual trees and the average numbers of

Table 1
Average daily catches of female and male southern pine beetles in 1986. Data are means and $\pm$ standard deviation

Date	Female		Male	
	Treated	Non-treated	Treated	Non-treated
May 29	0.8 (0.45)	2.0 (1.87)	6.2 (3.70)	9.4 (8.02)
30	0.2 (0.45)	0.0 (1.00)	0.6 (0.89)	0.2 (0.45)
31	2.0 (2.12)	0.6 (0.55)	11.2 (8.11)	12.8 (6.38)
June 1	3.2 (3.27)	7.4 (5.13)	16.6 (10.45)	22.6 (14.54)
2	11.2 (5.76)	9.0 (5.96)	23.6 (11.99)	19.4 (11.97)
3	11.0 (10.44)	10.8 (6.83)	12.4 (12.76)	15.8 (9.58)
4	4.4 (4.16)	3.2 (1.30)	12.2 (12.09)	8.6 (1.82)
5	2.6 (2.61)	2.2 (1.79)	3.8 (4.92)	2.4 (1.67)
6	0.8 (1.30)	0.2 (0.45)	1.6 (2.07)	1.2 (2.68)
7	1.0 (2.24)	0.6 (1.34)	0.8 (1.79)	2.8 (6.26)
8	0.2 (0.45)	0.0 (0.00)	0.4 (0.89)	2.4 (1.67)
9	0.4 (0.89)	1.2 (0.84)	0.4 (0.89)	1.2 (1.10)

Table 2

Average daily catches of female and male southern pine beetles in 1987. Data are mean and $\pm$ standard deviation

Date	Female		Male		
	Treated	Non-treated	Treated	Non-treated	
July	31	2.2 (2.28)	2.4 (1.52)	12.0 (6.20)	9.8 (8.07)
August	1	0.0 (0.00)	1.0 (1.73)	7.2 (10.18)	7.8 (6.91)
	2	1.6 (2.07)	1.8 (1.64)	8.0 (6.96)	8.2 (4.92)
	3	4.2 (0.84)	3.0 (1.00)	7.8 (4.76)	11.8 (6.76)
	4	1.8 (1.64)	4.0 (2.83)	7.0 (3.94)	9.6 (9.91)
	5	6.2 (2.59)	9.0 (4.06)	19.4 (12.18)	27.6 (17.08)
	6	7.8 (4.32)	14.8 (6.76)	23.4 (6.54)	22.2 (5.89)
	7	4.8 (3.83)	11.8 (5.40)	19.2 (9.68)	30.6 (14.42)
	8	5.8 (1.92)	9.8 (4.97)	12.6 (5.41)	19.0 (9.19)
	9	6.0 (2.55)	5.6 (3.05)	10.8 (6.06)	13.6 (10.26)
	10	5.2 (4.49)	8.0 (1.58)	11.6 (2.88)	11.0 (5.52)
	11	8.8 (3.56)	8.2 (5.26)	27.4 (10.33)	14.8 (9.73)
	12	9.5 (6.81)	9.4 (4.98)	20.5 (13.82)	19.2 (15.61)
	13	4.2 (2.86)	17.4 (8.99)	49.2 (39.82)	44.2 (25.52)
	14	9.4 (2.88)	16.8 (9.83)	35.8 (3.96)	38.2 (23.70)
	15	1.4 (2.07)	7.6 (4.93)	3.0 (4.00)	8.8 (7.60)
	16	0.6 (0.55)	7.0 (5.15)	1.6 (0.89)	9.2 (6.87)
	17	0.2 (0.45)	5.2 (5.89)	1.2 (1.79)	5.2 (4.32)
	18	0.2 (0.45)	1.0 (1.00)	0.2 (0.45)	2.8 (2.68)

females, males, and total beetles for each tree are presented in Table 1 for 1986 and in Table 2 for 1987. Daily means and standard errors of total beetles trapped per tree and by treatment within each year are shown in Figs. 5(A) and 5(B).

Tests of statistical significance at $P < 0.10$ increased detection of variables potentially affected by the treatments. However, tests at that level of probability indicated only two of the 17 attack or colonization variables examined differed between control and treated trees in 1986 (Table 3). Egg density (eggs laid per centimeter of gallery constructed) was higher in treated trees; and there were also greater numbers of miscellaneous insects in the bark samples taken to determine the number of late larval instars and pupae in those trees (Table 3). There were no differences between treatment and control trees in the parameters associated with the attack process.

Some differences were indicated in 1987 (Table 4), most notably associated with the early stages of attack. The number of unsuccessful attacks, length of resinous gallery, and total gallery length were reduced in the control trees (Table 4). The number of emerging progeny was also higher in the two control trees that actually

produced brood, while the number of miscellaneous insects was greater in the treated trees.

4. Discussion

Calculated monthly soil water balance data show how greatly environmental conditions differed in the 2 years of study, and how much each year differed from the long-term average (Fig. 1). In 1986, based on the calculated daily water balance, the study was initiated and carried out under well-watered conditions, with frequent showers during June keeping stored water above 12 cm, about 60% of available, through most of June (Fig. 2). However, in 1987, the study was carried out following several months of gradually accumulating moderate water deficits (Figs. 1(C) and 2(B)). Rainfall sufficient to recharge soil to field capacity occurred on day 203 (22 July). Rapid depletion reduced storage to 16 cm (80% of available) by day 210 (29 July), when treatments were applied (Fig. 2).

Table 3

Population parameters for Southern Pine Beetle in 1986

Variable	Treated			Control		
	n	Mean	SE	n	Mean	SE
Successful attacks	50	5.4	0.50	50	4.9	0.27
Unsuccessful attacks	50	0.4	0.11	50	0.4	0.11
Total gallery length (cm)	50	62.2	3.21	50	61.8	2.10
Resinous gallery length (cm)	50	41.9	3.25	50	45.8	1.60
Percent of gallery resin filled	50	62.9	3.14	50	75.3	2.04
Total eggs	50	149.9	7.47	50	130.1	4.66
Hatched eggs	50	141.4	7.33	50	123.1	4.55
Dead eggs	50	8.5	1.43	50	6.9	1.11
Gallery length per female (cm)	48	15.3	4.43	50	14.7	1.09
Eggs per female	48	39.5	4.34	50	30.5	2.18
Eggs per cm of gallery	50	2.5*	0.08	50	2.1	0.06
Immatures	50	15.9	1.27	50	15.5	1.56
Reemerged adults	47	8.4	0.70	50	5.8	0.51
Emergent adults	48	5.3	1.00	45	7.0	0.85
Predators in bark X-ray	50	3.1	0.30	50	3.2	0.45
Parasites in bark X-ray	50	0.8	0.14	50	0.9	0.15
Miscellaneous insects in bark X-ray	50	3.3*	0.41	50	2.1	0.28

n, number of bark samples (each 100 cm²) on which calculations are based.

A maximum of 50 samples were taken (ten per tree from five trees within each treatment).

Density data are expressed as mean number per 100 cm².

*Treated means differ from control means ($P = 0.10$, analysis of variance, Tukey's studentized range test).

Table 4
Population parameters for Southern Pine Beetle in 1987

Variable	Treated			Control		
	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
Successful attacks	48	3.4	0.36	45	4.0	0.40
Unsuccessful attacks	48	0.4 ^a	0.10	45	3.6	0.49
Total gallery length (cm)	48	49.2 ^a	3.46	19	85.9	5.10
Resinous gallery length (cm)	48	18.5 ^a	1.84	19	47.5	6.63
Percent of gallery resin filled	48	38.3	3.26	19	55.7	7.09
Total eggs	48	90.0	7.24	19	126.8	9.69
Hatched eggs	48	48.9	6.92	19	113.4	8.81
Dead eggs	48	11.1	1.09	19	13.4	2.02
Gallery length per female (cm)	43	17.3	1.57	18	18.6	1.77
Eggs per female	43	31.4	3.13	18	27.1	3.13
Eggs per cm of gallery	48	1.8	0.08	19	1.5	0.09
Immatures	50	5.7	0.74	20	6.3	1.46
Reemerged adults	47	3.6	0.45	19	8.4	1.28
Emerged adults	5	2.6 ^a	0.54	2	6.6	1.98
Predators in bark X-ray	50	4.9	0.51	20	6.0	1.25
Parasites in bark X-ray	50	0.3	0.08	20	0.3	0.12
Miscellaneous insects in bark X-ray	50	16.5 ^a	2.05	20	4.1	1.22

n, number of bark samples (each 100 cm²) on which calculations are based. A maximum of 50 samples were taken (ten per tree from five trees within each treatment).

For emerged adults, a maximum of five samples (one bolt per study tree) were taken.

Density data are expressed as mean number per 100 cm².

^aTreated means differ from control means ($P=0.10$, analysis of variance, Tukey's studentized range test).

Soil water steadily decreased during the study, dropping to 8 cm, about 39% of total available, by the end of August (day 243).

In relation to changes in tree water status following SPB attack, it has long been thought that mutualistic fungi contribute to the rapid death of bark beetle-attacked trees (Nelson, 1934; Craighead and St. George, 1940). However, Hetrick (1949) reported SPB-infested trees without evidence of bluestain, and Bridges et al. (1985) described several successful SPB infestations that lacked the bluestain fungus, *Ophiostoma minus* (Hedgcock) H.&P. Sydow. One theory has been advanced that includes this scenario: (1) initial beetle attacks result in fungal inoculation, (2) phytotoxic compounds are introduced or produced in tree tissue, (3) tree resistance decreases rapidly due to reduction in oleoresin exudation pressure and flow, (4) subsequent attacks meet little resistance and beetle survival is high, (5) tree dies and brood is produced (Hodges et al., 1985). Solutions of isocoumarins (fun-

gal metabolites) have been shown to stimulate transpiration in loblolly pine seedlings when administered through cut stems (DeAngelis et al., 1986). Apparently, if isocoumarins are produced in the early stages of beetle attack and fungal inoculation, and they function as found by DeAngelis et al. (1986) with seedlings and introduction through cut stems, they could adversely affect tree defense by lowering water content throughout the bole.

In our study there was a considerable delay in detection of measurable decreases in water potential of twigs detached from the crowns of attacked trees (Figs. 3(A) and 3(B)), which agrees with results from two unpublished studies. In one, Brown and Michael (1978) reported that afternoon xylem water potentials did not differ between attacked and non-attacked trees until about 14 days after initial attack. In another, Brown and Doraiswamy (1980) reported that morning needle water potentials did not begin to change until between 30 and 35 days following attack. These results differ in an expected fashion because midday measurements of xylem water potential, when evaporative demand is usually high, should detect onset of severe tree water deficits sooner than early morning measurements. Neither study was published, but a portion of Brown and Doraiswamy's work was included in Wagner et al. (1979). Those authors reported a derived prediction equation for morning xylem water potential, which indicated no difference between mean infested-tree values and control-tree values until after the mean egg stage of brood development (about 3 weeks after initial beetle attack).

Results of Brown and Michael (1978), Brown and Doraiswamy (1980), the results reported here, those of Bridges et al. (1985), and fungal inoculation studies with ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) by Parmeter et al. (1992), cast some doubt on the role that fungal associates of SPB may play in blocking the transpiration stream, and perhaps hastening desiccation and death of SPB attacked trees. If such a role exists, measurement of xylem water potential in twigs by the pressure chamber technique does not appear adequate to detect the effects.

Apparently, differences in water regimes between the two study years greatly influenced tree responses to treatment and SPB attack. Figs. 4(A) and 4(B) indicate that the dry-ice collars considerably reduced the potential for resin to flow in response to SPB attack in

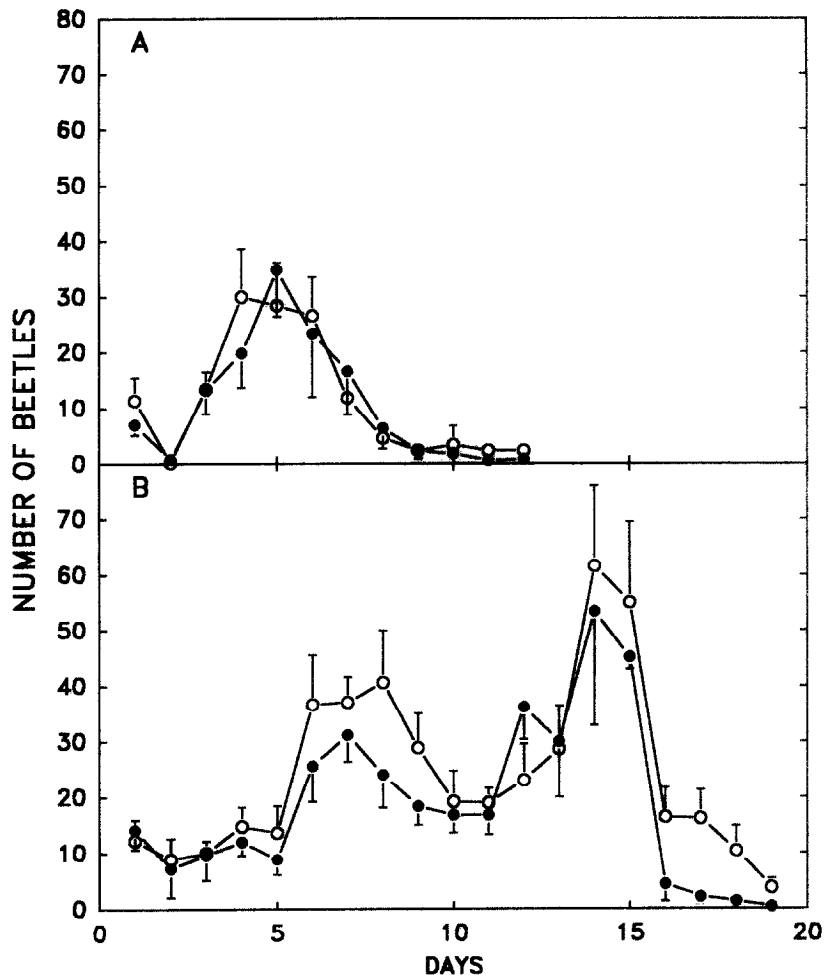


Fig. 5. Average daily catches of southern pine beetles in window traps for treated trees (filled circles) and control trees (open circles) in (A) 1986 and (B) 1987. Note that trap catches differed little between treatments within years, but that many more beetles were trapped, and for a much longer time, in 1987 than in 1986.

both years. However, under well-watered conditions in 1986, resin yields of control trees also dropped rapidly following SPB attack, whereas in 1987 yields decreased temporarily and then increased steadily. These trends in resin yield are in agreement with the levels of tree resistance to beetle attacks. In 1986 SPB were uniformly successful in attacking both treated and control trees (Table 3), but in 1987 three of the five control trees resisted attacks to the point that no brood was produced (Table 4; Stephen et al., 1988).

Treatment with dry-ice collars to induce acute water deficit can also result in death of phloem, cambial, and ray tissues in the outer xylem. This was clearly the case

in some trees in 1987 when temperatures as low as -25°C were measured at 8 cm deep into the xylem. Following thawing, the killed tissues may ferment; this was clearly so with one treated tree in 1986 in which a large number of ambrosia beetles (*Xyleborus* spp.) was observed attacking the lower bole. Such confounding effects could and probably did have negative effects on the development of brood in treated trees in both years, but especially in 1987 when the treatment technique was modified to ensure an effective freezing treatment.

In 1987 it appeared that study trees were not being attacked to the same degree as in 1986. Therefore, additional infested bark and bolts containing emerging

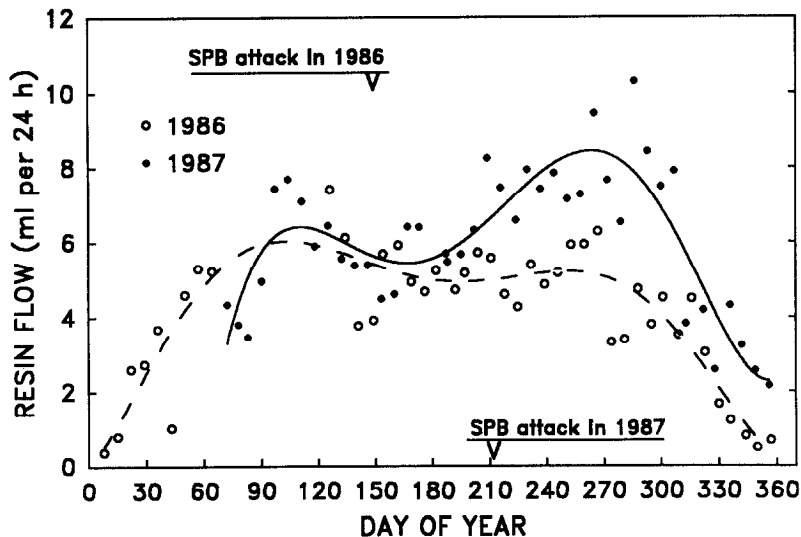


Fig. 6. Annual course of resin yield from bark wounds in 1986 ($n=11$) and in 1987 ($n=12$). Loblolly pines were at the same location, and of similar age and size as those used in the study of dry-ice treatment effects. Timing of SPB attack is indicated for each year. Curves are for 6th order polynomials (1986, dashed line; 1987, solid line). Note that in 1987 there was a strong positive trend in resin yield at the time the study was initiated in late July of that year.

SPB were brought to the study area. This resulted in many more beetles being caught in pheromone traps over a longer time span in 1987 than in 1986 (see Tables 1 and 2, and Fig. 5). If anything, trap data indicate that study trees were more severely challenged in 1987 by attacking SPB than in 1986. Further, attack densities were similar for both treated and control trees in 1986 (Table 3), but in 1987 control trees were attacked at twice the density (7.6 versus 3.8) with 47% judged unsuccessful compared with 11% unsuccessful in treated trees (Table 4). These observations agree with past research indicating that pheromone production is prolonged in trees which resist attacking beetles with abundant resin flow (Vité and Pitman, 1968; Coster and Vité, 1972; Payne, 1980; Raffa and Berryman, 1983; Dunn and Lorio, 1993). The relative responses of control trees are in general agreement with expectations based on the conceptual model proposed by Lorio et al. (1990). In 1986 study trees were well hydrated, and had not begun producing latewood and the major complement of the current year's vertical resin ducts commonly associated with latewood development. Conversely, in 1987 study trees experienced moderate levels of water deficits prior to the study, initiated about 6 to 8 weeks after the transition from earlywood to latewood formation, and the moderately

dry conditions during the study apparently increased the partitioning of energy to oleoresin synthesis. Such is indicated by the seasonal course of resin yield measured in comparable trees within the same stand in 1986 and 1987 shown in Fig. 6. Resin flow remained low during the 1986 study, but increased during the 1987 study.

Another factor affecting the potential flow of oleoresin from wounds made to the face of the xylem is the progressive displacement of the wound surface from the main reservoir of oleoresin as earlywood forms during rapid growth in the spring and early summer months. Until the transition to latewood occurs, and the current year's vertical resin ducts begin appearing, the band of earlywood formed in the current year represents an ever-increasing barrier to resin flow. Because the SPB excavates egg galleries at the xylem/phloem interface, conditions that enhance earlywood formation and extend its duration, such as abundant rainfall in late spring and early summer, may increase pine susceptibility to SPB attack (Lorio et al., 1990).

In 1986 results did not support the hypothesis that treatment with dry-ice collars to cause acute water deficit will enhance SPB attack success and brood production. Both treated and control trees were readily colonized and produced brood. In 1987 results sup-

ported the hypothesis, given that three of the five control trees resisted attack to the extent that all attacks eventually failed. These results illustrate the dynamic nature of host tree conditions and resistance to beetle attack from year-to-year and from time-to-time during a growing season.

Although one may question the vitality of SPB populations in 1987, when an outbreak apparently was declining, results support the secondary hypothesis that trees well into latewood formation would resist attack more strongly than trees still producing earlywood. Rainfall amount and distribution, and calculated water deficits, indicated conditions considered favorable for resin production, because as growth is limited by moderate water deficit more available energy is partitioned to resin synthesis (Lorio, 1986; Blanche et al., 1992). However, high levels of resin yield and resistance to attack as demonstrated in 1987 does not always occur (see Fig. 6, and Lorio et al., 1990), and different results probably would have been found in the summer of 1986 when severe water deficits developed (Figs. 1(B) and 2(A)).

In summary, results from this study indicate strongly that knowledge of environmental conditions and stage of growth and development of host trees is extremely important in attempts to assess the effects of manipulative treatments on tree susceptibility to beetle attacks. Without such knowledge of conditions preceding and during the study in both 1986 and 1987 adequate interpretation of results would be difficult. Indeed, explanation for the wide disparity in responses of control trees between years would be very unlikely. Further, results here indicate the dynamic nature of tree resistance to beetle attack even in the absence of abnormal stresses, and re-emphasize the need for studies of physiological changes associated with ontogeny of trees that affect their susceptibility to forest insects (Kozlowski, 1969).

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