

32. Environmental Effects on Pine Tree Carbon Budgets and Resistance to Bark Beetles

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Pine trees are a dominant component of primary production in natural and managed ecosystems throughout the southeastern United States. Because of the economic importance of pines in the Southeast, the southern pine beetle (*Dendroctonus frontalis* Zimmerman, Coleoptera: Scolytidae) can cause losses in excess of \$236 million per year by attacking and killing pine trees (Price et al., 1992), and is arguably the greatest source of natural disturbance in ecosystems of the southeast. Interactions between pine trees and bark beetles have become a focus of global change research because it has long been hypothesized that bark beetle outbreaks are linked to climatic patterns (Beal 1927; Beal, 1933; Berryman and Ferrel, 1988; Christiansen and Bakke, 1988; Craighead, 1925; Grégoire, 1988; Kalkstein, 1976; King, 1972; Kroll and Reeves, 1978; Michaels, 1984; Raffa, 1988; St. George, 1930; Wyman, 1924). This implies that climate change will probably alter the frequency and intensity of forest disturbance from pest outbreaks. However, the mechanisms by which climatic patterns impact bark beetle population dynamics have remained obscure (Martinat, 1987; Mattson, 1980; Reeve et al., 1995). The development of accurate, physiologically explicit models is an essential first step in assessing the ecological risks associated with global change (Ayres, 1993). The research reported in this chapter was designed to test and refine a model of environmental effects on tree carbon budgets that provides a promising tool for understanding and predicting the effects of global change on interactions between pine trees and the southern pine beetle (SPB) (Figure 32.1).

There are numerous pathways by which climatic change could affect trees and

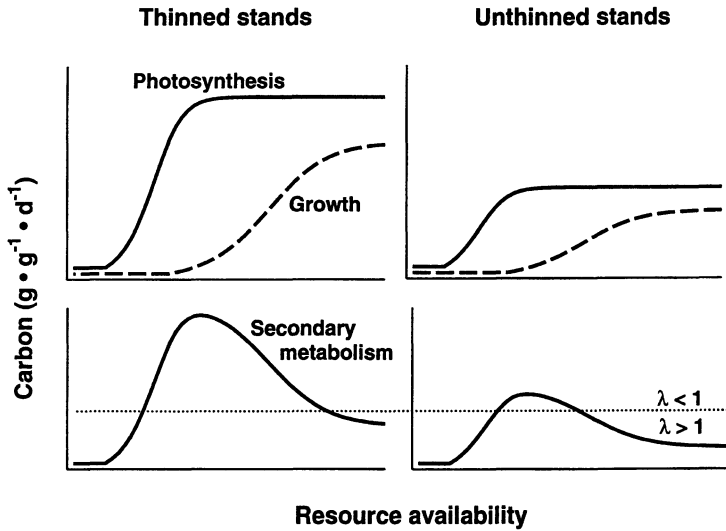


Figure 32.1. Hypothesized responses of loblolly pine in thinned and unthinned stands to changes in the availability of water and mineral nutrients. Moderate deficiencies of water or mineral nutrients are predicted to limit growth more than photosynthesis, and thus, carbon available for secondary metabolism (photosynthesis—growth) increases, oleoresin production rises, and attacking bark beetles suffer low reproductive success ($\lambda < 1$). Secondary metabolism is predicted to be low, and beetle reproductive success high ($\lambda > 1$), either at high resource availability (in which the majority of photosynthates go toward growth) or low resource availability (in which the total carbon budget is low). In dense, unthinned pine stands, the total carbon budget ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) is predicted to be less than in thinned stands, resulting in reduced secondary metabolism, and allowing reproductive success of attacking bark beetles across a broad range of resource availability.

influence pest resistance (Ayres, 1993). Precipitation patterns impact soil-water availability and thereby exert strong effects on trees. Any changes in precipitation patterns could impact the suitability of pine trees for bark beetles and influence beetle population dynamics. We have attempted to explain effects of soil moisture on bark beetles with a physiological model (Reeve et al., 1995) that is derived from principles of growth-differentiation balance in plants (Loomis, 1932; Loomis, 1953; Lorio, 1986; Wilkens et al., 1996a). There is a widely held perception that trees that are “vigorous” (a word that is often used interchangeably with “fast growing”), are also most resistant to insect attack. However, the model that we employed argues against this simple assumption, except under conditions of very low resources. The model predicts decreasing resistance when moving from conditions of moderate to high resources. In this model, moderate water deficiencies are predicted to limit growth more than they limit photosynthesis (Figure 32.1, upper) because growth is a function of cell division and expansion, which are strongly dependent upon water availability (Brown and Sommer, 1992).

As a consequence, trees experiencing moderate water deficits, compared to trees in well-watered conditions, are predicted to have a surplus of carbohydrates beyond that which can be invested in growth (the difference between photosynthesis and growth curves in Figure 32.1). Pine trees with relatively more surplus carbon are predicted to have higher rates of secondary metabolism (Figure 32.1, lower), produce more oleoresin (a mixture of monoterpenes and resin acids that impedes attacking bark beetles), and allow only limited reproductive success in attacking beetles. At low water availability, photosynthesis is predicted to drop, which should limit rates of secondary metabolism. Hence, our model predicts high reproductive success of attacking bark beetles (i.e., positive population growth, $\lambda > 1$) at either high water availability or low water availability.

Experimental and theoretical support for this general model of plant responses is accumulating (Ayres, 1993; Herms and Mattson, 1992; Wilkens et al., 1996a). As predicted, Lorio (1978) found that 72% of all infestations they observed were on moist sites that were closely associated with a high site index. Also as forecasted for loblolly pine, severe water stress can limit resin flow and promote beetle success (Lorio and Hodges, 1977; Lorio et al., 1995). More surprisingly (but also as predicted) moderate water stress can produce the opposite effect. Recently completed studies in central Louisiana (Reeve et al., 1995) showed that moderately water-stressed loblolly pine had markedly higher rates of secondary metabolism (but reduced growth) than either control or irrigated trees; the potential rate of increase in SPB was three to six times higher among those that attacked irrigated trees compared to moderately water-stressed trees. The magnitude of these effects indicates that even modest changes in precipitation patterns could have dramatic effects on bark beetle population dynamics. Furthermore, because the response of secondary metabolism appears to be nonlinear (Figure 32.1), the effect of changes in precipitation are not only dependent upon the direction of change (i.e., precipitation increases or decreases), but also on the extent of change and the initial conditions of the forest. For example, a 20% decrease in summer precipitation might lead to moderate water stress and limit bark beetle outbreaks, but a 40% decrease might lead to severe water stress and promote bark beetle outbreaks. Similarly, a decrease of 20% in summer precipitation might lead to moderate water stress and limit bark beetle outbreaks in Louisiana, but also might lead to severe water deficits and promote bark beetle outbreaks in east Texas where there is less average rainfall and moderate water deficits are presently the status quo.

Global change is also apt to produce changes in southern forests through alteration of mineral-nutrient availability (Anderson, 1991; Bassaz, 1990; Chapin, 1991; Pastor and Post, 1988). Mineralization rates and, therefore, the availability of mineral nutrients to plants are highly sensitive to temperature, moisture, and litter quality. In some forests, including large regions of the northeastern United States, soil-nutrient regimes are also changing as a result of the sustained deposition of airborne nitrogenous pollutants (Lovett and Kinsman, 1990; McNulty et al., 1990; Miller et al., 1993; Olliger et al., 1993). These pollutants are frequently deposited as ammonium and nitrate (Friedland et al., 1991), and hence, may be

expected to produce the same effects on tree growth and physiology as fertilization. A review of published studies (Ayres, 1993), indicates that of all the abiotic factors associated with global change (temperature, carbon dioxide (CO₂), water, cloud cover, and nutrient availability), changes in nutrient regime may produce the largest effects on tree resistance to herbivores. Changes in nutrient availability can alter patterns of secondary metabolism in many plants with consequences for populations of insect pests (Ayres 1993, and references within). However, the effects of nutrient availability on oleoresin production in loblolly pine are not known. Before developing land-use strategies that will be appropriate under future climatic regimes, we must understand the physiological responses to existing nutrient regimes and the effects of these responses on the interaction between SPB and southern pines. We hypothesized that our model (summarized in Figure 32.1 can be generalized to predict responses to changing nutrient availability, as well as changing water availability. Based on Figure 32.1, we predicted that the effect of fertilizing pines would be to increase growth more than it increases photosynthesis, which would limit carbohydrates available for secondary metabolism, lead to reduced oleoresin flow, and increase the reproductive success of attacking beetles. This prediction runs counter to predictions that any silvicultural practices that increase tree growth will necessarily increase tree resistance to herbivores (Mason et al., 1992; Raffa, 1988; Waring, 1983).

We emphasize, however, that Figure 32.1 does not indicate that fertilization will always reduce tree resistance. Indeed, the model indicates that fertilization can increase secondary metabolism in plants that are in extremely stressed conditions (Figure 32.1). We make our prediction of decreased tree resistance in response to fertilization with the assumption that the site is not extremely nutrient deficient. This assumption is supported by the site index for our study area, which was approximately 88, and which is midrange for loblolly pine forests in Louisiana and Arkansas (Carmean et al., 1989). Our assumption is further supported by foliar nitrogen (N) and phosphorus (P) concentrations in the study site (Gravatt, 1994), which generally fall at or above established sufficiency levels (Allen, 1987).

The risk of bark beetle outbreaks might be mitigated by appropriate silvicultural practices. We hypothesized that thinning of pine plantations would tend to elevate total carbon budgets in loblolly pine (because it increases the crown size and reduces shading), and would, therefore, increase rates of secondary metabolism at any given level of resource availability (Figure 32.1). If this is true, thinned plantations would only allow reproductive success in attacking bark beetles ($\lambda > 1$) at extremely low or high resource availability, unthinned plantations would allow beetle success across most conditions of water or nutrient availability. This prediction is consistent with reports that SPB infestations tend to be less severe in pine forests with low stand density than in "overstocked" pine forests with high stand density (Brown et al., 1987; Coster and Searcy, 1981; Gara and Coster, 1968; Lorio, 1980; Lorio et al., 1982; Lorio and Sommers, 1981; Mason et al., 1985; Nebeker et al., 1985). Our research aimed to test the hypotheses represented in Figure 32.1.

Materials and Methods

The study was conducted on a 1.1 hectare (ha) plantation on Beauregard silt loam soil located in the Johnson Tract of the Palustris Experimental Forest in the Kisatchie National Forest of central Louisiana. During 1981, the site was planted with loblolly pine seedlings at a 1.8×1.8 m spacing (6×6 ft), yielding a rectangular grid of seventy rows and ninety columns containing 6,300 trees. Before the growing season of 1989, treatments were randomly assigned to eight plots (each plot containing thirteen rows of thirteen trees); two plots were left as controls, two were fertilized with diammonium phosphate, two were thinned, and two were thinned and fertilized. Thinned plots were reduced to 748 trees per ha from the original density of 2990 trees/ha (Haywood, 1994). In April of 1989, fertilizer was applied at the rate of 746 kg/ha, that is, 150 kg P and 134 kg N per ha. We selected experimental trees from each of these plots; nine from each thinned plot and eleven from each unthinned plot, for a total of 80 trees. Experimental trees in the unthinned plots were drawn equally from trees classified in May of 1993 as codominant (tall enough to share the upper canopy) or intermediate (being partly overgrown by neighboring trees). The thinned plots, because of the thinning treatment, contained only codominant trees. Immediately after treatments were applied in 1989, the basal areas were 28 to 29 m²/ha for the unthinned plots and 6 to 7 m²/ha for the thinned plots. In 1992 when our measurements began, the basal areas were 37 to 39 m²/ha for the unthinned plots and 14 to 17 m²/ha for the thinned plots (Haywood, 1994).

At intervals throughout the growing season in 1993 and 1994, we measured oleoresin flow, phloem thickness, photosynthesis, height growth, and cambial growth. On each sampling date, oleoresin flow was measured from standardized wounds (125 mm²; 2/tree) to the xylem face (Dunn and Lorio, 1993). Phloem discs (125 mm²), which were removed to produce the wounds, were returned to the laboratory, freeze-dried, and then weighed to yield estimates of phloem specific mass (mg/125mm²), which is a correlate of thickness.

We measured carbon assimilation rates with a portable photosynthesis system (Li-6200, Li-Cor Corporation). On each sampling occasion, we measured two sets of two fascicles from each tree. The sampled needle tissue was freeze-dried, weighed, and subsequently analyzed for total nitrogen using a Carlo-Erba carbon/nitrogen analyzer. For each sampled tree, we recorded the average length and mass of fascicles (four fascicles per tree), and the number of fascicles per 10 cm of shoot. These data allowed us to express photosynthesis as 1) $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; (2) $\mu\text{moles} \cdot \text{g}^{-1} \cdot \text{s}^{-1}$; (3) $\mu\text{moles} \cdot \text{g N}^{-1} \cdot \text{s}^{-1}$; (4) $\mu\text{moles} \cdot \text{fascicle}^{-1} \cdot \text{s}^{-1}$; and (5) $\mu\text{moles} \cdot 10 \text{ cm shoot}^{-1} \cdot \text{s}^{-1}$.

Cambial growth was measured every seven to nine days during the growing season from dendrometer bands permanently affixed to each experimental tree at 1.5 m aboveground. Height was measured twice per year, once in the first week of June and again in late fall after height growth had ceased for the year.

We tested for patterns in carbohydrate partitioning by tracking the fate of labeled carbon (¹⁴C) assimilated by photosynthesizing needles as CO₂. In late

summer of 1993 (September 2) and in spring of 1994 (May 12), two branches from each of three trees in each of four treatment groups were exposed to 200 μ Curies (740k Bq) of labeled CO_2 for thirty minutes within a plastic bag (long enough to assimilate about 90% of the label). Five days later, the branches were harvested, and then separated into basal and distal regions (the distal region was within the bag during label uptake). Tissue for analysis included a mixture of the inner bark and recently formed xylem cells. Xylem tissue was obtained by carefully removing the phloem tissue, and then scraping the last-formed cells from the xylem. Extraction of the tissues was done in such a way that labeled material could be separated into one of two fractions, which were 1) hexane soluble (mainly monoterpenes and resin acids) and 2) structural compounds. Liquid scintillation counts were performed on each sample; one was performed on the hexane extract (representing the oleoresin fraction), and one on the residue (after oxidation in a carbon oxidizer). Resulting data allowed us to compare the proportion of assimilated carbon that was distributed to primary vs secondary metabolism.

Treatment effects were evaluated by analysis of variance (ANOVA) with a statistical model that tested for effects of 1) thinning (thinned and unthinned), 2) fertilization (fertilized and unfertilized), 3) crown class (codominant and intermediate), and 4) sampling date (varies by measurement). Data were analyzed as a partial factorial (Milliken and Johnson, 1984) because one treatment combination (i.e., thinned plot, intermediate crown class) did not exist. Measurements of resin flow, phloem thickness, photosynthesis, and needle morphology involved subsampling within trees, so the ANOVAs were modified to include nesting within trees. Preliminary analyses included treatment plots as a blocking factor, but the effects of blocking were always small and usually nonsignificant, so blocking was eliminated from the models for simplicity.

Results

Photosynthesis

Thinning elevated the rate of photosynthesis when considered on a per fascicle or per 10 cm shoot basis; however, other measures of photosynthesis were not affected (Table 32.1; Figure 32.2). Crown class had no discernible effect on photosynthesis for any scale measured (Table 32.1). Photosynthesis was consistently higher in fertilized trees, yielding significant differences for most contrasts (Table 32.1; Figure 32.2). However, on a per gram basis (A/g), fertilizer had no effect. Among unthinned intermediate trees, fertilization increased photosynthesis on a per mole N basis (A/mole N), but not the others (Table 32.1; Figure 32.2).

Needle Morphology and Chemistry

Nitrogen concentration was higher in unthinned trees (Table 32.2; Figure 32.3). Among the codominants, however, thinning did not affect nitrogen concentration

Table 32.1. Statistical Contrasts for the Effects of Thinning,¹ Fertilization, and Crown Class (Codominants vs Intermediates) on Carbon Assimilation Rates (A = $\mu\text{moles CO}_2/\text{s}$) of *Pinus taeda*

Treatment contrast	F-statistics				
	A/m ²	A/g	A/fascicle	A/10 cm shoot	A/mole N
Thinned vs unthinned	3.58	0.16	9.34**2	9.17**	0.02
Thinned vs unthinned codominants	3.32	0.00	5.05*	3.98	0.06
Fertilized vs unfertilized	11.60**	2.12	20.87***	9.33**	21.32***
Fertilized vs unfertilized in thinned	6.03*	2.10	8.72**	7.14*	10.42**
Fertilized vs unfertilized in unthinned	6.50*	0.77	12.97***	4.14*	12.08**
Fertilized vs unfertilized in unthinned codominants	4.71*	1.41	13.78***	2.52	7.22*
Fertilized vs unfertilized in unthinned intermediates	2.26	0.02	2.50	1.74	5.31*
Codominants vs intermediates in unthinned	0.08	0.48	0.50	1.19	0.41
Fertilizer $\times$ crown class interaction in unthinned	0.06	0.43	1.41	0.00	0.02
Fertilizer $\times$ thinning interaction in codominants	0.01	0.00	0.95	0.23	0.04
Trees (Treatment)	6.50***	5.97***	9.41***	14.83***	

¹ Corresponds to data in Figure 32.2. Measurements included two replicates per tree (each based on a different pair of fascicles drawn from the same shoot) for all except A/mole N. All treatment contrasts used MS_{tree} (degrees of freedom = 48) as the F-test denominator except for Trees (Treatment), which used MS_{error} (degrees of freedom = 65).

² * $P < .05$, ** $P < .01$, *** $P < .001$

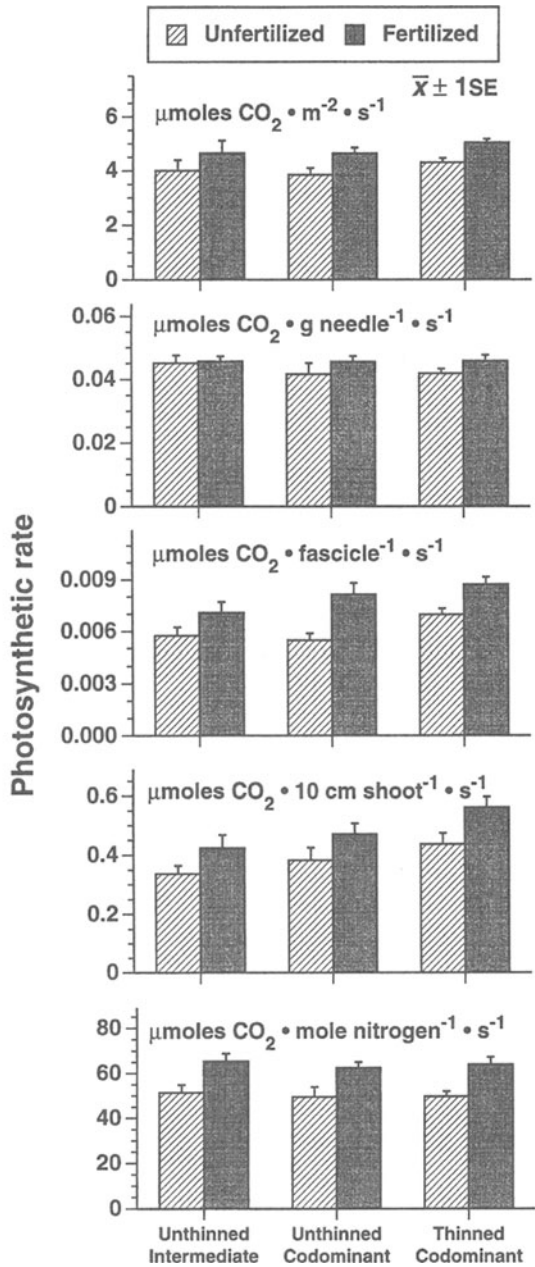


Figure 32.2. Photosynthetic rate of fertilized or unfertilized trees in thinned and unthinned plots (note: unthinned plots contain both codominant and intermediate trees and will be the case whenever unthinned and thinned trees are compared) as measured by several different methods. Starting from the top: on a per area basis, on a per gram basis, on a per fascicle basis, on a per shoot basis, and on a per unit of nitrogen basis.

Table 32.2. Statistical Contrasts for the Effects of Thinning, Fertilization, and Crown Class (Codominants vs Intermediates) on Needle Morphology and Chemistry of *Pinus taeda*¹

Treatment contrast	F-statistics			
	Fascicle length	Fascicle mass	Fascicles / 10 cm	% Nitrogen
Thinned vs unthinned	10.54**	14.80***	0.18	4.18*
Thinned vs unthinned codominants	3.45	6.60*	0.06	1.37
Fertilized vs unfertilized	14.75***	14.80***	0.75	28.36***
Fertilized vs unfertilized in thinned	3.54	4.92*	0.17	10.20**
Fertilized vs unfertilized in unthinned	11.22**	10.08**	1.44	18.58***
Fertilized vs unfertilized in unthinned codominants	16.77***	8.68**	3.76	13.70***
Fertilized vs unfertilized in unthinned intermediates	0.86	2.79	0.00	6.56*
Codominants vs intermediates in unthinned	2.70	1.76	1.08	1.26
Fertilizer × crown class interaction in unthinned	3.74	0.39	1.70	0.09
Fertilizer × thinning interaction in codominants	3.81	0.73	3.08	0.34
Date				5.15*
Date × treatment ³				0.73
Trees (treatment)				2.16**

¹ Corresponds to data in Figure 32.3. Nitrogen measurements included two dates (June 3, 1993 and July 5, 1995). All treatment contrasts used MS_{tree} as the F -test denominator (degrees of freedom = 48) except for Date, Date × Treatment, and Trees (Treatment), which used MS_{error} (degrees of freedom = 41).

² * $P < .05$, ** $P < .01$, *** $P < .001$

³ The treatment classes included the six possible combinations of thinning, crown class, and fertilization (unthinned intermediate unfertilized, unthinned intermediate fertilized, unthinned codominant unfertilized, unthinned codominant fertilized, thinned codominant unfertilized, and thinned codominant fertilized).

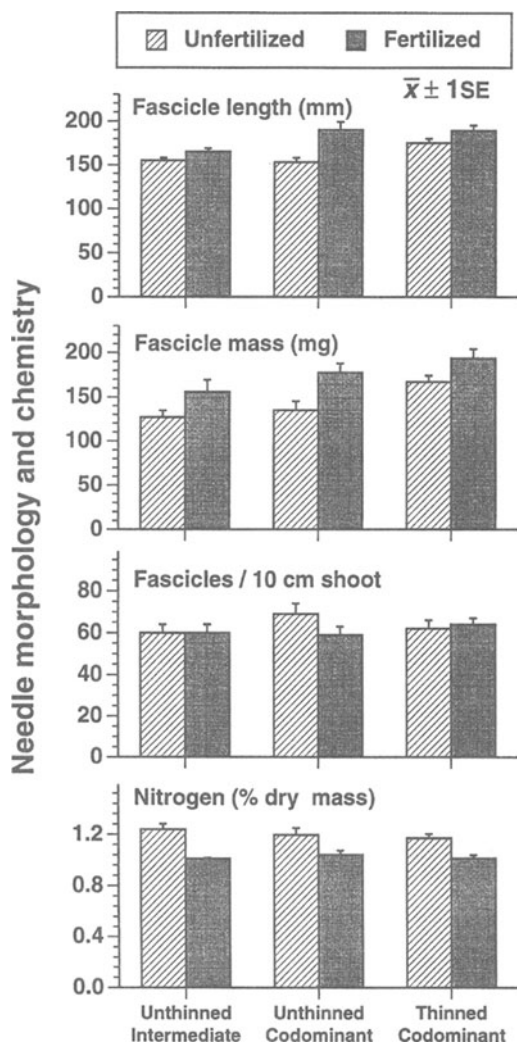


Figure 32.3. Needle morphology and chemistry of fertilized or unfertilized trees in thinned and unthinned plots.

(Table 32.2; Figure 32.3). Thinning resulted in greater fascicle length and mass (Table 32.2; Figure 32.3). Among the codominants, thinning increased fascicle mass but not fascicle length (Table 32.2; Figure 32.3). The number of fascicles per 10 cm was not affected by thinning or any other treatment (Table 32.2; Figure 32.3). Crown class had no discernible effect on needle morphology or chemistry (Table 32.2; Figure 32.3), but fertilization tended to increase the mass and length of the fascicles (Table 32.2; Figure 32.3). Fertilized trees had consistently lower nitrogen concentrations than the unfertilized trees (Table 32.2; Figure 32.3),

which was also discovered by Gravatt (1994) at the same site in a different study. This result is consistent with a dilution effect. That is, fertilized trees had bigger needles than the unfertilized trees (mean $\pm$ standard error = 180 ± 7 vs 147 ± 6 mg per fascicle) but the same total amount of nitrogen per fascicle (mean $\pm$ standard error = 1.84 ± 0.09 vs. 1.76 ± 0.08 mg), and therefore, lower needle nitrogen concentrations (mean $\pm$ standard error = 1.022 ± 0.016 vs 1.200 ± 0.025).

Diameter Growth

Four years after treatments were applied, in 1988 trees in thinned plots had markedly larger trunks than those in unthinned plots (mean $\pm$ standard error = 18.01 ± 0.32 vs 15.45 ± 0.35 cm diameter, respectively). Thinned trees continued to show greater cambial growth than unthinned trees throughout the 1993 (not shown) and 1994 growing seasons (Table 32.3, Figure 32.4). Within the unthinned plots, trunk diameter in spring of 1993 was greater in codominant trees than intermediate trees (mean $\pm$ standard error = 15.45 ± 0.35 vs 11.76 ± 0.14 cm). Subsequent diameter growth in the unthinned plots continued to be greater for codominant trees than for intermediate trees throughout the 1993 and 1994 growing seasons (Table 32.3, Figure 32.4). Fertilizer had no effects on cambial growth (Table 32.3, Figure 32.4); cambial growth in all treatments was highly episodic. For example, trees in the thinned plot gained nearly 0.8 mm/week of cambial growth during three weeks in April and May of 1993, but barely grew at all (< 0.2 mm/week) during the five weeks that separated these bouts of rapid growth (Figure 32.4). Periods of cambial growth were closely associated with short-term changes in soil moisture as each episode of cambial growth during 1993 occurred immediately following a significant rainfall event. The majority of cambial growth in all treatments occurred during the same brief episodes (Figure 32.4). Differences among treatments in cumulative cambial growth resulted largely from differences in the rate of growth during these episodes. Cambial growth patterns for 1993 (not shown) were nearly identical to those of 1994.

Height Growth

In 1992, four years after treatments were applied, unthinned trees were taller than thinned trees, codominant trees were significantly taller than intermediate trees, and fertilized trees were taller than unfertilized trees (Table 32.4; Figure 32.5). From 1993 to 1994, thinned trees grew more than unthinned trees in three of the four time-periods analyzed, thinned codominants grew more than unthinned codominants in one of the time-periods, and fertilized trees grew more in three of four time-periods (Table 32.4; Figure 32.6). Fertilizer increased height growth least in unthinned intermediate trees (Table 32.4; Figure 32.6).

Resin Flow

There were no significant differences in resin flow between thinned and unthinned trees (Table 32.5; Figures 32.7 and 32.8). Similarly, there were no differences in

Table 32.3. Statistical Contrasts for the Effects of Thinning, Fertilization, and Crown Class (Codominants vs Intermediates) on Trunk Diameter Growth in *Pinus taeda*

Treatment contrast	<i>F</i> -statistics					
	Diameter in 1992 (cm)		Incremental diameter growth (mm)			
			Spring 1993	Summer 1993	Spring 1994	Summer 1994
Thinned vs unthinned	145.04*** ¹		256.86***	215.31***	178.22***	184.32***
Thinned vs unthinned codominants	34.55***		121.85***	98.73***	79.47***	78.19***
Fertilized vs unfertilized	0.08		0.69	1.32	0.14	0.01
Fertilized vs unfertilized in thinned	0.74		0.97	0.65	0.01	0.18
Fertilized vs unfertilized in unthinned	0.63		2.23	0.76	0.13	0.12
Fertilized vs unfertilized in unthinned codominants	0.20		2.78	1.06	0.20	0.24
Fertilized vs unfertilized in unthinned intermediates	0.45		0.22	0.05	0.01	0.00
Codominants vs intermediates in unthinned	56.86***		18.90***	18.33***	16.95***	20.99***
Fertilizer × crown class interaction in unthinned	0.03		0.66	0.30	0.06	0.11
Fertilizer × thinning interaction in codominants	0.79		3.68	0.09	0.08	0.42

¹ * $P < .05$; ** $P < .01$; *** $P < .001$

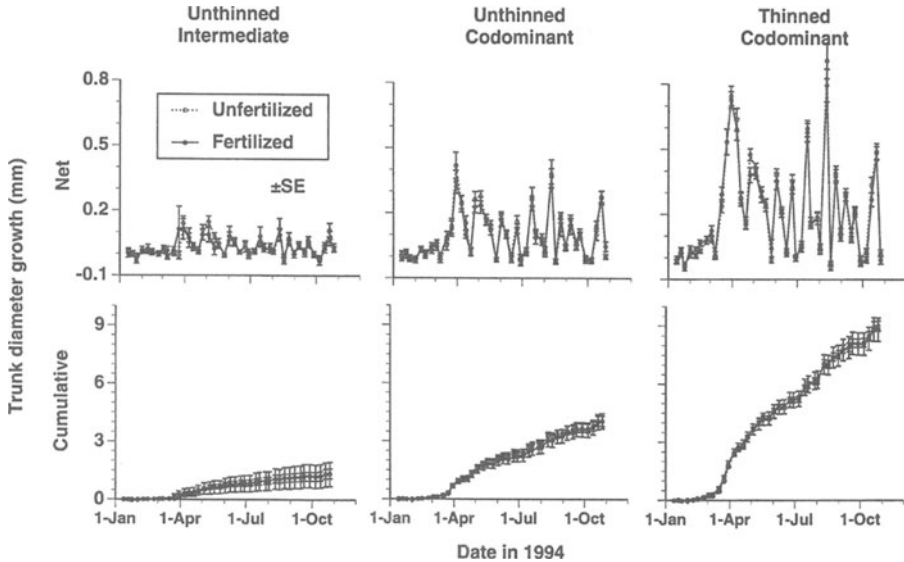


Figure 32.4. Diameter growth in 1994 of fertilized or unfertilized trees in thinned and unthinned plots presented in two different ways. Upper figure: The net growth, or incremental increase in growth after each seven to ten day period. Lower figure: The cumulative diameter growth over the growing season. Patterns of diameter growth for the 1993 growing season were nearly identical to the 1994 data shown here.

resin flow between codominant and intermediate crown classes (Table 32.5). In contrast, fertilizer generally reduced resin production (Table 32.5; Figures 32.7 and 32.8). However, there was a significant fertilizer $\times$ crown class interaction in the unthinned plots as fertilization affected resin flow in unthinned intermediates, but had no effect in the unthinned codominants (Table 32.5; Figures 32.7 and 32.8).

Phloem-Specific Mass

Phloem-specific mass was nearly twice as high in unthinned trees (Table 32.6; Figures 32.7 and 32.8). As the season progressed, there was a gradual decline in phloem-specific mass, especially in thinned codominants (Figures 32.7 and 32.8). Phloem-specific mass was greater in unthinned codominants than in unthinned intermediates, and fertilizer had no discernible effect on phloem specific mass (Table 32.6; Figures 32.7 and 32.8). All patterns were consistent across years. Phloem is a major storage site for starch and sugars in the tree, and is a primary food source for attacking beetles and their developing broods.

Labeled Carbon Patterns

Labeled carbon studies indicated strong seasonal shifts in partitioning of carbon to growth vs secondary metabolism. In the spring, during a period of rapid growth of

Table 32.4. Statistical Contrasts for the Effects of Thinning, Fertilization, and Crown Class (Codominants vs Intermediates) on Height Growth in *Pinus taeda*

Treatment contrast	<i>F</i> -statistics					
	Height in 1992 (m)		Incremental height growth (cm)			
	Spring 1993	Summer 1993	Spring 1993	Summer 1993	Spring 1994	Summer 1994
Thinned vs unthinned	4.86* ¹		0.97	4.52*	26.49***	4.70*
Thinned vs unthinned codominants	31.15***		0.07	1.16	12.99***	0.67
Fertilized vs unfertilized	29.14***		6.89*	6.30*	16.65***	1.34
Fertilized vs unfertilized in thinned	11.19**		0.28	7.50**	9.62**	0.57
Fertilized vs unfertilized in unthinned	18.66***		7.30**	1.84	8.70**	0.82
Fertilized vs unfertilized in unthinned codominants	13.68***		6.66*	1.56	7.59**	5.49*
Fertilized vs unfertilized in unthinned intermediates	5.96*		1.62	0.47	2.09	0.97
Codominants vs intermediates in unthinned	43.39***		0.99	1.60	1.67	3.18
Fertilizer × crown class interaction in unthinned	0.62		0.74	0.14	0.74	5.44*
Fertilizer × thinning interaction in codominants	0.65		2.83	0.54	0.05	1.85

¹ * $P < .05$; ** $P < .01$; *** $P < .001$

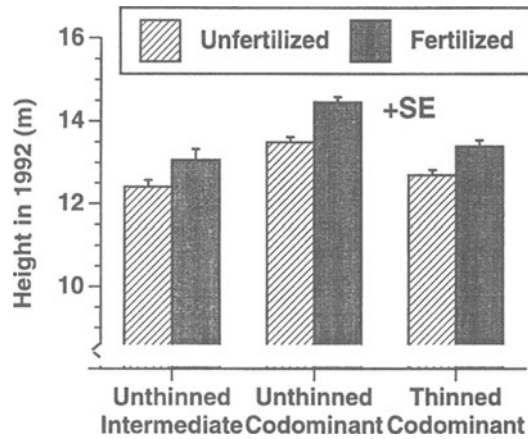


Figure 32.5. Height in 1992 of fertilized or unfertilized trees in thinned and unthinned plots. These heights were measured four years after treatments were applied and just before our intensive measurements began.

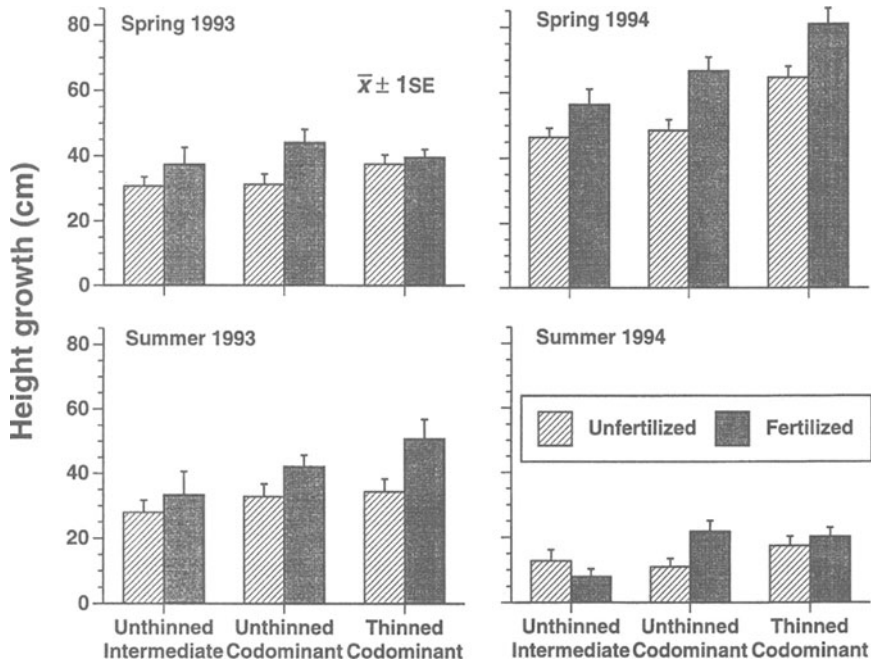


Figure 32.6. Height growth of fertilized or unfertilized trees in thinned and unthinned plots in the spring and fall of 1993 and 1994.

Table 32.5. Statistical Contrasts for the Effects of Thinning, Fertilization, and Crown Class (Codominants vs Intermediates) on Resin Flow in *Pinus taeda*¹

Treatment contrast	d f	Error term	F	P
Thinned vs unthinned	1	MS _{tree}	1.63	0.21
Thinned vs unthinned codominants	1	MS _{tree}	1.33	0.25
Fertilized vs unfertilized	1	MS _{tree}	5.69	0.0196
Fertilized vs unfertilized in thinned	1	MS _{tree}	4.22	0.0436
Fertilized vs unfertilized in unthinned	1	MS _{tree}	2.53	0.12
Fertilized vs unfertilized in unthinned codominants	1	MS _{tree}	0.14	0.70
Fertilized vs unfertilized in unthinned intermediates	1	MS _{tree}	6.54	0.0126
Codominants vs intermediates in unthinned	1	MS _{tree}	0.02	0.89
Fertilizer × crown class interaction in unthinned	1	MS _{tree}	4.46	0.0381
Fertilizer × thinning interaction in codominants	1	MS _{tree}	2.50	0.11
Treatment ²	5	MS _{tree}	73.85	0.0001
Date	14	MS _{error}	9.83	0.0001
Date × treatment	70	MS _{error}	1.42	0.0352
Tree(treatment)	74	MS _{error}	29.03	0.0001

¹ Data include nine dates in 1993 and six in 1994.

² The treatment classes included the six possible combinations of thinning, crown class, and fertilization (unthinned intermediate unfertilized, unthinned intermediate fertilized, unthinned codominant unfertilized, unthinned codominant fertilized, thinned codominant unfertilized, and thinned codominant fertilized).

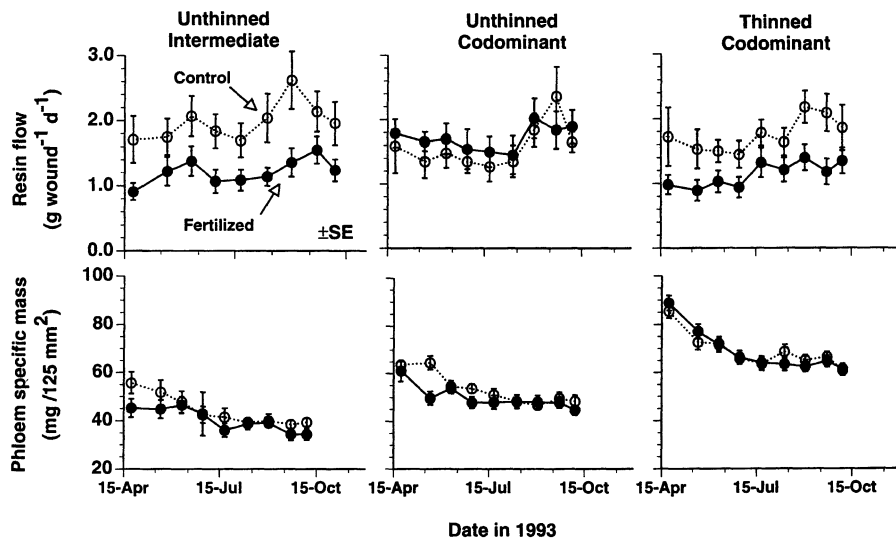


Figure 32.7. Resin flow and phloem-specific mass, in 1993, of fertilized or unfertilized trees in thinned and unthinned plots. The size of the wound made to measure resin flow and collect phloem samples was 125 mm².

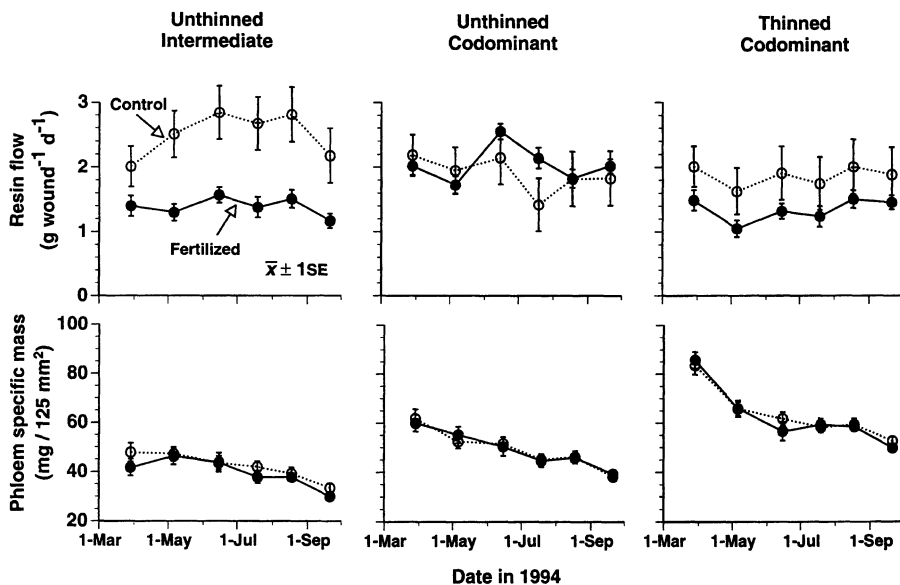


Figure 32.8. Resin flow and phloem-specific mass in 1994. See Figure 32.7 legend for details.

Table 32.6. Statistical Contrasts for the Effects of Thinning, Fertilization, and Crown Class (Codominants vs Intermediates) on Phloem Thickness (mg/125 mm²) in *Pinus taeda*¹

Treatment contrast	d f	Error term	F	P
Thinned vs unthinned	1	MS _{tree}	190.95	0.0001
Thinned vs unthinned codominants	1	MS _{tree}	83.01	0.0001
Fertilized vs unfertilized	1	MS _{tree}	2.18	0.14
Fertilized vs unfertilized in thinned	1	MS _{tree}	0.00	0.96
Fertilized vs unfertilized in unthinned	1	MS _{tree}	2.90	0.09
Fertilized vs unfertilized in unthinned codominants	1	MS _{tree}	0.91	0.34
Fertilized vs unfertilized in unthinned intermediates	1	MS _{tree}	2.06	0.16
Codominants vs intermediates in unthinned	1	MS _{tree}	21.05	0.0001
Fertilized × crown class interaction in unthinned	1	MS _{tree}	0.17	0.68
Fertilizer × thinning interaction in codominants	1	MS _{tree}	0.61	0.44
Treatment ²	5	MS _{tree}	41.22	0.0001
Date	10	MS _{error}	58.27	0.0001
Date × treatment	50	MS _{error}	3.03	0.0001
Tree (treatment)	74	MS _{error}	6.56	0.0001

¹ Data include five dates in 1993 and six dates in 1994.

² The treatment classes included the six possible combinations of thinning, crown class, and fertilization (unthinned intermediate unfertilized, unthinned intermediate fertilized, unthinned codominant unfertilized, unthinned codominant fertilized, thinned codominant unfertilized, and thinned codominant fertilized).

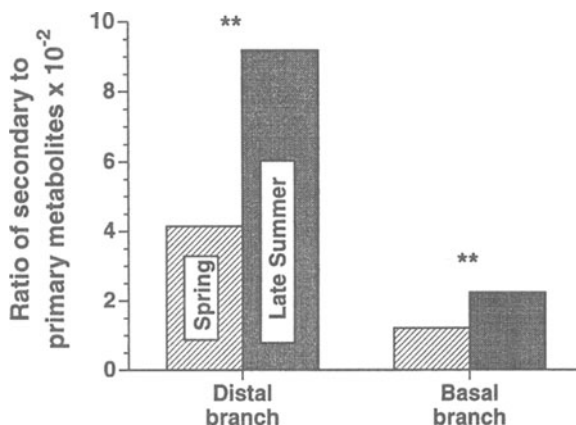


Figure 32.9. Ration of ^{14}C incorporated into secondary compounds relative to primary compounds (structure) in distal and basal branch portions in the spring (May 12 to 16, 1994) and in the late summer (September 2 to 7, 1993). Asterisks above bars indicate significant difference between the summer and spring measurements. (* $P = 0.01$).

shoots, the ratio of ^{14}C allocated to secondary compounds relative to structure was approximately 0.04 in the distal (inside the bag) part of branches and about 0.01 in the basal portion (Figure 32.9). Conversely, in late summer, during a very hot and dry period when shoot growth was negligible, the ratio of ^{14}C in secondary to primary metabolites was about 0.09 in the distal portion of branches and about 0.02 in the basal part (Figure 32.9).

Discussion

Patterns of Growth and Resin-Based Defenses

Figure 32.1 predicts that fertilization will ease nutrient limitations on tree growth, and result in lower allocation of carbon to resin-based defenses. As predicted, fertilized trees grew more than unfertilized trees. This was evident in height growth (Figures 32.5 and 32.6), fascicle growth (Figure 32.3), and root growth (Sword et al., Chapter 11), but not in cambial growth (Figure 32.4). Also as predicted fertilized trees had consistently lower resin flow than unfertilized trees. An exception to this pattern was that fertilization had no effect on resin flow in codominants found in unthinned plots (Figures 32.7 and 32.8). One explanation for this result is that fertilization increased photosynthesis and growth of codominants such that unfertilized and fertilized trees straddled the peak of the secondary metabolism curve in Figure 32.1.

A decrease in resin flow in response to fertilization is consistent with many studies that demonstrate a reduction in secondary defenses in response to fertilization (Bryant et al., 1987; Dudt and Shure, 1994; Larsson et al., 1986; Wilkens et

al., 1996a; but see Honkanen, 1995 for exceptions). Pines in this study exhibited reductions in monoterpenes and resin acids in response to fertilization. Two other studies conducted at this site have also indicated a marked reduction in resin flow in response to fertilizer. The effects of fertilization ran counter to predictions that any silvicultural practices that increase tree growth and "vigor" will also increase tree resistance to herbivores (Raffa, 1988; Waring, 1983; Waring, et al., 1992). Our results indicate that increasing productivity using fertilizer may actually increase susceptibility to SPB damage through reduced resin flow. Resin flow has been shown to negatively affect SPB (Lorio et al., 1995; Reeve et al., 1995) and is widely considered to be the most important defense against bark beetles in general (Christiansen et al., 1987; Nebeker et al., 1993). Nevertheless, forestry practices are typically aimed at maximizing stand productivity; however, maximizing pine productivity through fertilization or by initiating plantations on highly productive sites may ultimately result in greater SPB damage. Indeed, Lorio (1978) found that 72% of all infestations observed were on moist productive sites. Our results, however, must be evaluated with the knowledge that this experiment was conducted on a single site of juvenile pines. More research is needed to evaluate the generality of these patterns. Nonetheless, these results suggest that it may be necessary to balance the desire for rapid tree growth against concomitant decreases in resin flow, and increases in the risk of SPB damage.

Changes in soil fertility, resulting from changes in climate patterns, could decrease or increase the suitability of pines for SPB. The direction of this change will depend on whether global climate changes increase or decrease mineralization rates, and whether the affected population is under severe, moderate, or limited nutrient stress (Figure 32.1). Although it is difficult to predict how global change will influence soil-nutrient availability, the general pattern might be that of lower soil-nitrogen availability (Bazzaz, 1990). Our results suggest that this would tend to increase resin flow (and decrease success of attaching bark beetles) in pine populations experiencing moderate to little nutrient stress.

Soil moisture and, therefore, rainfall patterns also have strong effects on the physiology and resin production of loblolly pine (Lorio, 1986; Lorio et al., 1990). Water deficits lead to the development of latewood in which resin ducts are more plentiful (Lorio, 1993), and which leads to higher resin production (Lorio et al., 1990). In contrast, water surplus is associated with greater growth, but decreased resin flow (Lorio et al., 1990). Thus, fast-growing pines in well-watered sites may have increased susceptibility to SPB resulting from reduced resin flow. Because of this, foresters and planners must weigh the benefit of increased growth with the risk of decreased resistance to SPB. For instance, the placement of pine plantations on well-watered sites, such as bottomlands, may increase the risk of severe SPB problems.

The results of the ^{14}C study conducted in the spring and fall provide additional physiological evidence of shifts in carbon partitioning between primary and secondary metabolites associated with ontogeny and environmental conditions. These results are consistent with the principles of growth-differentiation balance (Loomis, 1932; Lorio, 1986), because rapid growth in the spring was associ-

ated with reduced carbon allocation to secondary metabolism (Figure 32.9). These represent the first data we know of that test the predictions of the growth-differentiation balance hypothesis using labeled carbon.

Figure 32.1 predicts that trees in thinned stands will have a larger carbon budget ($\text{g of fixed carbon} \cdot \text{g}^{-1} \text{ of plant tissue} \cdot \text{d}^{-1}$), will invest relatively more carbon in resin-based defenses, and will have increased resistance to southern pine beetles. Increased secondary chemistry in response to light has also been shown in numerous studies (Coley, 1993; Dudd and Shure, 1994; Larsson et al., 1986; Shure and Wilson, 1993; Wilkens et al., 1996b; Wilkens et al., 1996a). However, our data did not support this hypothesis. Trees in thinned and unthinned plots had very similar resin flow (Figures 32.7 and 32.8). Three possible explanations for the similarity in resin flow between thinned and unthinned plots are identified in the next section.

Explanation 1

Resin production was similar between thinned and unthinned trees because thinned trees did not have a larger carbon budget on a per gram basis ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) than unthinned trees as predicted by Figure 32.1. On a per gram of needle-tissue basis, photosynthesis was similar between thinned and unthinned plots (Table 32.1; Figure 32.2). However, photosynthesis was higher in thinned trees on a per fascicle and per 10-cm shoot basis because of larger needles (Table 32.2; Figure 32.3). Visual assessment suggested that crowns were larger in thinned trees. Thus, it is probable that a larger crown containing more robust needles will produce more carbon per unit time (i.e., $\text{g} \cdot \text{d}^{-1}$). We predicted, however, that the rate of carbon fixation would increase on a per gram of plant-tissue basis (i.e., $\text{g of fixed carbon} \cdot \text{g}^{-1} \text{ of plant tissue} \cdot \text{day}^{-1}$), which includes the bole and the root system, in addition to the crown. There was much greater bole growth (Figure 32.4), and somewhat greater root growth in thinned plots (Sword et al., Chapter 11). Furthermore, faster-growing trees probably had greater respiration and maintenance costs (Kozlowski et al., 1991; Ryan 1991). If the increase in bole and root growth were commensurate with the increase in crown size, then the larger pool of fixed carbon in thinned trees would be partitioned between larger sinks, which would result in similar photosynthesis on a $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ basis between thinned and unthinned trees and, thus, similar resin production on a $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ basis. Although this explanation is plausible, it seems improbable that the response of trees to vastly improved light and nutrient conditions would lead to exactly proportional increases in crown, bole, and root systems. Empirical evidence repeatedly demonstrates that plants exposed to increased light have altered root/shoot ratios. Furthermore, Donner and Running (1986) found that the increased leaf hydration and light availability associated with thinned plots of lodgepole pine led to a 21% increase in photosynthesis. Thus, there are several reasons to believe that photosynthesis on a whole plant basis ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) was indeed higher in thinned trees, and we are inclined to reject explanation 1.

Explanation 2

Resin production was similar between thinned and unthinned trees because growth in unthinned trees was more limited by nutrients, water, and space than by carbon and, therefore, had a relative surplus of carbon to support secondary metabolism. Based on soil-moisture measurements, unthinned trees experienced more severe water shortages than the thinned trees, which is consistent with published results on the effect of thinning for loblolly pine (Basset, 1964; Zahner and Whitmore, 1960). If water and nutrient shortages in unthinned trees led to growth inhibition, the proportion of fixed carbon available for secondary metabolism would then increase (Figure 32.1). This shift to secondary metabolism might enable trees in unthinned plots to match the resin flow levels of the trees on thinned plots with larger carbon budgets.

Explanation 3

Resin production was similar between thinned and unthinned trees because thinned trees allocated proportionally more carbon to storage than thinned trees. Thinned trees had a dramatically higher phloem-specific mass, which indicates greater carbohydrate storage (Figures 32.7 and 32.8). Increased allocation to storage in thinned trees could explain why thinned and unthinned trees had similar levels of resin flow even though thinned trees had greater total carbon budgets.

Regardless of the physiological explanation, our results suggest that thinning does not affect tree physiology in a way that increases resistance to SPB attack. Thus, alternative explanations must be explored as to why SPB infestations tend to be less severe in pine forests with low stand density than in “overstocked” pine forests. One explanation is that attacking adult beetles are able to aggregate on host trees more efficiently in dense stands than in thinned stands (Gara and Coster, 1968; Johnson and Coster, 1978; Showalter and Turchin, 1993; Turchin, 1989; Turchin and Thoeny, 1993).

Summary

Our results indicate that increased nutrient availability leads to an increase in growth and a reduction in resin-based defenses. Because of this, we recommend that foresters and planners consider the effect of fertilization and site fertility on both tree growth and SPB risk. Unfortunately, increased tree growth may frequently be associated with increased SPB risk. The mechanism for the usefulness of thinning as a silvicultural technique to limit SPB infestations remain unclear.

If, as expected, global change alters precipitation patterns and soil-nutrient availability in the southern United States, patterns of growth and secondary metabolism in southern pines will also change, and this will probably produce changes in the spatial and temporal pattern of SPB infestations. Because SPB have such a large impact on southern forests, even modest changes in SPB activity can have significant economic and ecological repercussions. Our theoretical and empirical

understanding of environmental effects on the physiology of southern pine remains imperfect but is growing. With this study, we now have some basis for predicting the direction and magnitude of changes in risk of SPB attack, anticipating how these patterns will vary from region-to-region or site-to-site, and suggesting appropriate changes in land-use strategies. Further testing and parameterization of such physiologically explicit models as depicted in Figure 32.1 should increase our ability to manage southern forests in a changing world.

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