The Productivity & Sustainability of Southern Forest Ecosystems in a Changing Environment
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11. Ecophysiological Response of Managed Loblolly Pine to Changes in Stand Environment

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Anticipated shifts in our global climate may expose southern pine ecosystems to such environmental stimuli as elevated carbon dioxide and water and nutrient deficiencies (Hansen et al., 1988; Kirschbaum et al., 1990; Peters, 1990). Global climate change may also increase the degree of stress to which trees are presently exposed (Kirschbaum et al., 1990; Peters, 1990). For example, the western extent of loblolly pine (*Pinus taeda* L.), now dictated by moisture availability for seedling establishment, is predicted to shift eastward with temperature and precipitation changes that may occur with global climate change (Miller et al., 1987).

Forest management practices that most effectively respond to global climate change can be identified only if we understand how the physiological and growth processes of trees in forest stands are affected by climate-mediated shifts in such essential resources as light, carbon dioxide, water, and mineral nutrients. The interdependence of above ground and root system processes, and the interactions between these processes and the availability of site resources, emphasize the need to simultaneously study above ground, root-system, and soil responses to environmental change. Tree responses to silvicultural manipulation should also be intensively evaluated so that cultural scenarios that maintain stand productivity and ecosystem integrity can be implemented in the event of global climate change.

Unfortunately, the physiology and growth of large trees in forest stands is poorly understood. The study of trees larger than seedlings has long been avoided because of the expense and logistical problems encountered when accessing large tree crowns on a continuous basis. Because microenvironmental variation within

the canopy of a forest stand strongly influences crown physiology, the study of crown processes requires intensive measurement vertically within the forest canopy. Also, most physiological studies conducted on large trees have relied on information derived from only one to five trees, and have excluded observations of root system dynamics.

Materials and Methods

Study Establishment

The study is located on the Palustris Experimental Forest in Rapides Parish, LA, on a Beauregard silt loam soil (fine-silty, siliceous, thermic, plinthaquic paleudult) with a one to three percent slope (Kerr et al., 1980). In 1981, container-grown loblolly pine were planted (1.83 x 1.83 m). Percent survival and diameters at breast height (DBH), measured during September of 1987, indicated that initial survival (92%) and tree size were evenly distributed.

During April of 1988, twelve treatment plots, thirteen rows of thirteen trees each, were established (Haywood, 1994). Blocking was not considered necessary because initial stand productivity was homogenous. Thinning and fertilization treatments were randomly assigned to the plots in a two by two factorial design with three replications. Levels of thinning were either maintenance of the original stocking (2,732 trees ha^{-1}) or removal of every other row of trees and every other tree in residual rows during November of 1988 (721 tree ha^{-1}). Levels of fertilization were either no fertilization or broadcast application of 747 kg ha^{-1} diammonium phosphate (150 kg ha^{-1} P and 135 kg ha^{-1} N) during April of 1989. The fertilization rate was based on recommendations for loblolly pine grown on the inherently nutrient-poor soil in this study (Kerr et al., 1980; Shoulders and Tiarks, 1983).

Tree Growth, Canopy Environment, and Crown Physiology

Height and DBH measurements of the interior twelve trees on each plot were repeated quarterly through 1993 (Haywood, 1994). Outside-bark stem volume per tree was calculated (Baldwin and Feduccia, 1987), and stem volume per hectare was determined.

Two replications were chosen as blocks for intensive measurement of the stand environment and tree physiology. Blocks were identified based on the influence of topography on soil drainage with one block appearing more poorly drained than the other. Free-standing, steel, radio towers that supported wooden walkways in the lower and upper one-third of the canopy were installed to access at least eight dominant or codominant trees on the interior of each plot.

Canopy environmental measurements were limited to one block that was chosen based on the proximity of plots relative to each other. At three north-facing and three south-facing locations in both the upper and lower one-third of measure-

ment plot canopies air temperature and photosynthetic photon flux density (PPFD) were monitored using custom-designed sensor units that were wired to one data acquisition system per plot (Model 576, Keithley/Metrabyte/Asyst/DAC Inc.). Sample branches were randomly selected from those that were logistically available, which resulted in measurement of the microclimate of two to four trees per plot and canopy level.

Sensor units consisted of two sensor housings, 50 cm apart, that were attached to polyvinyl chloride pipe (1.5 cm diameter). Sensor units were affixed to the towers and positioned adjacent to sample branches. Each sensor housing contained one shielded, solid-state temperature sensor (AD-592C, Analog Devices), and two photodiodes (BS500B, Sharp Electronics Corp.) which were positioned on opposite sides of the sensor housing. Sensors were wired so that mean branch temperature and mean branch PPFD were recorded. Sensor units were reassigned to different sample trees and branches, and PPFD sensors were calibrated twice per year against a recently calibrated quantum sensor.

Using walkways, crown physiological processes were monitored in the upper and lower one-third of the canopies of two blocks. Once during 1992 and four times during 1993, three upper and lower crown branches from each of three trees were randomly chosen from logistically available branches. Time and sampling procedure constraints prevented measurement of all treatments on the same day. Thus, data were collected over a two-day period with each fertilization treatment being measured in one day. One set of measurements was collected from both blocks in the morning and a second set of measurements was collected in the afternoon. The plot measurement sequence in the afternoon was the reverse of that in the morning.

Net photosynthesis measurements were conducted on two to three fascicles (six to nine needles) from the mature foliage on south-facing, terminal, or adjacent lateral shoots. In situ net needle carbon dioxide (CO_2) uptake rate was quantified under ambient conditions with a portable photosynthesis system (LI-6200, Li-Cor Inc.), and expressed as the mean of data collected at each of three branches per canopy level and treatment.

Branch carbon exchange index (BCEI), was calculated to express the net amount of carbon assimilated by the most recently mature internode. To develop this index, the mean fascicle length and projected needle surface area (PNSA) of ten fascicles on each of three randomly selected terminal shoots per treatment and canopy level of one block were quantified once during 1993. Linear regression equations that predicted PNSA per fascicle from fascicle length were developed for each treatment and canopy level. Equations for each treatment had significantly different slopes. Therefore, separate equations were used to predict PNSA of fascicles used for physiological measurements. After completion of physiological measurements 1) the mean fascicle length of foliage used for the physiological measurements was quantified, 2) PNSA was predicted using the appropriate equation, and 3) BCEI was calculated by multiplying the total number of fascicles on the shoot by the predicted PNSA, and then multiplying by the mean rate of net CO_2 uptake per unit of projected needle surface area.

Soil Environment and Root System Growth

On the two blocks used for physiological measurements, vertical Plexiglass@ rhizotrons were installed at three interior locations per plot. Rhizotron locations were randomly chosen from those that had a stable microtopography and were associated with a dominant or codominant tree that was not adjacent to a missing or dead tree, or a tree that was heavily infected with *Cronartium fusiforme* Hedge & Hunt (fusiform rust). At each location, one longitudinal side of an excavated area (35 x 20 x 80 cm) was patched with a mortar prepared with sieved soil from the site. Sheet metal screws were placed at 10 cm intervals around the periphery and down the center of Plexiglass@ sheets (0.3 x 35.4 x 76 cm) to secure rhizotrons onto the soil face. Rhizotrons were insulated with Styrofoam between root observations.

Soil temperature was measured with solid-state temperature sensors (AD592C, Analog Devices), embedded in epoxy resin inside 5 cm pieces of stainless steel tubing that were insulated with waterproof electrical sealant. Insulated sensors were inserted at 5, 15, and 30 cm through ports in rhizotrons. Sensors were also installed at two randomly chosen locations, independent of rhizotrons, for a total of five series of soil temperature sensors per measurement plot. Soil temperatures were measured at ten-day intervals beginning in June of 1992 and continuing through the study.

In all replications, one set of stationary time-domain reflectometry sensors was installed vertically at plot centers to quantify volumetric soil-water content in 0 to 20 and 20 to 40 cm depths of the soil. Measurements were taken at ten- to fourteen-day intervals beginning in June of 1992 and continuing through the study. Volumetric soil-water content was also measured with sensors inserted horizontally at 5, 15, and 30 cm through ports in one rhizotron per plot of one block. These measurements, taken at six-hour intervals, began in May of 1993 and continued through the study. Climate data were recorded in an open field 25 m from the study with an electronic weather station (Omnidata International, Inc.).

At ten-day intervals beginning in April of 1993, the long lateral new root length observed in rhizotrons was traced with permanent marker onto heavy-duty acetate sheets (2 1.6 x 30 cm) attached to left and right sides of the plexiglass. Observations were recorded cumulatively. After each measurement date, acetate sheets were photocopied, and a computer image tile of each photocopy was created using a desktop scanner. The length of the lines contained in each image file was quantified using GSROOT software (PP Systems Inc.). Net lateral root elongation occurring in the 0 to 30 cm depth of rhizotrons was calculated by subtraction. After each measurement period, the number of new roots ($\geq$ 0.5 cm) initiated in the 0 to 30 cm depth was also quantified.

On June 17 (day 168), August 29 (day 241), and December 6, 1993 (day 340), visible lateral roots were traced and their lengths were quantified as described. These lengths, expressed as a fraction of the length of lateral roots that had accumulated since April 13, 1993, described lateral root persistence. When roots were traced for lateral root persistence measurements, ectomycorrhizai and non-

mycorrhizal roots were differentiated by marker color. Roots were considered ectomycorrhizal by the presence of one or more ectomycorrhizae or swollen short roots. Ectomycorrhizal colonization was expressed as the percentage of lateral root length that appeared ectomycorrhizal.

Data Analyses

During December of 1993, tree height, DBH, and stem volume, as well as stem volume per hectare, were subjected to analyses of covariance using a completely random, two by two factorial experimental design with three replications (Haywood, 1994). The factors were two levels each of fertilization and thinning. Covariates were initial height, DBH, stem volume, and stem volume per hectare measured in early March of 1989 before height-growth began.

For each fertilization treatment, branch air temperature and PPFD were subjected to analyses of variance using a repeated measures split-split-plot design with two replications. Whole plots were level of thinning and subplots were canopy level (upper or lower crown). Net needle CO, uptake rate and BCEI were analyzed by fertilization treatment using a repeated measures, split-split-split-plot design with four replications. Whole plots were level of thinning (thinned or not thinned), and subplots were canopy level and time of day (morning or afternoon). Analyses of variance were conducted by measurement date on soil temperature (5, 15, 30 cm) and water content (0 to 20, 20 to 40 cm) using a randomized complete block design with two blocks, and a completely random design with three replications, respectively. Significant treatment effects were noted if trends were consistent over time. Net root elongation and root initiation were analyzed using a randomized complete block, split-plot in time design with two blocks. Two levels each of thinning and fertilization were the whole plot treatments, and time was the subplot treatment. Lateral root persistence and ectomycorrhizal colonization were analyzed by measurement date using a randomized complete block design with two blocks. Main and interaction effects were considered significant at $p \leq 0.05$ unless otherwise noted.

Results

Tree Growth, Canopy Environment, and Crown Physiology

Analyses of covariance indicated that thinning significantly increased tree DBH and volume (Table 11.1). Fertilization significantly increased tree height, DBH and volume, as well as stand volume. Nearly significant interactions between thinning and fertilization were observed in tree DBH ($p = 0.0559$) and volume ($p = 0.0571$), with fertilization causing a greater increase in these variables on the thinned plots than on plots that were not thinned.

On plots that were not fertilized, lower canopy PPFD was significantly greater on thinned plots when compared to those that were not thinned (Figure 11.1).

Table 11.1. Growth and Yield of Loblolly Pine Before, and Four Years After Fertilization With Nitrogen and Phosphorus, and Manipulat Stand Density With Row Thinning. Analyses of Covariance Were Conducted on Data Collected in the Thirteenth Growing Season. For E Variable, the Covariant Was the Same Variable at the Start of the Study in March of 1989

Treatment	Trees Surviving in 1993 (number ha $^{-1}$)	March 1989, 9th growing season				December 1993, 13th growing		
		Height (m)	DBH (cm)	Tree Volume (m^3)	Total Volume (m^3 ha^{-1})	Height (m)	DBH (cm)	Tree Volume (m^3)
Not Thinned, Not Fertilized	2,783	9.1	11.2	0.0488	135.8	13.1	13.2	0.1009
Not Thinned, Fertilized	2,600	9.1	11.4	0.0514	133.7	14.1	13.9	0.1220
Thinned, Not Fertilized	731	8.9	10.9	0.0483	35.4	12.4	16.5	0.1446
Thinned, Fertilized	711	8.6	10.6	0.0420	29.8	13.4	18.4	0.1897

	Analysis of Variance		Analyses of Covariance		
	df	MS	df	MS	
Thinning(T)	1	11,647,3 11.6	1	0.670 1	34.414	0.0082
Fertilizer(F)	1	30,947.3	1	3.2858	5.916	0.0037
T × F	1	19,806.3	1	0.0222	1.757	0.0009
Error mean square	8	15,783.1	7	0.1258	0.3356	0.00017
Covariant			1	0.4691	0.8000	0.0005
	(Probability > F – value)				(Probability > F – value
Thinning(T)	0.000 1			0.0543	0.0001	0.0002
Fertilizer(F)	0.1990			0.0014	0.0040	0.0022
T × F	0.295 1			0.6866	0.0559	0.0571

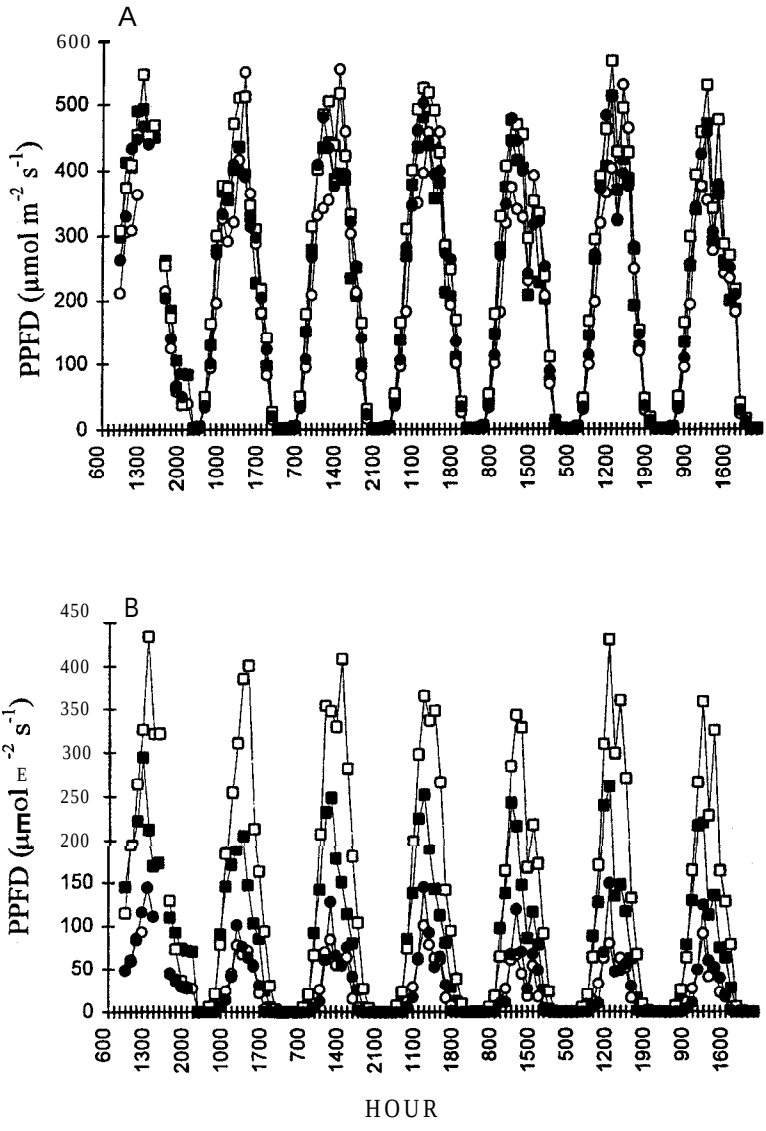

Figure 11.1. Typical photosynthetic photon flux density (PPFD) (µmol m-2 s- 1) in the upper (A) and lower (B) one-third of the canopy between 0600 and 2300 hours during one week in August of 1993. Data are hourly means of four 15-minute measurements collected at six branch locations on plots that were not thinned and either were fertilized (●) or were not fertilized (○), and plots that were thinned and either were fertilized (■) or were not fertilized (0).

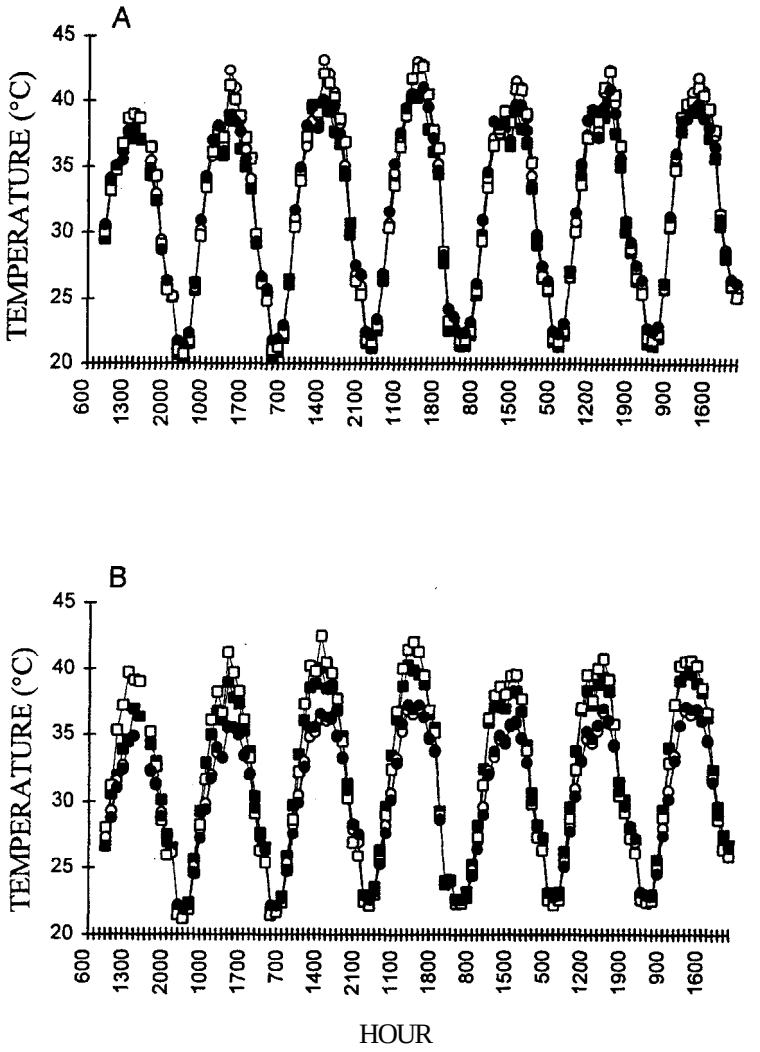

Figure 11.2. Typical branch temperature (°C) in the upper (A) and lower (B) one-third of the canopy between 0600 and 2300 hours during one week in August of 1993. Data are hourly means of four 15-minute measurements collected at six branch locations on plots that were not thinned and either were fertilized (●) or were not fertilized (○), and plots that were thinned and either were fertilized (■) or were not fertilized (□).

Although a similar trend was found, thinning did not significantly increase PPFD in the lower canopy of fertilized plots. Branch temperature in the lower canopy of both fertilization treatments was significantly increased by thinning with midday branch temperature differences of 2 to 5 °C on sunny days (Figure 11.2). Upper canopy PPFD and branch temperature were not affected by thinning in either fertilization treatment.

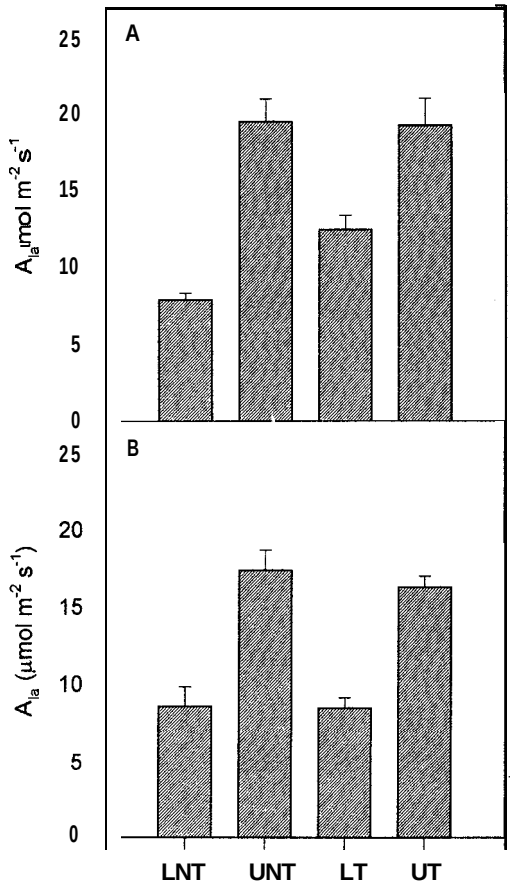

Figure 11.3. Typical net needle CO, uptake (A,,) (µmol m^{-2} s^{-1}) on plots that either were fertilized (A) and were not fertilized (B). Data are the mean of three measurements collected in the upper (U) and lower (L) one-third of the canopy on plots that were either thinned (T) or were not thinned (NT). Vertical bars indicate the standard error of the mean.

In both fertilization treatments, the rate of needle net photosynthesis was significantly higher in the upper crown than in the lower crown (Figure 11.3). Thinning did not affect needle net photosynthesis in either fertilization treatment. Although experimental design limitations prevented direct statistical comparison, needle net photosynthesis appeared slightly higher on plots that were fertilized when compared to plots that were not fertilized.

Upper crown BCEI was significantly higher than that of the lower crown (Figure 11.4). In both fertilization treatments, BCEI was significantly higher in the lower crown of the thinned plots when compared to the lower crown of plots that were not thinned. Thinning did not significantly affect BCEI in the upper crown of either fertilization treatment. Although experimental design limitations prevented statistical comparison, BCEI in both thinning treatments and in both

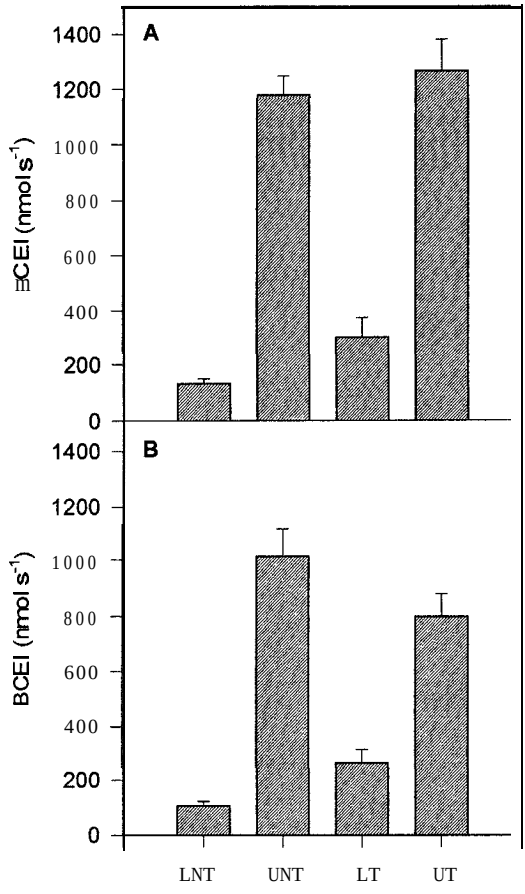

Figure 11.4. Typical branch carbon exchange index (BCEI) (nmol s^{-1}) on plots that either were fertilized (A) or were not fertilized (B). Data are the mean of three measurements collected in the upper (U) and lower (L) one-third of the canopy on plots that either were thinned (T) or were not thinned (NT). Vertical bars indicate the standard error of the mean.

crown levels appeared to be higher in response to fertilization. This effect was most pronounced in the upper crown of the thinned plots in which BCEI was 68% higher four years after fertilization.

Soil Environment and Root System Growth

During 1992 and 1993, 146 and 138 cm of precipitation were received, respectively. Approximately 57% of the precipitation in both years occurred during March through September. In June through September, the volumetric soil-water content at depths of 0 to 20 and 20 to 40 cm averaged 27.3 and 24.5%, respectively during 1992, and 26.5 and 23.6%, respectively during 1993. Between October of 1992 and May of 1993, the volumetric soil-water content at depths of 0 to 20 and

20 to 40 cm averaged 35.4 and 30.5%. Between late June and September of 1992, the volumetric soil-water content at the 0 to 20 cm depth was significantly greater on the thinned plots when compared to plots that were not thinned. Otherwise, thinning and fertilization treatments did not significantly affect volumetric soil water content.

Volumetric soil-water content, measured biweekly, decreased 32 and 27% at depths of 0 to 20 and 20 to 40 cm, respectively, between June and September of 1993. Daily measurements allowed greater resolution of soil-water content trends. Lack of precipitation between late May and mid-June, and between mid-July and early August were associated with 59 and 70% reductions, respectively, in soil-water content measured at 15 cm (Figure 11.5). A similar trend was observed at depths of 5 and 30 cm.

Soil temperature at the 15 cm depth was significantly higher (0.7 "C) on the thinned plots during the growing season; in winter, the soil temperature was significantly higher (0.6 "C) on plots that were not thinned (Figure 11.6). A similar response was observed at depths of 5 and 30 cm. Throughout the year, soil temperatures were significantly lower (0.4 "C) at depths of 15 and 30 cm on plots that were fertilized than on plots that were not fertilized.

Lateral root elongation and initiation in the 0 to 30 cm depth of the soil exhibited a multimodal pattern between April of 1993 and March of 1994 with the greatest growth in spring and early summer (Figures 11.7 and 11.8). During peak root growth, lateral root elongation exhibited a bimodal pattern. Root elongation and initiation declined 92 and 87%, respectively, in midsummer and continued at a reduced rate through fall and winter with several short periods of accelerated growth.

The thinning operation, which had been conducted during the fall of 1988, significantly increased lateral root elongation and initiation in the 0 to 30 cm depth of the soil during 1993 (Table 11.2). Fertilization did not significantly affect lateral root elongation or initiation. However, lateral root elongation was significantly affected by an interaction between time, thinning, and fertilization. Analyses of variance by day indicated that on the thinned plots, lateral root elongation was greater in response to fertilization on five of eighteen measurement days between June and January (Figure 11.7). Significant treatment effects during peak root growth corresponded to lower coefficients of variation and more stable soil environmental conditions relative to seasonal trends (Figure 11.9).

Of the lateral root length that accumulated in rhizotrons during 1993, approximately 99, 79, and 48% persisted and were visually observed on June 17 (day 168), August 29 (day 241), and December 6, 1993 (day 340), respectively. Losses were attributed to both mortality and obstruction of roots from view, Thinning did not significantly affect the persistence of lateral roots in rhizotrons, but fertilization significantly increased their persistence between April 13 and August 29, 1993 (Figure 11.10). The percentage of lateral root length with visible signs of ectomycorrhizal colonization increased from approximately 29 to 45% between June 17 (day 168) and December 6, 1993 (day 340), but was not significantly affected by thinning or fertilization.

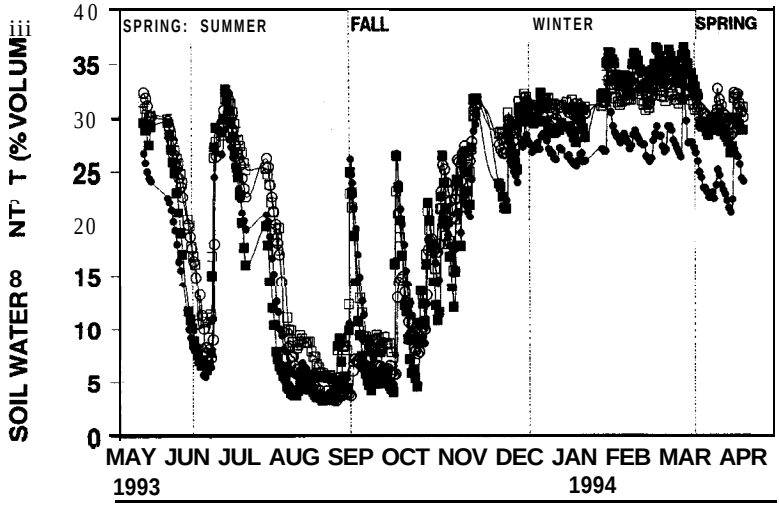

Figure 11.5. Daily percent volumetric soil-water content at 15 cm between May of 1993 and March of 1994. Data are the mean of four measurements collected at six-hour intervals at one location in each plot of one replication (not thinned and not fertilized (0); not thinned and fertilized (0); thinned and not fertilized (0); thinned and fertilized (■)).

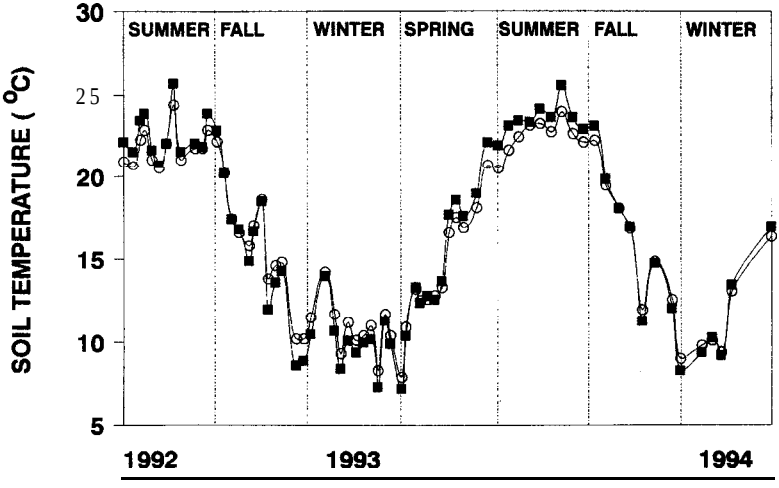

Figure 11.6. Soil temperature (“C) at 15 cm between June 1992 and March 1994 on plots that either were thinned (W), or were not thinned (0). Data are the mean of two replications of five measurements that were collected at approximately two-week intervals.

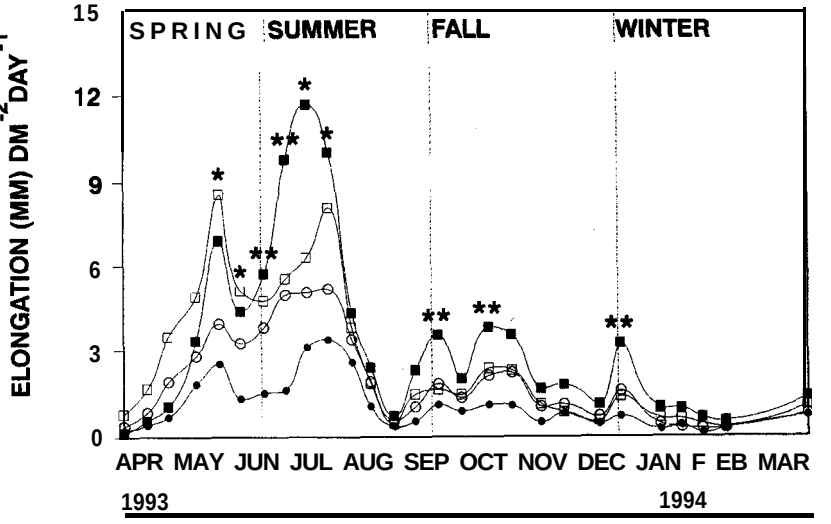

Figure 11.7. Seasonal rate of long lateral root elongation (mm dm^{-2} day-^{1}) in rhizotrons between April of 1993 and March of 1994. Data are the mean of two replications of six measurements (not thinned and not fertilized (0); not thinned and fertilized (0); thinned and not fertilized (□); thinned and fertilized (■)). The thinning effect was significant on dates noted with "*", and both thinning and T × F ($P \leq 0.07$) effects were significant on dates noted with "**".

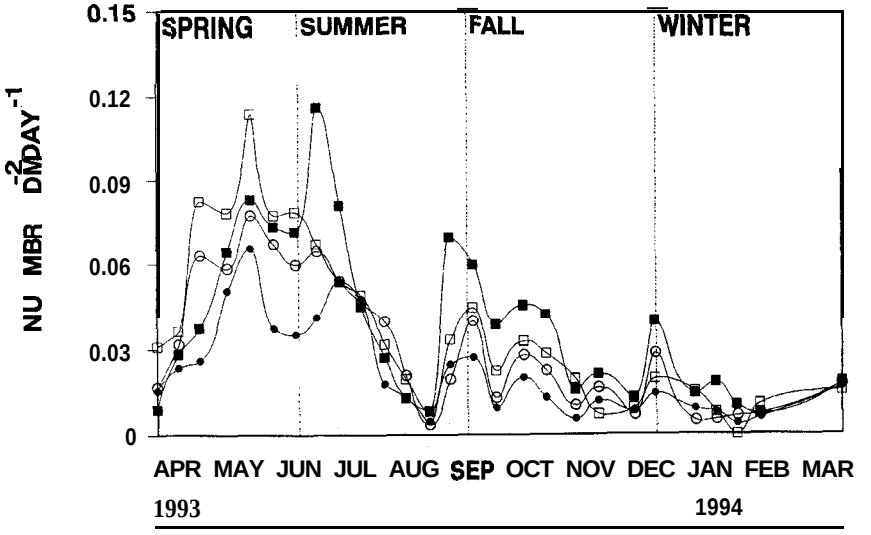

Figure 11.8. Seasonal rate of long lateral root initiation (number dm-^{2} day-^{1}) in rhizotrons between April of 1993 and March of 1994. Data are the mean of two replications of six measurements (not thinned and not fertilized (0); not thinned and fertilized (0); thinned and not fertilized (□); thinned and fertilized (■)).

Table 11.2. Analyses of Variance of Long Lateral Root Elongation (mm dm^{-2} day^{-1}), and Initiation (number dm^{-2} day^{-1}) at the 0 to 3
Depth of the Soil During April 1993 through March 1994

Source of Variation	Long Lateral Root Elongation			Long Lateral Root Initiation		
	df	MS	Probability > F − value	df	MS	Probability >
Block (B)	1	22.5764	0.1502	1	0.00065	0.21
Thinning (T)	1	110.4932	0.0238	1	0.00739	0.01
Fertilization (F)	1	0.7444	0.7500	1	0.00034	0.34
T × F	1	30.45 16	0.1117	1	0.00159	0.09
B x T x F (error a)	3	6.1057		3	0.00027	
Time	26	29.3242	0.000 1	26	0.00428	0.00(
Time x B (error b)	26	0.869 1		26	0.00016	
Time x T	26	4.4926	0.000 1	26	0.00024	0.26
Time × F	26	1.0868	0.1688	26	0.00030	0.07
Time x T x F	26	2.2345	0.0003	26	0.00019	0.50
Time × T × F x B (error c)	78	0.8173		78	0.00020	

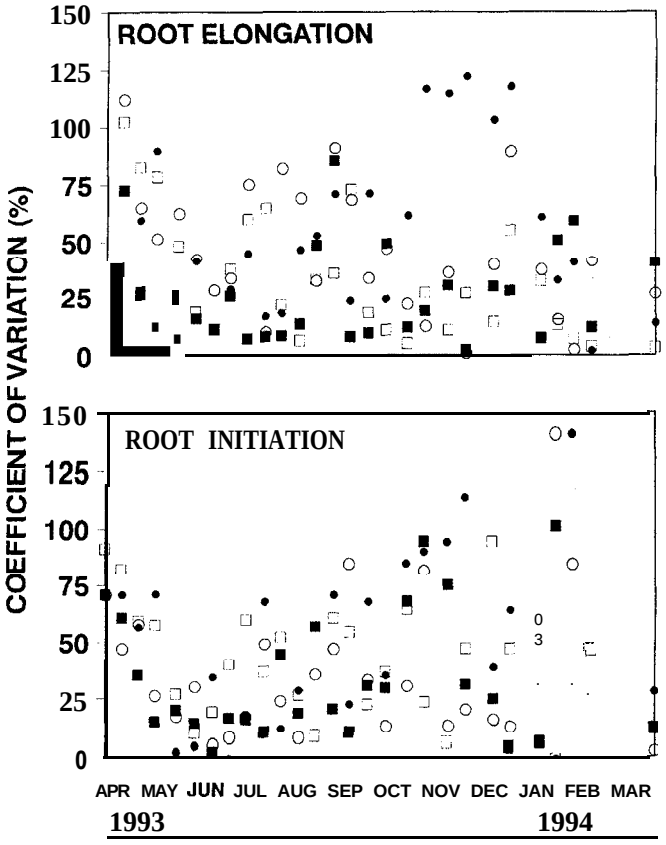

Figure 11.9. Coefficients of variation of root elongation (mm dm-^{2}) and initiation (number dm^{-1}) observed between April of 1993 and March 1994. Data are coefficients of variation associated with the mean of two replications.

Discussion

Thinning significantly increased both aboveground productivity and root growth. Significant increases in aboveground growth were consistently observed in response to fertilization, and on 25% of the measurement days between May and October, root growth on the thinned plots was significantly stimulated by fertilization. This is in contrast to the results of others who have found an inverse relationship between fine root production and such variables as site quality and fertilization (Comeau and Kimmins, 1989; Gower et al., 1992; Haynes and Gower, 1995; Keyes and Grier, 198 1; Santantonio and Santantonio, 1987; Vogt et al., 1983; Vogt et al., 1987). The difference between our observations and those reported elsewhere demonstrate the complexity of growth responses to the forest stand environment.

Thinning and fertilization reduce the competition among trees for such es-

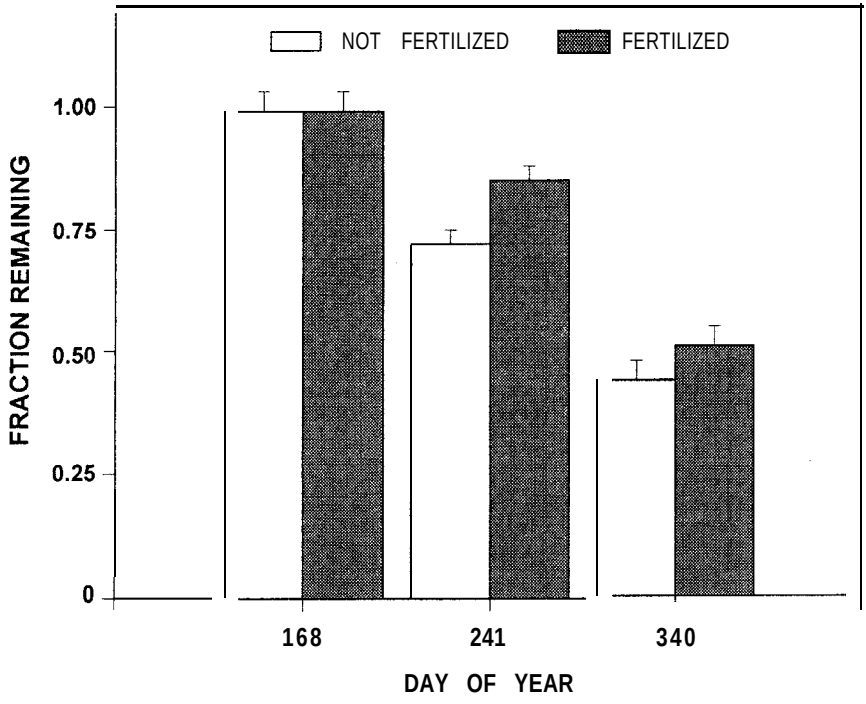

Figure 11.10. Fraction of the long lateral root length on plots that were and were not fertilized, that persisted in rhizotrons when compared to that accumulated between April 13, 1993 and each of three dates (June 17, day 168; August 29, day 241; December 6, day 340). Vertical bars indicate the standard error of the mean.

sential resources as light, water, and mineral nutrients (Kozlowski et al.. 199 1). By age thirteen, the plots that were not thinned were overstocked and had live-crown ratios less than 36%. Smith (1986) suggested that stands with live-crown ratios below 30 to 40% may not be vigorous enough to respond positively to thinning. In our study, light competition and reduced rates of photosynthate production in the canopies of plots that were not thinned may have limited the availability of carbohydrates for root metabolism, and therefore, root growth.

Beauregard silt loam soils are generally low in available phosphorus, and loblolly pine has responded well to the amounts of nitrogen and phosphorus applied in this study (Shoulders and Tiarks, 1983; Tiarks, 1982). Typically, nitrogen fertilization favors aboveground rather than root growth and phosphorus amendments stimulate root growth (Marschner, 1986). Four years after fertilization, insufficient phosphorus on plots that were not fertilized may have reduced root growth. Stimulation of root growth may be one mechanism by which phosphorus fertilization has eliminated this inhibition and has increased the growth of

loblolly pine on some coastal plain soils (Haywood and Burton, 1990; Pritchett and Gooding, 1975). Our results suggest that conclusions about carbon partitioning to the root system in response to silvicultural treatments cannot be made without information on the environmental and physiological status of a stand.

Anticipated shifts in the earth's climate include significantly higher global temperatures (Hansen et al., 1988; Peters, 1990), and a simultaneous reduction in precipitation (Hansen et al., 1988). Furthermore, elevated atmospheric temperature and carbon dioxide, together with reduced precipitation, may alter the chemistry of organic matter in soil (Johnson, 1995; Van Cleve and Powers, 1995). Because the cycling of mineral nutrients through forest ecosystems is strongly influenced by the quantity and quality of organic matter deposited in the soil (McColl and Gressel, 1995), mineral nutrient availability may also be affected by global climate change.

Carbon partitioning among plant organs is the principal mechanism by which plants respond to seasonal patterns of water, mineral nutrient, and carbohydrate availabilities (Dickson, 1989). For example, water and mineral nutrient limitations generally result in a shift in biomass accumulation from the crown and bole to the root system (Gower et al., 1992; Santantonio and Santantonio, 1987; Vogt et al., 1983); under water and mineral nutrient sufficiency, but light limitation, however, crown growth is favored (Waring, 1991). To use these relationships to manipulate forest responses to climate change, interactions between physiological and growth processes within whole trees in a stand environment must be understood. With this information, it may be possible to use silvicultural treatments to manipulate both resource availabilities and internal tree physiological relationships in an effort to compensate for potential effects of global climate change on forests.

Older woody roots and newly elongated roots provide both water and mineral nutrients for tree growth (Eissenstat and Van Rees, 1994; MacFall et al., 1991; Van Rees and Comerford, 1990). However, the absorption of water and mineral nutrients in environments where these resources are limited may primarily rely on the growth of new roots (Eissenstat and Van Rees, 1994). Furthermore, calcium uptake primarily occurs apoplastically through the immature endodermis of newly elongated roots (Russell and Clarkson 1976). In our study, 63 and 62% of the lateral root elongation and initiation, respectively between April of 1993 and March of 1994, occurred from May to July, 1993. Because new roots that were produced during this twelve-week period not only supplied resources for tree growth, but also provided a foundation from which additional new roots grew, it is probable that environmental and physiological variables during this period affected root function throughout the year.

A 36% reduction in the rate of root elongation, which was observed in late spring of 1993, was associated with rapid expansion of new shoots and fascicles. Root growth is a weaker photosynthate sink than branch growth, and a complementary pattern of shoot and root growth is typical of such species with recurrent shoot growth as loblolly pine (Dickson, 1989; Dickson, 1991). The drop in root

elongation that we observed could have been a response to reduced carbohydrate availability for root metabolism. However, a similar simultaneous reduction in new root initiation was not observed in late spring, which suggests that carbohydrates were not limited for root growth. Reduced root elongation with no effect on root initiation was also associated with twenty-two days of drought in June that caused a 59% decrease in soil-water content. Similarly, others have reported that water deficits reduce lateral root elongation but have minimal effects on root initiation (Hipps et al., 1995; Teskey and Hinckley, 1981). These results suggest that the extension of new loblolly pine roots into the soil during peak root growth may be strongly influenced by fluctuations in soil moisture.

Four years after thinning and fertilization, temperatures of the soil and lower crown were elevated in response to thinning but were reduced by fertilization. Temperature responses appeared to be related to changes in shading caused by branches and foliage in the canopy that were either removed with the thinning operation or produced in response to fertilization. Only a small increase in soil-water content in response to thinning was observed, and no significant soil-water response to fertilization. Lack of a stronger effect on soil-water content may have been caused by reequilibration of the foliage distribution in the canopy, and similarity of transpiration potentials that evolved after application of silvicultural treatments (Cregg et al., 1990).

Gower et al. (1993) found that new foliage was predominantly produced in the mid- and lower canopy of a ponderosa pine *(Pinusponderosa* Dougl. ex P. Laws.) stand, but was produced in the upper and mid-canopy of a similarly stocked red pine (*Pinus resinosa* Ait.) stand. This phenomenon was attributed to the open nature of the ponderosa pine crown compared to that of red pine. In our study, the upper canopy received significantly more light than the lower canopy, and PPFD in the upper canopy was unaffected by silvicultural treatment. In the lower canopy, however, we found that loblolly pine responded to a thinning-induced increase in PPFD by increasing foliage production. Similar to the observations of Vose (1988), we also found that on the thinned plots, fertilization increased loblolly pine foliage production in the lower canopy. However, as the lower canopy became more dense, PPFD was reduced. Comparable relationships have been presented between fertilization, canopy leaf areas, and light levels in pine forests (Gower et al., 1993; Vose and Allen, 1988).

Changes in the canopy environment with crown depth were positively related to rates of photosynthesis. Similar to the results of Teskey et al. (1994), rates of photosynthesis within upper and lower portions of the canopy were only slightly affected by silvicultural treatment. However, fertilization increased fascicle production in both the upper and lower canopies and thinning increased fascicle production in the lower canopy. As a result, when rates of photosynthesis were expanded to express branch level carbon exchange, it was apparent that thinning and fertilization greatly increased carbon fixation in the crown. Clearly, an understanding of crown processes that control forest productivity requires the simultaneous measurement of environmental, physiological, and growth variables vertically within the forest canopy.

Our results present the potential for manipulation of root growth using silvicultural tools that alter photosynthate production in tree crowns. Starch accumulates in root parenchyma cells in fall and winter and is a primary carbohydrate source for root growth early in the growing season (Ericsson and Persson, 1980; Ford and Deans, 1977; Gholz and Cropper, 1991). In addition to early growth, a fall peak in root activity has been reported (Dickson, 1991; Grier et al., 1981; Santantonio and Santantonio, 1987). However, the consistent occurrence of a second peak in root growth is strongly dependent, in part, on environmental conditions earlier in the growing season (Dickson, 1991). A larger amount of carbon fixation in the canopy may stimulate root growth throughout the growing season by increasing the amount of photosynthate translocated to, and the amount of starch stored in, the root system.

In our study, canopy environmental responses to silvicultural treatments were isolated in the lower portion of the crown. It may be possible to manipulate carbon fixation in the lower canopy alone to affect the amount of photosynthate translocated to the root system. In a young tree, photosynthate produced by the most recently matured foliage is translocated acropetally to be metabolized by developing internodes and fascicles, whereas, that which is produced by older foliage is partitioned basipetally to support root growth (Dickson, 1991; Dickson, 1989; Watson and Casper, 1984). A similar pattern of carbon partitioning has been found within the branches of *Populus* trees (Dickson, 1986). Dickson (1986) suggested that the terminal shoot and lateral branches in the crowns of young *Populus* trees contributed more photosynthate for root growth than did the lateral branches of the lower crown. However, they also stated that the magnitude of this relationship may change with light levels in the canopy. Research should be conducted to determine if maintenance and stimulation of a positive carbon balance in the lower canopy of a managed forest stand contributes significantly to the amount of photosynthate allocated for root growth.

In addition to root elongation and initiation, the rate of fine root anatomical development also may be influenced by resource availability. Accelerated transformation of primary roots into secondary roots could reduce the susceptibility of new roots to such environmental extremes as water deficit. This would result in reduced mortality, and lead to a larger infrastructure from which new roots could initiate as conditions became favorable. In our study, the persistence of lateral roots that grew in rhizotrons between April and August was greater in plots that were fertilized than in those that were not fertilized. Because of dissimilarity between root environments in undisturbed soil and in rhizotrons, we cannot make inferences about tine root mortality based on the persistence of lateral roots in rhizotrons. However, increased lateral root persistence in response to fertilization may be attributed to the developmental status that roots achieved in response to mineral nutrient availability.

This relationship is apparent in the data presented by Gower et al. (1993), in which biomass partitioning by Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) was quantified in response to five levels of soil amendment. Although biomass partitioned to the root system was greater on control than on amended

plots, a larger proportion of the total small ($> 2 \leq 5$ mm diameter) plus very tine (≤ 2 mm) root biomass occurred in the small, rather than the very fine category, on the amended plots. The reverse was true on the control plots.

We found that under present-day climate conditions, the potential exists for water limitations to reduce root growth. If global climate change significantly alters the pattern or amount of precipitation received by southern pine forests, the growth of tree roots could be inhibited. In the event of global climate change, factors that may strongly influence root system function are the amount of root growth that occurs before the onset of water deficits, and the rate at which primary roots undergo secondary development. Our results provide important insight on how stand-management practices could be used to manipulate these factors.

Summary

Many of the potential negative impacts of global climate change on southern pine forests will manifest through reduced availabilities of soil resources. We found that during the period of peak root growth, the elongation of new loblolly pine roots was closely related to the rate at which soil moisture declined. This level of responsiveness was also noted by Vogt et al. (1993) who emphasized the sensitivity of tine roots to environmental change, in part, because of their direct contact with the soil.

The ability of tree root systems to procure key resources in a changing climate may be limited. Thus, aggressive forest management strategies that maintain optimum stand conditions will be needed as climate change occurs. Such silvicultural treatments as thinning and fertilization are effective through their influence on stand environment and resource variables, many of which are similar to those expected to shift with global climate change. We found that silvicultural manipulation of stand density influenced the vertical distribution of light in the canopy. The intensity and distribution of light in the canopy, in addition to the branch carbon exchange indices suggest that carbon fixation at the canopy level was stimulated by manipulation of stand density. Elevated root growth observed in response to thinning may have been caused by an increase in the amount of photosynthate translocated from either the entire crown or the lower crown alone. This suggests that such silvicultural tools as thinning and fertilization offer an opportunity to manipulate relationships between light, water, and mineral nutrient availabilities in forest stands, and carbohydrate partitioning within trees to buffer the possible negative effects or enhance the potential positive effects of global climate change on southern pine forests.

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