ORIGINAL ARTICLE

Mary Anne Sword Sayer · James D. Haywood

Fine root production and carbohydrate concentrations of mature longleaf pine (*Pinus palustris* P. Mill.) as affected by season of prescribed fire and drought

Abstract The historical range of longleaf pine (*Pinus palustris* P. Mill) has been greatly reduced, in part, by lack of fire. Recently, the application of fire has become an accepted practice for the restoration of longleaf pine to former parts of its natural range. This study was designed to evaluate the effects of season of prescribed fire on the root growth and nonstructural carbohydrate concentrations of longleaf pine, and identify the time of year when fire has the least negative effect on longleaf pine root processes. We found that root growth was generally less on July-burned plots than on either March- or May-burned plots and we attribute these responses to the effect of fire on interaction between root processes and the soil environment. Specifically, soil water and temperature conditions may have been less favorable for root growth on the July-burned plots compared to the March- and May-burned plots. With two years of information on the seasonal dynamics of foliage production, root growth, and root carbohydrates, we determined that at our study site, optimal prescribed fire would impact tree growth less in November through March compared to other times of the year. We also observed that severe drought during the 1998 growing season was associated with a 3-month delay in peak root growth, and prolonged drought in 1999 through 2000 coincided with a reduction in root starch storage. We conclude that season of prescribed fire potentially affects root processes, but that severe or prolonged drought may either interact with or override these effects.

Keywords Leaf area index · Net root elongation · Nonstructural carbohydrates · Prescribed burning · Root phenology

M. A. S. Sayer (✉) · J. D. Haywood
USDA Forest Service, Southern Research Station, Alexandria Forestry Center,
2500 Shreveport Highway, Pineville, LA 71360, USA
e-mail: msword@fs.fed.us
Tel.: +318-473-7275
Fax: +318-473-7273

Introduction

Longleaf pine (*Pinus palustris* P. Mill.) ecosystems dominated as much as 37.2 million hectares of the southeastern United States in the late 1800s (Landers et al. 1995). By 1935, logging reduced this area 78%. Early efforts to reestablish longleaf pine were unsuccessful due to the difficulty of regeneration and exclusion of fire as a management tool (Barnett and Dennington 1992; Boyer 1989; Outcalt 2000). Gradually, the natural range of longleaf pine was converted to plantations of loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.), and today, less than 2 million hectares of longleaf pine forests exist (Landers et al. 1995; Outcalt 2000; Outcalt and Sheffield 1996).

Fortunately, regeneration research has recently identified successful approaches to establish longleaf pine (Barnett and McGilvray 1997; Boyer 1989; McGuire et al. 2001; Ramsey et al. 2003; Rodríguez-Trejo et al. 2003), and fire is now considered an effective longleaf pine management tool (Brockway and Lewis 1997; Brockway and Outcalt 2000; Gilliam and Platt 1999; Haywood et al. 2001). As a result, successful restoration of longleaf pine to portions of its natural range is ongoing.

The native flora and fauna of longleaf pine ecosystems benefit from fire every two to four years (Brockway and Lewis 1997; Haywood et al. 2001; Landers et al. 1995; Outcalt 2000). Longleaf pine is adapted to withstand fire, in part, by a thick bark that protects the vascular cambium from excessive heat. Because this species is highly intolerant of shade, a primary benefit of repeated fire is the control of competing vegetation. The benefits of repeated fire, however, have not always been observed in longleaf pine stemwood growth. Brockway and Lewis (1997) found that the stem diameter and tree height of longleaf pine was unaffected by prescribed fire in winter that was repeated annually, biennially, or triennially over a 40-year period. Boyer (1983, 1987), however, compared the absence of fire and the application of biennial fire in winter, spring, and summer in a longleaf pine stand and found that after 10 years, stem diameter, tree height, stand basal area, and stemwood volume were reduced by fire regardless of season.

Inconsistent growth responses to fire may be due to interaction between branch phenology and the season of fire (Glitzenstein et al. 1995). The effect of season of fire on stem growth was demonstrated by Weise et al. (1987) who defoliated 4-year-old loblolly and slash pine in January, April, July, or October. Stem growth was unaffected by defoliation in January when foliage was limited to fascicles produced in the previous year (Chung and Barnes 1980; Sword et al. 1996; Tang et al. 1999). Stem growth was also unaffected by defoliation in July and October which was several months after the initiation of new shoot growth. In April, however, when first flush fascicle expansion was ongoing, foliage removal led to reduced stem growth. Furthermore, stem growth reductions were proportional to the amount of defoliation. Perhaps removal of young first flush foliage decreased tree growth by eliminating the primary source of carbon for the growth of subsequent flushes (Dickson 1991).

Because current photosynthate is the main source of energy for conifer root metabolism (Ritchie and Dunlap 1980; van den Driessche 1987), root growth could also be directly affected by fire damage to foliage. In an earlier study, we found that severe crown scorch in September lowered the amount of sucrose and starch in the roots of mature longleaf pine for more than 1 year (Sword and Haywood 1999). A similar response was observed by Guo et al. (2004) with a reduction in the total nonstructural carbohydrates of 22-year-old longleaf pine fine roots 2 months after 80% of the foliage was scorched in June. In both of these studies, fine root production was not greatly affected by crown scorch. Guo et al. (2004) suggested that if stored energy (e.g., starch) is available for root metabolism and foliage recovery is rapid then root growth will be maintained after crown scorch. However, root mortality may eventually occur if stored energy and photosynthetic capacity remain low. We hypothesize that fire damage to longleaf pine foliage affects carbon allocation to root carbohydrates and therefore, new root growth but that this effect is dependent on the seasonal development of foliage at the time of fire application. Our first objective was to document the seasonal dynamics of longleaf pine foliage and new root growth, and root nonstructural carbohydrates. Our second objective was to evaluate the effect of prescribed fire in March, May, and July on relationships between foliage production, fine root growth, and root nonstructural carbohydrate levels.

Materials and methods

Study site

The study is located on the Palustris Experimental Forest in the Kisatchie National Forest, Rapides Parish, Louisiana (approximately 92°30′W longitude, 31°N latitude). The study area was naturally regenerated by the seed tree silvicultural system in 1950–1955 with seed trees harvested in 1956 (Grelen 1975). In 1962, longleaf pine seedlings were released by mechanical removal of woody plants over 30 cm tall. Soils at the study site are Ruston fine sandy loam (Fine-loamy, siliceous, semiactive, thermic Typic Paleudults), McKamie fine sandy loam (Fine, mixed, superactive, thermic Vertic Hapludalfs), and Gore silt loam (Fine, mixed, active, thermic Vertic Paleudalfs). The soils are moderately well drained to well drained, moderately slowly permeable to moderately permeable, and have a 1–5% slope. The humid, subtropical climate is characterized by mean daily summer and winter air temperatures of 27.4°C and 11.4°C, respectively. Mean annual precipitation is 1560 mm with 700 mm received in spring and summer and 860 mm received in fall and winter (SRCC 2005).

The objective of the original study, established in 1962, was to monitor long-term changes in woody and herbaceous vegetation in response to no fire or biennial prescribed burning in March, May, or July (Grelen 1975; Haywood et al. 2001). There were 16 plots, 0.13 ha each, installed using a randomized complete block design with four replications blocked by topography. By age 43 years, prescribed burning treatments had significantly affected stocking, stemwood production, and vegetation diversity. For example, absence of fire over 37 years converted the dominant pine species from longleaf pine to loblolly pine. In the present study, therefore, the non-burned treatment was excluded. Non-uniform stand density and low stocking on two of the four replications also eliminated those plots from the present study. Measurement plots were one large cluster or patch of six or seven trees and one small cluster or patch of three or four trees within each plot of the remaining two replications. Trees in the large and small tree clusters were unevenly distributed and approximately 1–2 m apart. Two tree clusters per plot were required so that destructive root sampling in the large tree clusters did not affect observations of seasonal root growth in the small tree clusters. Tree clusters on each plot were randomly chosen from those that contained an adequate number of trees and were isolated from neighboring trees. Treatments were biennial prescribed burning in March, May, or July. Plots were prescribe burned with strip-headfires on March 25, May 19, or July 22, 1998. Prescribed fires scheduled for 2000 were delayed until 2001 due to a drought-driven federal burning restriction in 2000. At study initiation in 1998, basal areas of large and small tree clusters among the plots did not differ significantly by treatment.

Measurements

Stand environment

Precipitation was measured between July 1997 and December 2000 with an electronic weather station (Omnidata International, Inc., Logan, UT) in an open field approximately 6 km from the study site. Immediately before and during prescribed fires, soil temperature (°C) was measured in the center of each small tree cluster of one replication using 20-gauge, type T thermocouples placed at 2, 5, and 10 cm depths of the mineral soil (Omega Engineering, Inc., Stamford, CT). Thermocouples were monitored at

10-min intervals using an Easylogger (Omnidata International, Inc., Logan, UT).

Foliage dynamics

Projected leaf area index (LAI) was measured monthly between April 1998 and June 2000 at ten permanent locations 1 m apart along a southeast-facing transect in each large tree cluster. Simultaneously, data were recorded at a height of 137 cm between 0700 and 0900 CST along transects and in an adjacent open field using two Li-Cor LAI-2000 plant canopy analyzers (Li-Cor, Inc., Lincoln, NE) (Li-Cor, Inc. 1991). Measurements were made with a 45° view cap and exclusion of data associated with the fifth optical ring. The 10 measurements along each transect were averaged and monthly LAI was expressed as meter squared of projected surface area per meter squared of forest floor surface area.

Fine root dynamics

New root phenology was documented monthly between April 1998 and June 2000 by the rhizotron technique (Sword et al. 1998). Three rhizotrons were installed in January 1998 at random locations at least 1 m from trees in each small tree cluster. Rhizotrons were constructed of Plexiglas sheets (0.3 cm × 32 cm × 30 cm), secured to one side of an excavated area (35 cm × 20 cm × 35 cm). New pine lateral roots, ≥0.5 cm in length, were traced with a permanent marker onto acetate sheets (21.6 cm × 30 cm) attached to the Plexiglas. Pine roots were distinguished from non-pine roots based on diameter, the appearance of surface color and texture, ephemeral roots and ectomycorrhizae, and lateral root branch angles, as well as comparison of parent and lateral root diameters. Observations were recorded cumulatively. After each measurement date, a computer image file of each acetate sheet was created, the length of the lines contained in each file was quantified using GSROOT software (PP Systems, Inc., Bradford, MA) and net lateral root elongation was calculated by subtraction. Measurements in each small tree cluster were averaged and net root elongation in the 0–30 cm depth was expressed as millimeters of length per decimeter squared of rhizotron per day. Monthly cumulative root elongation in the 0–30 cm depth between May and December of 1998 and 1999 was expressed as millimeters of length per decimeter squared of rhizotron.

Seasonal live and dead fine root biomass were quantified by the in-growth core method (Vogt and Persson 1991). A 30-cm^2 grid was established in each large tree cluster. In-growth cores were constructed of heavy-duty plastic netting (1 cm × 0.5 cm mesh), 6 cm in diameter and 10 cm in length, containing 283 cm^3 of air dried, sieved mineral soil from the 0–10 cm depth at the study site. In each large tree cluster, 60 in-growth cores were installed at grid coordinates no farther than 5 m from a longleaf pine tree during a 1-week period in late January using a metal-coring device (Veihmeyer 1929). Six in-growth cores were randomly excavated in each large tree cluster at 2-month intervals between August 1998 and February 2000 and composited.

Pine fine roots, ≤2 mm in diameter, were removed from cores by wet sieving. Because pine fine root biomass is characterized by a high degree of natural variation (Bengough et al. 2000), roots were separated into categories to better resolve fine root biomass responses. Pine roots were distinguished from non-pine roots based on diameter, surface color and texture, plasticity, the appearance of ephemeral roots and ectomycorrhizae, and lateral root branch angles. Pine roots were further categorized as live and vigorous, live and senescent, or dead based on color, the appearance of root tips, elasticity, turgor, and adherence of the cortex to the vascular cylinder. Roots in each category were oven-dried (70°C) to equilibrium, ground in a Wiley mill (1 mm^2-mesh), and combusted (450°C, 8 h) to obtain ash weights. Fine root biomass by root category was expressed as grams of ash-free root tissue per cubic centimeters of soil volume. Vigorous and senescent fine root biomass were summed for live fine root biomass, and live and dead fine root biomass were summed for total fine root biomass. Fractions of vigorous, senescent, dead, and live fine root biomass were calculated.

Root nonstructural carbohydrate relations

Root starch, glucose, and sucrose concentrations were measured monthly between March 1998 and April 2001. At each measurement interval, five soil cores, 6.5 cm in diameter and 10 cm deep, were extracted from the periphery of small tree clusters using a metal-coring device and composited (Veihmeyer 1929). Approximately 1 h after sampling, live pine coarse roots, >2 ≤ 5 mm in diameter, were washed from the soil and packed in dry ice. Frozen roots were freeze-dried and ground in a Wiley mill (1 mm^2 mesh). Using a modification of the procedure of Jones et al. (1977), root starch, glucose, and sucrose concentrations were quantified and expressed as mg per g of ash-free dry weight.

Statistical analysis

The normal distribution of all variables was assessed by the Shapiro–Wilk statistic (SAS Institute, Inc. 1991). Values of LAI, net root elongation, and cumulative root length were transformed to natural logarithms, and root sucrose and starch concentrations, and dead, vigorous, senescent, and live fine root biomass were transformed to square roots to establish normality. Values of LAI, monthly net and cumulative root elongation, coarse root carbohydrate concentrations, and fine root biomass by root category were evaluated by analyses of variance using a repeated measures, completely random design with the Mixed procedure of SAS Version 8.1 (SAS Institute Inc., Cary, NC). Repeated measures were measurement date, and treatments were prescribed burning in March, May, or July. A similar analysis was conducted on fine root biomass and fractions of fine root biomass by root category for measurements taken after a steady state of fine root production was achieved in December 1998. Main and interaction effects were considered significant at $P \leq 0.05$ unless otherwise noted. Means

were compared with the least significant difference (LSD) test and considered significantly different at $P \leq 0.05$ unless otherwise noted.

The linear relationship between monthly net root elongation and precipitation between April and October of 1998 and 1999 was evaluated by ordinary least-squares regression. The slope of regression equations was considered significant at $P \leq 0.05$ unless otherwise noted.

Results

Stand environment

Immediately before burning, soil temperature exhibited little variation by depth with means across the 2–10 cm depth in March, May, and July of 15.2, 22.7, and 27.2°C, respectively. Equipment failure prevented measurement of soil temperature during the March burn. During the May burn, mean soil temperature at the 2, 5, and 10 cm depths increased by 36% (29.7°C), 18% (26.3°C), and 5% (23.9°C), respectively, with a maximum soil temperature of 37.5°C at the 2 cm depth. During the July burn, soil temperature was only elevated by 7% at the 2 cm depth (29.3°C).

When compared to the 30-year regional mean between 1971 and 2000 (SRCC 2005), annual precipitation was reduced by 22, 29, and 20% in 1998, 1999, and 2000, respectively (Fig. 1a). Precipitation during the active growing season (i.e., March-October) was 47% less than normal in 1998 and 28 and 21% less than normal in 1999 and 2000, respectively.

Foliage dynamics

Leaf area index was significantly affected by measurement date but not by prescribed burning treatment (Table 1). Mean LAI on the March-burned plots, however, appeared to be consistently higher than that on the May- and July-burned plots (Fig. 1b). Failure to detect a significant difference in LAI among the months of prescribed burning may have been due to the low number of replications in the study. The magnitude of peak LAI was similar between 1998 and 1999 with a mean peak LAI of 1.97 m^2/m^2. The duration of peak LAI extended over 4 months in 1998 (July through October) and over 2 months in 1999 (August and September). A significant interaction between prescribed burning treatment and measurement date was observed for LAI. However, prescribed burning treatment did not affect LAI within a measurement date.

Fine root dynamics

Net root elongation was significantly affected by measurement date, and cumulative root length between May and December was significantly affected by measurement date and interaction between measurement date and prescribed burning treatment ($P=0.0914$) (Table 1). Net root elongation was modal with maximums in August through October
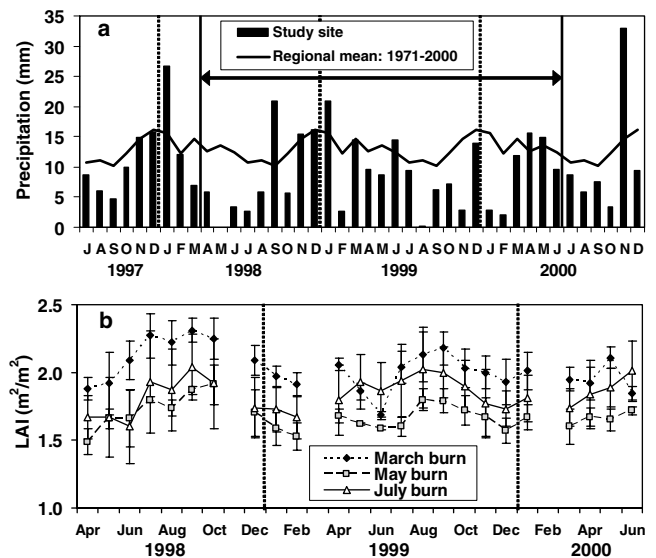

Fig. 1 (**a**) Mean monthly precipitation (mm) between 1971 and 2000 in central Louisiana, and total monthly precipitation between July 1997 and December 2000 in a mature longleaf pine stand on the Palustris Experimental Forest in Rapides Parish, Louisiana, and (**b**) monthly projected leaf area index (LAI) (m^2/m^2) of mature longleaf pine between April 1998 and June 2000 in response to prescribed burning in March, May, or July. Bars represent the standard error of the mean ($n=2$). The dotted lines represent the beginning of a new year, and the solid lines and arrows represent the time frame of precipitation measurements when LAI was measured. Data were not collected in November 1998, March 1999, and February 2000

of 1998 and May through July of 1999 (Fig. 2a). Net root elongation during these peaks did not differ significantly between years. Cumulative root elongation between May and December was significantly greater in 1999 than 1998 for all months except October (Fig. 2b). However, we cannot attribute these differences to year alone because the time between rhizotron installation and root observation differed by year. Between September and December of 1998, cumulative root elongation was significantly greater on the March-burned plots than on the July-burned plots (Fig. 2c).

During May through October which is the range of months that maximum root elongation occurred in 1998 and 1999, monthly root elongation tracked closely with precipitation during the month of, and month prior to root elongation measurement in 1998 (Fig. 3a), and 1999 (Fig. 3b). Linear relationships between monthly root elongation and precipitation during the month of root elongation measurement ($P=0.0537$, $R^2=0.3234$, $S_{y \cdot x}$ (root-mean square error) $=1.1727$ mm/dm²/day), and precipitation in the month prior to root elongation measurement ($P=0.0182$, $R^2=0.4426$, $S_{y \cdot x}=1.0644$ mm/dm²/day) were significant. Inclusion of both precipitation variables in the regression equation explained 69% of the variation in monthly peak root elongation rate ($P=0.0054$). Partial coefficients of determination for precipitation during the month of, and month prior to root observations were 24% ($P=0.0263$) and 44% ($P=0.0182$), respectively.

Total, live, vigorous, senescent, and dead fine root biomass were significantly affected by measurement date

Table 1 Probabilities of a greater F value (Pr > F) for leaf area index (LAI), net root elongation, cumulative root length, fine root production and root carbohydrate concentrations of mature longleaf pine in central Louisiana after prescribed burning in March, May, or July

Variable	Effect	Degrees of freedom	Pr > F
LAI	Burning treatment (T)	2	0.3765
	Measurement date (D)	24	0.0001
	T×D	48	0.0106
Net root elongation	Burning treatment	2	0.4770
	Measurement date	22	0.0001
	T×D	44	0.6125
Cumulative root length since May	Burning treatment	2	0.6142
	Measurement date	14	0.0001
	T×D	28	0.0914
Total fine root biomass	Burning treatment	2	0.5708
	Measurement date	9	0.0001
	T×D	18	0.1628
Live fine root biomass	Burning treatment	2	0.5123
	Measurement date	9	0.0048
	T×D	18	0.1458
Vigorous fine root biomass	Burning treatment	2	0.7181
	Measurement date	9	0.0201
	T×D	18	0.3838
Senescent fine root biomass	Burning treatment	2	0.0634
	Measurement date	9	0.0001
	TxD	18	0.4053
Dead fine root biomass	Burning treatment	2	0.7752
	Measurement date	9	0.0001
	T×D	18	0.5092
Root starch concentration	Burning treatment	2	0.7072
	Measurement date	30	0.0001
	T×D	60	0.0807
Root glucose concentration	Burning treatment	2	0.9898
	Measurement date	29	0.0001
	T×D	58	0.8778
Root sucrose concentration	Burning treatment	2	0.6561
	Measurement date	29	0.0001
	T×D	58	0.7731

(Table 1). A steady state of total fine root biomass at the 0–10 cm depth was reached by December 1998, 11 months after in-growth core installation (Fig. 4). Between August 1998 and February 2000, maximum values of vigorous, senescent, and dead fine root biomass occurred in December 1998 through April 1999, June through August 1999, and June through December 1999, respectively. Prescribed burning treatment significantly affected senescent fine root biomass (P=0.0634) with more senescent fine root biomass on the March-burned (33% increase) and May-burned (120% increase) plots than on the July-burned plots.

When fine root biomass data collected before a steady state of total fine root production were excluded from the analyses, total, live, vigorous, senescent, and dead fine root biomass and fractions of live, vigorous, senescent, and dead fine root biomass were significantly affected by measurement date (P values not shown). In addition, interaction between measurement date and prescribed burning treatment significantly affected live (P=0.0518) and total (P=0.0843) fine root biomass. Live fine root biomass was significantly higher on the May-burned plots than on the

March-burned plots on two dates, and on the July-burned plots on three dates (Fig. 5). Total fine root biomass was higher on the May-burned plots than on the March- and July-burned plots on one date (April 1999) (March burn: 0.18 g/cm^3, May burn: 0.40 g/cm^3, July burn: 0.16 g/cm^3).

Root nonstructural carbohydrate relations

Coarse root starch, glucose, and sucrose concentrations differed significantly by measurement date (Table 1). Concentrations of root starch and glucose exhibited complementary seasonal patterns (Fig. 6a, b). Maximum and minimum concentrations of root starch were in February through May, and September through November, respectively. Maximum and minimum concentrations of root glucose were in July through December, and March through April, respectively. Starch depletion from roots occurred between May and October, whereas, an accumulation of glucose in roots generally occurred between May and November. The maximum concentration of root starch was significantly less in 1999, 2000, and 2001 than in 1998, and
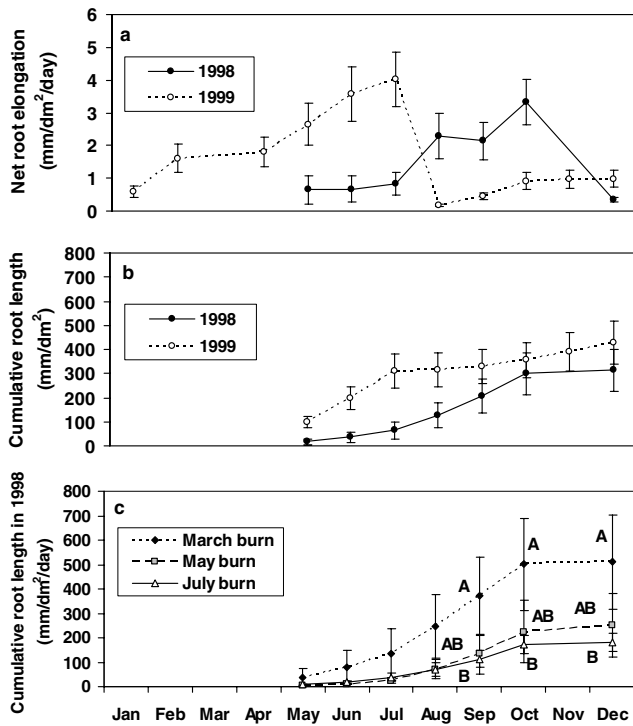
Fig. 2 At the 0–30 cm depth, (**a**) mean monthly net root elongation (mm/dm^2/day) (*n*=6) and (**b**) mean monthly cumulative root length since May (mm/dm^2) (*n*=6) during 1998 and 1999, and (**c**) monthly cumulative root length (*n*=2) since May 1998 after prescribed burning in March, May, or July 1998 in a mature longleaf pine stand. Means associated with a different letter are significantly different at *P*≤0.10 by the least significant difference test. Bars represent the standard error of the mean. Data were not collected in November 1998 and March 1999
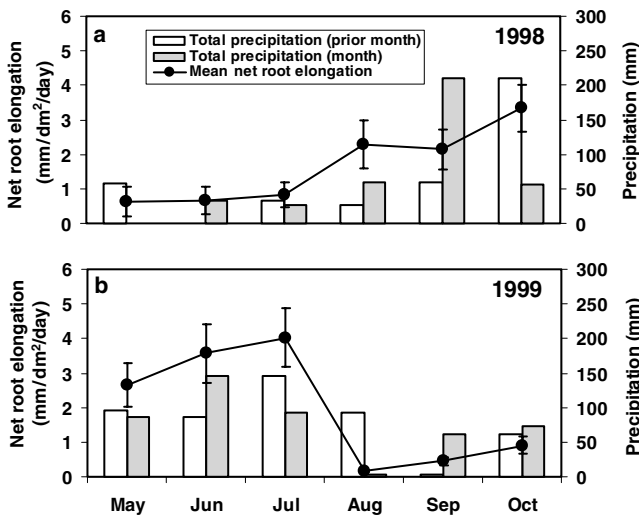

Fig. 3 Mean monthly net root elongation (mm/dm^2/day) (*n*=6), and monthly precipitation (mm) in the month prior to, and month of root elongation measurement in 1998 (**a**) and 1999 (**b**). Bars represent the standard error of the mean
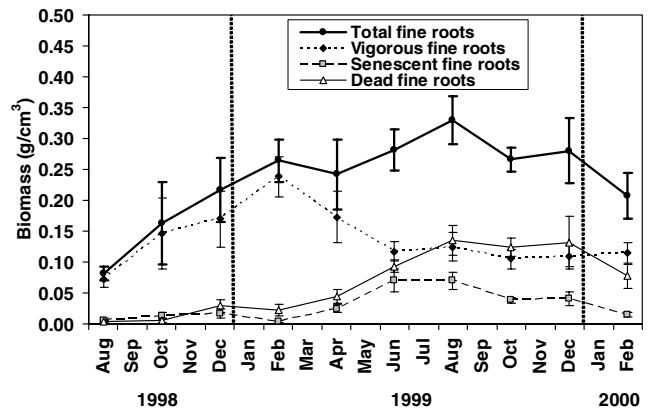

Fig. 4 Mean bimonthly fine root biomass (g/cm^3) in in-growth cores at the 0–10 cm depth between August 1998 and February 2000 in a mature longleaf pine stand. Bars represent the standard error of the mean (*n*=6). The dotted lines represent the beginning of a new year
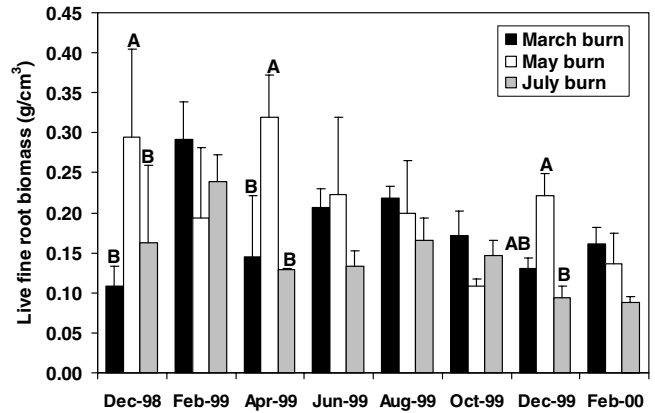

Fig. 5 Live (vigorous + senescent) fine root biomass (g/cm^3) in in-growth cores at the 0–10 cm depth after a steady state of fine root production was reached in December 1998 in response to prescribed burning in March, May, or July 1998. Means within a measurement date associated with a different letter are significantly different at *P*≤0.10 by the least significant difference test. Bars represent the standard error of the mean (*n*=2)

root glucose concentration was significantly less in April, May, November, and December of 2000 compared to 1998 and 1999. Root sucrose concentration did not exhibit a distinct seasonal pattern among years (Fig. 6c). After April 2000, however, root sucrose concentration was significantly higher than in 1998 or 1999. Prescribed burning treatment had a significant effect on coarse root starch concentration (*P*=0.0807). Mean comparisons by the LSD test indicated that root starch concentration was significantly affected by prescribed burning treatment on seven of 31 measurement dates. Consistent effects were observed on four measurement dates between June and August 1998 and in June 2000 with significantly lower (38–68%) root starch concentrations on the May-burned plots than the July-burned plots.
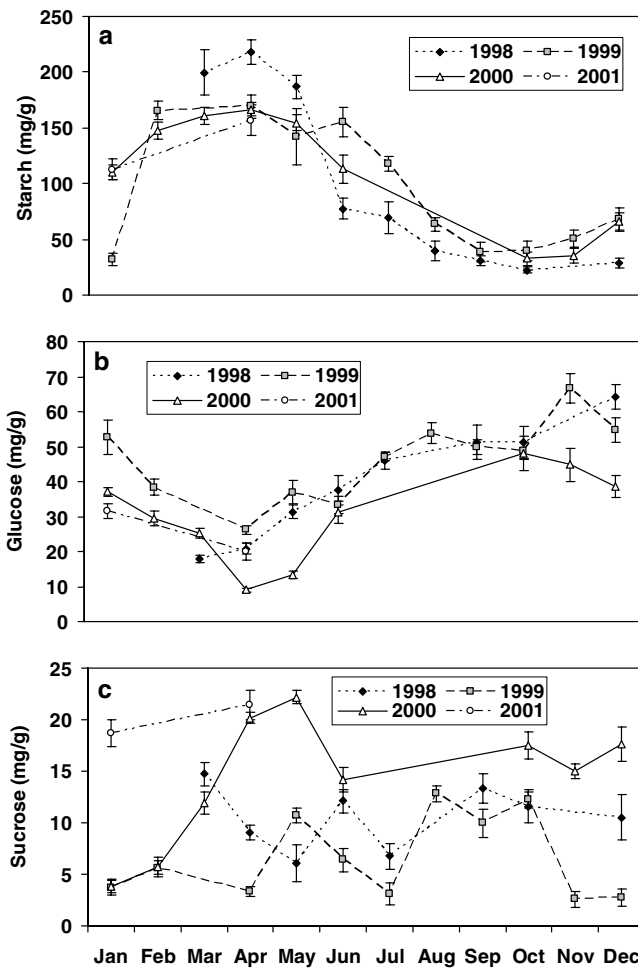
Fig. 6 Monthly longleaf pine coarse root ($>2 \leq 5$ mm in diameter) (**a**) starch, (**b**) glucose and (**c**) sucrose concentrations (mg/g) in 1998, 1999, 2000, and early 2001 in a mature longleaf pine stand. Bars represent the standard error of the mean (*n*=2). Data were not collected in November 1998, March 1999 and July through September 2000

Discussion

Prescribed fire and soil environment × root interactions

The month that prescribed fire was applied did not affect foliage dynamics and therefore, we were unable to evaluate relationships between fire-induced changes in leaf area, and both root growth and root carbohydrate concentrations. As the prescribed fires were ignited, it became apparent that fire intensities and damage to foliage would be low. Three years after the treatments were applied, Haywood et al. (2001) concluded that repeated biennial burning since 1962 at our study site created understory vegetation that favored low, rather than high intensity burns. Future research to evaluate relationships between foliage and fine root dynamics in response to prescribed fire should be done with younger trees characterized by smaller heights to the crown and in stand conditions conducive to moderate fire intensity.

Although foliage dynamics was not affected by prescribed fire, fine root production and starch concentration responded to month of prescribed fire. On the July-burned plots, we found less cumulative root length in rhizotrons during 1998 compared to the March-burned plots, a lower amount of live fine root biomass compared to the May-burned plots, and higher coarse root starch concentrations during the period of starch depletion in 1998 compared to the May-burned plots.

Three conditions unique to 1998 may have caused interaction between the soil environment and root phenology such that fine root production was less on the July-burned plots compared to the March- or May-burned plots. First, a rainfall deficit in 1998 progressively worsened between March and August (Fig. 1a), and burning may have exacerbated water limitations by increasing soil evaporation (Neary et al. 1999; Pritchett 1979; Wells et al. 1979). Because root growth is sensitive to water availability (Kaufmann 1968; Torreano and Morris 1998), it is likely that the impact of water deficit and post-fire soil evaporation on fine root production was greater in July than in March or May. Second, burning causes a temporary elevation of surface soil (i.e., 0–10 cm depth) temperature which occurs more rapidly in dry soil compared to wet soil (Campbell et al. 1995). Thus, the duration of temperatures lethal to surface roots in the drier month of July was longer than in the wetter months of March and May. Third, root elongation was delayed by 3 months in 1998 with the onset of peak root growth at the time of the July burn (Fig. 2a). We suggest that less fine root production was observed on the July-burned plots compared to the March- or May-burned plots because of the simultaneous occurrence of water deficit, exposure of existing surface roots to an extended period of high temperature during fire, and changes in root phenology that increased the exposure of new roots to water deficit and high surface soil temperature. Although precipitation was below-normal in 1999, season of burn did not affect longleaf pine root growth. However, since we did not burn in 1999, we did not expect to see a root elongation response similar to that observed in 1998.

Another factor possibly affecting longleaf pine fine root production in response to month of prescribed fire is post-fire soil warming. Because longleaf pine new root growth and soil temperature are positively correlated (Jones et al. 2003; Sword Sayer et al. in press), and combustion of the understory and forest floor increases soil insolation and heat absorption (Neary et al. 1999; Pritchett 1979; Wells et al. 1979), we propose that fine root production was stimulated by post-fire soil warming. In general, optimum temperatures for the root growth of woody plants range between 20°C and 25°C (Kozlowski et al. 1991). In an earlier study, 12- and 1.8-fold increases in the new root growth of longleaf pine seedlings were observed over a 28-day period as soil temperature increased from 13°C to 18°C and 18°C to 23°C, respectively (Sword Sayer et al. in press). Before burning in March, May, and July, soil temperatures averaged 15°C , 22°C , and 27°C, respectively. When ambient soil temperature was sub-optimal (i.e., March and May) new root growth may have been stimulated by post-fire

soil warming. Similar observations were made by Balisky and Burton (1997) who found that soil warming of out-planted lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings stimulated new root growth. In addition, a small post-fire increase in soil temperature after burning in May could have accelerated coarse root starch metabolism between May and October on the May-burned plots compared to the July-burned plots.

Potential benefits of soil warming to new root growth are possible. However, the seasonal nature of new root growth indicates that these benefits vary in magnitude depending on the synchrony of prescribed fire and maximum rates of new root growth. Past research has shown that in the absence of severe drought, maximum rates of new loblolly pine root growth occur between May and July (Farrish 1991; Sword Sayer and Tang 2004). Similarly in 1999, the peak fine root growth of longleaf pine occurred in May through July (Fig. 2a). Biennial increases in soil temperature during the late winter or early spring of years characterized by normal root phenology could stimulate early fine root growth, and therefore, soil resource uptake and tree growth intermittently throughout the lifetime of a stand. However, because the stemwood growth and root carbohydrate status of *Pinus* are sensitive to foliage loss (O'Neil 1962; Sword and Haywood 1999; Weise et al. 1987), the beneficial effects of soil warming on fine root production may be contingent on a minimum amount of fire-induced damage to foliage.

Prescribed fire and leaf area × Root interactions

Optimal prescribed fire results in desirable understory and forest floor changes with a minimum amount of crown scorch, and the absence of temperatures that are lethal to the bole and roots of managed trees. With information on the seasonal dynamics of foliage production, root growth, and root carbohydrates, we can deduce the time of the year when optimal prescribed burning has little effect on longleaf pine growth at our study site. Photosynthate stored as root starch is an important source of energy for internode and fascicle growth (Dickson 1989; Dickson 1991; Friend et al. 1994), and root metabolism if current photosynthate is limiting (Noland et al. 1997; Philipson 1988). At our study site, starch accumulated in longleaf pine roots between December and February (Fig. 6a). We suggest that maximum starch storage in longleaf pine roots at our study site requires the retention of foliage through February of the previous phenological year (e.g., March–February). Furthermore, our observation of longleaf pine root phenology (Fig. 2a) and those reported for loblolly pine (Farrish 1991; Sword Sayer and Tang 2004) provide evidence that the majority of new pine root growth normally occurs between May and July. Because current photosynthate is the primary source of energy for root metabolism (Ritchie and Dunlap 1980; van den Driessche 1987; Wargo 1979), we propose that longleaf pine root growth is vulnerable to an energy shortfall caused by foliage damage before July.

Using loblolly pine as a surrogate for longleaf pine, it is possible to further define the timeframe when longleaf pine growth is least vulnerable to fire damage to foliage with information from Weise et al. (1987). They found that the stemwood growth of loblolly pine was reduced by defoliation in April, but was unaffected by defoliation in January, July, or October. It appears as though foliage, either present or produced between February and June, was important for loblolly pine stemwood growth. Other research indicates that expansion of the first flush fascicles and second flush internodes of loblolly pine occurs between March and June (Chung and Barnes 1980; Sword et al. 1996; Tang et al. 1999). In two mature longleaf pine stands, Sheffield et al. (2003) reported the occurrence of only one consistent flush over a 3-year period and the expansion of first flush fascicles between April and July or August depending on site moisture regime. If the physiological function of foliage during the expansion of first flush fascicles is necessary for the normal stemwood growth of longleaf pine, damage to first flush fascicles must be minimized between April and August.

This information suggests that fire damage to foliage could adversely affect stemwood growth between December and February by reducing starch storage in roots, or between April and August by either limiting the amount of photosynthate available for root metabolism or reducing the physiological function of foliage during first flush fascicle expansion. We hypothesize, therefore, that prescribed fire at our study site would have little effect on stemwood growth in March or September through November. Since lower intensity fires with less crown scorch are expected in fall and winter compared to other times of the year (Glitzenstein et al. 1995; Wade and Johansen 1986), this window could be expanded to September through March. Although we have proposed a seasonal window when optimal prescribed fire has little effect on longleaf pine growth at our study site, further research is required to test and validate our hypotheses, and apply these results to other locations.

Root response to prolonged drought

As previously discussed, peak root elongation was delayed by 3 months in 1998, and we partially attribute this shift in root phenology to water limitations. The amount of root elongation was also affected by water availability. Specifically, monthly root elongation in rhizotrons during May through October of 1998 and 1999 was positively correlated with precipitation during the month of measurement and month before measurement (Fig. 3). Partial coefficients of determination for precipitation during the month of (24%), and month prior to (44%) root observations were significant but relatively small. Similar responses of tree root growth to water availability during drought have been observed but are variable in magnitude. For example, Jones et al. (2003) found that during drought, less longleaf pine fine root production occurred on drier compared to wetter microsites in a Georgia coastal plain forest. Joslin et al. (2000), however, reported only small and non-significant

decreases in fine root production in response to water deficit in an upland *Quercus* forest. It is apparent that in addition to soil water availability, other microsite variables as well as their spatial and temporal variability influence fine root production during drought (Jones et al. 2003; Joslin et al. 2000; Sword and Tiarks 2002).

In addition to a direct effect, water deficit may indirectly affect fine root growth by interfering with root carbohydrate relations. As prolonged drought continued at our study site, we found two root carbohydrate responses. First, relatively high levels of root starch in March through May 1998 were associated with normal precipitation during the period of starch accumulation between December 1997 and February 1998 (Figs 1a and 6a). However, when severe drought overlapped the period of starch accumulation, maximum starch concentrations were reduced. Jose et al. (2003) found that the photosynthetic rate of longleaf pine seedlings is sensitive to water deficit, and other studies have shown that the photosynthetic rate of plantation loblolly pine is reduced by drought (Ellsworth 2000, Tang et al. 2004). At our study site, therefore, drought-induced decreases in the photosynthesis of longleaf pine trees may have reduced both the accumulation and maximum concentration of coarse root starch in 1999 and 2000.

By 2000 which was the third consecutive year of drought, we also found that in general, coarse root glucose concentration was lower (29%) and coarse root sucrose concentration was higher (127%) than the mean of values in 1998 and 1999 (Figs 6b and c). Because root metabolism requires glucose derived from translocated sucrose, low root glucose together with an accumulation of root sucrose suggests that either enzymatic conversion of sucrose into glucose was inhibited, or the amount of sucrose translocated to the root system exceeded that demanded by both coarse and fine root metabolism. Tree roots can survive and grow in dry surface soil if deep soil water is available (Kosola and Eissenstat 1994; Caldwell et al. 1998). By the third year of drought at our study site, however, if deep soil water approached depletion, hydraulic limitations to deep fine root survival and as a result, root mortality may have increased leading to a lower energy demand for root maintenance respiration and growth. We hypothesize that by the third year of drought, fine root desiccation throughout the soil profile led to less fine root enzymatic activity and high rates of fine root mortality. As a result, the demand for glucose by root maintenance respiration and growth was low and sucrose translocated from the crown accumulated in the coarse roots that were proximal to fine roots. Further development of this hypothesis will require simultaneous measurement of the seasonal growth and carbohydrate relations of coarse and fine roots in response to long-term water sufficiency and deficiency.

Summary

In this study, we were unable to address our original goal which was to evaluate how fire-induced changes in leaf area at different times of the year affect longleaf pine root processes. However, our post-fire observations of foliage production, root growth, and root carbohydrates over 2 years provide information useful for the development of new research to determine the physiological mechanisms of how repeated fire affects the root processes and stand productivity of longleaf pine.

We estimated the seasonal pattern of longleaf pine root growth at our study site with peak production of vigorous fine root biomass between December and April followed by maximum root elongation between May and July. Seasonal concentrations of coarse root starch and glucose were modal and complementary, but coarse root sucrose was not characterized by a seasonal pattern. Severe drought during the growing season delayed the period of maximum root elongation in 1998. Furthermore, drought between 1998 and 2000 altered concentrations of coarse root starch in 1999 and 2000, and concentrations of coarse root glucose and sucrose in 2000. Also, longleaf pine fine root growth was generally less on the July-burned plots than on the March- and May-burned plots. We speculate that season of prescribed fire influenced longleaf pine root growth and carbohydrate concentrations by affecting relationships between fine root growth and soil water and temperature conditions. Analysis of the seasonal dynamics of foliage production, root growth, and root carbohydrates over two years, suggested that potential negative effects of fire on root and shoot growth at our study site are less when fire is prescribed in November through March rather than April through October.

References

Balisky AC, Burton PJ (1997) Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in interior British Columbia. New Forest 14:63–82

Barnett JP, Dennington RW (1992) Return to longleaf. Forest Farm 52:11–12

Barnett JP, McGilvray JM (1997) Practical guidelines for producing longleaf pine seedlings in containers. General Technical Report SRS-14. USDA Forest Service Southern Research Station, Asheville, NC, 28 p

Bengough AG, Castrignana A, Pagès L, van Noordwijk M (2000) In: Smit AL, Bengough AG, Engles C, van Noordwijk M, Pellerin S, van de Geijn (eds) Root methods: a handbook. Springer-Verlag, New York, pp 147–173

Boyer WD (1983) Growth of young longleaf pine as affected by biennial burns plus chemical or mechanical treatments for competition control. In: Jones EP Jr (ed) Proceedings of the second biennial Southern Silvicultural Research Conference. General Technical Report SE-24. USDA Forest Service Southeastern Forest Experiment Station, Asheville, NC, pp 62–65

Boyer WD (1987) Volume growth loss: a hidden cost of periodic prescribed burning in longleaf pine? South J Appl For 11:154–157

174

Boyer WD (1989) Response of planted longleaf pine bare-root and container stock to site preparation and release: fifth-year results. In: Miller JH (comp) Proceedings of the Fifth Biennial Southern Silvicultural Research Conference. General Technical Report SO-74. USDA Forest Service Southern Forest Experiment Station, New Orleans, LA, pp 165–168

Brockway DG, Lewis CE (1997) Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For Ecol Manage 96:167–183

Brockway DG, Outcalt KW (2000) Restoring longleaf pine wiregrass ecosystems: hexazinone application enhances effects of prescribed fire. Forest Ecol Manage 137:121–138

Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151–161

Campbell GS, Jungbauer Jr. JD, Bristow KL, Hungerford RD (1995) Soil temperature and water content beneath a surface fire. Soil Sci 159:363–374

Chung H, Barnes RL (1980) Photosynthate allocation in *Pinus taeda*. II. Seasonal aspects of photosynthate allocation to different biochemical fractions in shoots. Can J For Res 10:338–347

Dickson RE (1989) Carbon and nitrogen allocation in trees. In: Dreyer E, Aussenac G, Bonnett-Masimbert M, Dizengremel P, Favre JM, Garrec JP, Le Tacon F, Martin F (eds) Forest tree physiology. Annual Science Forum 46(suppl.). Elsevier/INRA, Paris, pp 631s–647s

Dickson RE (1991) Assimilate distribution and storage. In: Raghavendra AS (ed) Physiology of trees. Wiley, New York, pp 51–85

Ellsworth DS (2000) Seasonal CO_2 assimilation and stomatal limitations in a *Pinus taeda* canopy. Tree Physiol 20:435–445.

Farrish KW (1991) Spatial and temporal fine-root distribution in three Louisiana forest soils. Soil Sci Soc Am J 55:1752–1757

Friend AL, Coleman MD, Isebrands JG (1994) Carbon allocation to root and shoot systems of woody plants. In: Davis TD, Haissig BE (eds) Biology of adventitious root formation. Plenum, New York, pp 245–273

Gilliam FS, Platt WJ (1999) Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf pine) forest. Plant Ecol 140:15–26

Glitzenstein JS, Platt WJ, Streng DR (1995) Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol Monogr 65:441–476

Grelen HE (1975) Vegetative response to twelve years of seasonal burning on a Louisiana longleaf pine site. Research Note SO-192. USDA Forest Service Southern Forest Experiment Station, New Orleans, LA, 4 p

Guo DL, Mitchell RJ, Hendricks JJ (2004) Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140:450–457

Haywood JD, Harris FL, Grelen HE, Pearson HA (2001) Vegetative response to 37 years of seasonal burning on a Louisiana longleaf pine site. South J Appl For 25:122–130

Jones RH, Mitchell RJ, Stevens GN, Pecot SD (2003) Controls of fine root dynamics across a gradient of gap size in a pine woodland. Oecologia 134:132–143

Jones MGK, Outlaw WH, Lowry OL (1977) Enzymatic assay of 10^{-7} to 10^{-14} moles of sucrose in plant tissues. Plant Physiol 60:379–383

Jose S, Merritt S, Ramsey CL (2003) Growth, nutrition, photosynthesis and transpiration responses of longleaf pine seedlings to light, water and nitrogen. Forest Ecol Manage 180:335–344

Joslin JD, Wolfe MH, Hanson PJ (2000) Effects of altered water regimes on forest root systems. New Phytol 147:117–129

Kaufmann MR (1968) Water relations of pine seedlings in relation to root and shoot growth. Plant Physiol 43:281–288

Kosola KR, Eissenstat DM (1994) The fate of surface roots of citrus seedlings in dry soil. J Exp Bot 45:1639–1645

Kozlowski TT, Kramer PJ, Pallardy SG (1991) The physiological ecology of woody plants. Academic Press, New York, 657 p

Landers JL, Van Lear DH, Boyer WD (1995) The longleaf pine forests of the southeast: Requiem or renaissance? J Forest 93:39–44

Li-Cor, Inc. (1991) LAI-2000 plant canopy analyzer, Instructions manual. Li-Cor, Inc. Lincoln, NE

McGuire JP, Mitchell RJ, Moser EB, Pecot SD, Gjerstad DH, Hedman CW (2001) Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can J Forest Res 31:765–778

Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. For Ecol Manage 122:51–71

Noland TL, Mohammed GH, Scott M (1997) The dependence of root growth potential on light level, photosynthetic rate, and root starch content in jack pine seedlings. New Forest 13:105–119

O'Neil LC (1962) Some effects of artificial defoliation on the growth of jack pine (*Pinus banksiana* Lamb.) Can J Bot 40:273–280

Outcalt KW (2000) The longleaf pine ecosystem of the south. Native Plants J 1:42–53

Outcalt KW, Sheffield RM (1996) The longleaf pine forest: Trends and current conditions. USDA Forest Service Resource Bulletin SRS-9. USDA Forest. Service Southern Research Station, Asheville, NC, 23 p

Philipson JJ (1988) Root growth in sitka spruce and Douglas-fir transplants: dependence on the shoot and stored carbohydrates. Tree Physiol 4:101–108

Pritchett WL (1979) Properties and management of forest soils. Wiley, New York, 500 p

Ramsey CL, Jose S, Brecke BJ, Merritt S (2003) Growth response of longleaf pine (*Pinus palustris* Mill.) seedlings to fertilization and herbaceous weed control in an old field in southern USA. Forest Ecol Manage 172:281–289

Ritchie GA, Dunlap JR (1980) Root growth potential: its development and expression in forest tree seedlings. NZ J Forest Sci 10:218–248

Rodríguez-Trejo DA, Duryea ML, White TL, English JR, McGuire J (2003) Artificially regenerating longleaf pine during a year of drought. Forest Ecol Manage 180:25–36

SAS Institute, Inc. (1991) SAS procedures guide, release 6.03 edition. SAS Institute, Inc., Cary, NC, 441 p

Sheffield MC, Gagnon JL, Jack SB, McConville DJ (2003) Phenological patterns of mature longleaf pine (*Pinus palustris* Miller) under two different soil moisture regimes. Forest Ecol Manage 179:157–167

SRCC (2005) Southern Regional Climate Center Southern Climate Atlas. URL: http://www.srcc.lsu.edu/southernClimate/atlas/images/LAprcp.html (accessed 5 July 2005). Baton Rouge, LA: Louisiana State University

Sword MA, Gravatt DA, Faulkner PL, Chambers JL (1996) Seasonal branch and fine root growth of juvenile loblolly pine five growing seasons after fertilization. Tree Physiol 16:899–904

Sword MA, Chambers JL, Gravatt DA, Haywood JD (1998) Ecophysiological responses of managed loblolly pine to changes in stand environment. In: Mickler RA (ed) The productivity and sustainability of Southern Forest Ecosystems in a changing environment. Springer-Verlag, New York, pp 185–206

Sword MA, Haywood JD (1999) Effects of crown scorch on longleaf pine fine roots. In: Haywood JD (ed) Proceedings of the Tenth Biennial Southern Silvicultural Research Conference. General Technical Report SRS-30. USDA Forest Service, Southern Research Station, Asheville, NC, pp 223–227

Sword MA, Tiarks AE (2002) Local soils information needed to define the root zone in process models on the Gulf coastal plain. General Technical Report SRS-58. USDA Forest Service Southern Research Station, Asheville, NC, 15 p

Sword Sayer MA, Tang Z (2004) Long-term root growth response to thinning, fertilization, and water deficit in plantation loblolly pine. In: Connor KF (ed) Proceedings of the Twelfth Biennial Southern Silvicultural Research Conference. General Technical Report SRS-71. USDA Forest Service Southern Research Station, Asheville, NC, pp 458–464

Sword Sayer MA, Brissette JC, Barnett JP (in press) Root growth and hydraulic conductivity of southern pine seedlings in response to soil temperature and water availability after planting. New Forest

Tang Z, Chambers JL, Guddanti S, Yu S, Barnett JP (1999) Seasonal shoot and needle growth of loblolly pine responds to thinning, fertilization, and crown position. Forest Ecol Manage 120:117–130

Tang Z, Sword Sayer MA, Chambers JL, Barnett JP (2004) Interactive effects of fertilization and throughfall exclusion on the physiological responses and whole-tree carbon uptake of mature loblolly pine. Can J Bot 82:850–861

Torreano SJ, Morris LA (1998) Loblolly pine root growth and distribution under water stress. Soil Sci Soc Am J 62:818–827

van den Driessche R (1987) Importance of current photosynthate to new root growth in planted conifer seedlings. Can J Forest Res 17:776–782

Veihmeyer FJ (1929) An improved soil sampling tube. Soil Sci 27:147–152

Vogt KA, Persson H (1991) Measuring growth and development of roots. In: Lassoie JP, Hinckley TM (eds) Techniques and approaches in forest tree ecophysiology. ACRC Press, Boston, MA, pp 477–501

Wade DD, Johansen RW (1986) Effects of fire on southern pine: observations and recommendations. General Technical Report SE-41. USDA Forest Service Southeastern Forest Experiment Station, Asheville, NC, 14 p

Wargo PM (1979) Starch storage and radial growth in woody roots of sugar maple. Can. J For Res 9:49–56

Weise DR, Johansen RW, Wade DD (1987) Effects of spring defoliation on first-year growth of young loblolly and slash pines. Research Note SE-347. USDA Forest Service Southeastern Forest Experiment Station, Asheville, NC, 4 p

Wells CG, Campbell RE, DeBano LF, Lewis CE, Fredriksen RL, Franklin EC, Froelich RC, Dunn PH (1979) Effect of fire on soil, A state-of-knowledge review. General Technical Report WO-7. USDA Forest Service, Washington, DC, 34 p