HOW DOES FIRE AFFECT LONGLEAF PINE ROOT CARBOHYDRATES, FOLIAR NUTRIENTS, AND SAPLING GROWTH?

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Abstract—In central Louisiana, we conducted a prescribed-fire study in a 5-year-old longleaf pine (*Pinus palustris* P. Mill.) stand to evaluate the effects of fire on fine-root (2- to 5-mm diameter) carbohydrates, dormant season foliar nutrients, and sapling growth. Control, burn, and nonburned vegetation control treatments were studied using a randomized complete block design with five blocks. Prescribe fire was applied in May 2003. Root starch concentration was significantly lower and root glucose concentration significantly greater in the burned plots than in control and nonburned plots 1 month after treatment. Foliar potassium concentration was significantly greater after treatment in the burned plots compared to control and nonburned plots. Annual groundline diameter growth was also significantly greater in the burned plots than in the control plots. Our data suggest that fire shifts root carbohydrate and foliar potassium concentrations of longleaf pine saplings to restore leaf area and/or strengthen the tree stem.

INTRODUCTION

In the Southeastern United States, prescribed fire is commonly used to control brown-spot needle blight (caused by *Mycosphaerella dearnessii* M.E. Barr.) and competing vegetation, and to alter the structure of young longleaf pine (*Pinus palustris* P. Mill.) stands. Plant growth is influenced, in part, by nutrition-dependent foliar physiology and carbohydrate translocation from the foliage to other plant components. Because fire can cause early foliage senescence by scorching the crown (Haywood and others 2004), the production and supply of energy needed for forest productivity may be adversely affected by repeated use of prescribed fire. Our research evaluated the effects of prescribed fire on three factors that are important to longleaf pine production: root carbohydrate concentration, foliar nutrition, and stemwood growth. We hypothesize that prescribed fire affects root carbohydrate dynamics and foliar nutrition and that these responses are linked to sapling growth.

METHODS

Study Site

The study was in the west gulf region of the Southeastern United States on two sites in Rapides Parish in central Louisiana. The climate is humid and subtropical with mean January and July temperatures of 8 and 28 °C, respectively. Mean annual precipitation is 1525 mm with > 965 mm occurring between March and November. Soils range from very fine sandy to silt loam and are classified as Beauregard silt loam (fine-silty, siliceous, thermic Plinthaquic Paleudult), Malbis fine sandy loam (fine-loamy, siliceous, thermic Plinthic Paleudult), Ruston fine sandy loam (fine-loamy, siliceous, thermic Typic Paleudult), and Gore very fine sandy loam (fine, mixed, thermic Vertic Paleudult). The two sites are generally flat to gently sloping with < 10 percent slope.

Container-grown longleaf pine seedlings from seed sources in Mississippi (3 blocks) and Louisiana (2 blocks) were planted at 1.83 by 1.83 m in 1997. Treatment plots measure 22 by 22 m and contain 12 rows of 12 seedlings each. Measurement plots are the interior 10 rows of 10 trees each; the outer 2 rows of trees serve as a buffer.

Treatments

We studied three silvicultural treatments. Control plots (C) had no silvicultural activities. In the burn-only plots (B), prescribed burns were conducted in May 1998, June 2000, and most recently, on May 21, 2003, using the striphead fire method. In the nonburned, vegetation-control plots (N), herbicides were applied after planting to control herbaceous and woody plants, and nondesirable woody regrowth was hand felled.

Measured Variables

We quantified nonstructural carbohydrate concentrations of longleaf pine roots that were 2 to 5 mm in diameter. One root sample was collected from each of three randomly selected buffer trees per plot by following roots from the base of the tree until root diameter was between 2 and 5 mm, then excising a 5- to 10-cm length of root. Because this sampling method was destructive to roots, we selected a different set of three trees on each collection date. Sampled roots were excised with shears, placed on dry ice within 10 minutes of collection, and freeze-dried. Root samples were collected the day before, 1 month after, and again 7 months after the May 2003 prescribed fire. Freeze-dried roots were ground to pass through a #30 mesh screen and analyzed using an enzymatic assay modified for pine (Jones and others 1977, Kuehler and others 1999). Root starch, glucose, and sucrose concentrations were quantified as mg g^{-1} tissue dry weight.

Foliage was collected for nutrient analyses from the upper one-third of the south-facing crown of three trees per measurement plot on March 3, 2003, and January 23, 2004. We collected foliage during the dormant season, when nutrient reallocation fluxes are at a minimum (Dickson 1989). Sample trees were of mean height (± 10 percent) per plot. Ten fascicles from the last fully expanded flush of the previous year were collected from each tree, dried at 70 °C, and ground to pass through a #30 mesh screen. Nitrogen (N) concentration was determined using a C, N, S elemental analyzer (LECO

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Corporation, St. Joseph, MI) and expressed as percentage of dry weight. Phosphorus (P) was determined colorimetrically and expressed as mg g^{-1} tissue dry weight (John 1970). Foliar concentrations of potassium (K), calcium (Ca), and magnesium (Mg) were determined by atomic absorption spectrophotometry and expressed as mg g^{-1} tissue dry weight (Isaac and Kerber 1971).

In January 2003 and February 2004, we quantified total tree height in meters and groundline diameter in centimeters of all longleaf pine trees in each measurement plot. We determined annual growth increments by subtracting tree height and diameter in 2003 from those in 2004.

Experimental Design

Our study used a randomized complete block design with five blocks and three silvicultural treatments. Treatment differences regarding fine-root carbohydrate concentration and annual growth increment were statistically tested by analysis of variance procedures using the statistical analysis software, SAS (SAS Institute, Cary, NC). Where treatment differences were statistically significant, we used Tukey's Studentized Range Test as a means separation procedure. Analysis of covariance was applied to foliar nutrient concentrations using the nutrient concentrations in 2003 as the covariate; comparison using Bonferroni's pairwise comparison test was made on adjusted treatment means. Statistical significance was determined at $P \leq 0.05$.

RESULTS AND DISCUSSION

One month after burning, root starch concentration was significantly affected by treatment ($P = 0.0036$), with lower values on the B plots than on the C and N plots (fig. 1A). At this time, root starch concentration on the B plots was 35 percent lower than before the burn, while values on the C and N plots were unchanged. Root glucose concentration increased in all treatments 1 month after the burn. At this time, root glucose concentration was significantly affected by treatment ($P = 0.0066$), with 50 percent more root glucose on the B plots than on the C and N plots (fig. 1B). Root sucrose concentration 1 month after the burn (fig. 1C) and root starch, glucose, and sucrose concentrations 7 months after the burn were not significantly affected by any of the treatments.

These data indicate that, in longleaf pine saplings, root carbohydrate reserves may be mobilized to support the restoration of leaf area after scorch and fire-induced senescence. Sword Sayer and others (2006) report that these saplings averaged > 50-percent crown scorch. Also, at peak leaf area in July, a larger percentage of total leaf area in the upper crown was second-flush foliage on the B plots than on the C and N plots. Perhaps root starch was mobilized to support the second-flush production until the foliage had matured enough to change from an energy sink to an energy source.

It is also possible that the increase in root glucose concentration induced the production of secondary metabolites for root protection through the shikimic acid pathway. Tschaplinski and Blake (1994) found an increase in root glucose, shikimic acid, and the phenolic compound salicyl alcohol 4 days after shoot decapitation of hybrid poplar (*Populus* spp.). They speculated that the increase in glucose concentration induced the production of these protective compounds.

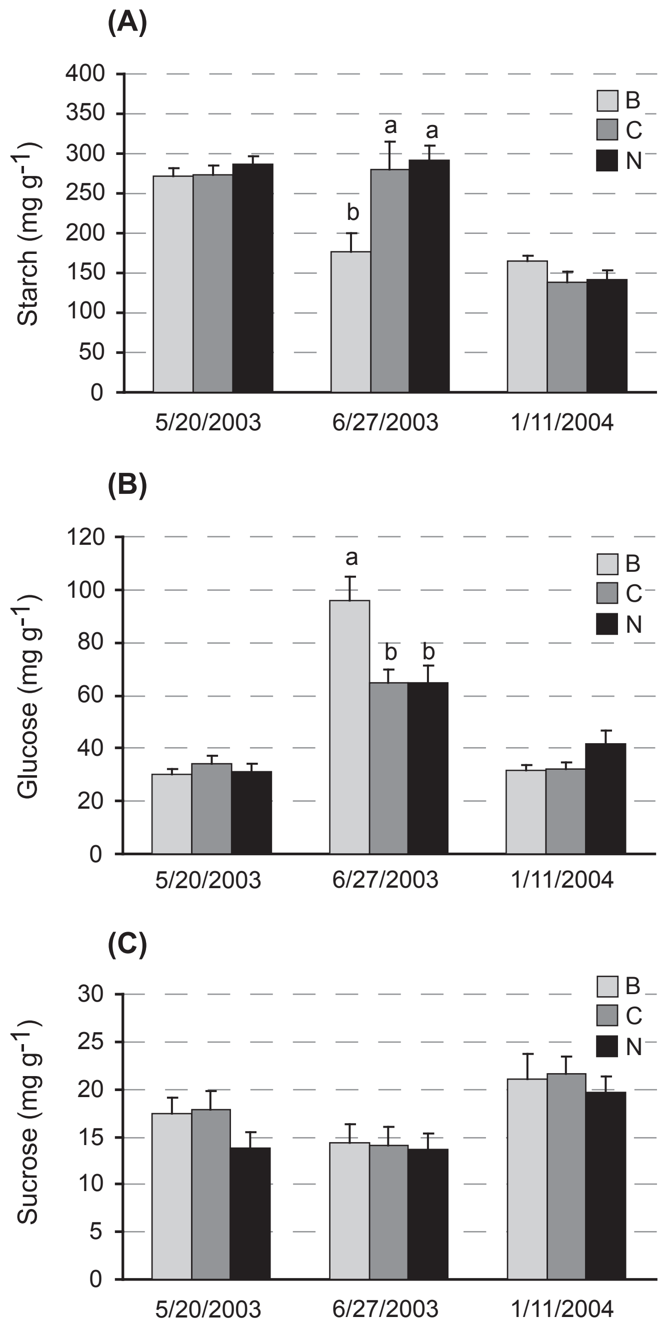

Figure 1—Mean (+1 standard error) longleaf pine root starch (A), glucose (B), and sucrose (C) concentration (mg g^{-1}) before (5/20/2003) and after (6/27/2003 and 1/11/2004) prescribed fire for burn (B), control (C), and nonburned vegetation control (N) treatments. Letters above the bar indicate statistically significant differences at $P \leq 0.05$ using Tukey's Studentized Range Test.

Current photosynthate translocated from foliage is the energy source for new root production and elongation (Dickson 1991, van den Driessche 1987). With the loss of foliage by scorch, we expected to see a postburn decline in root sucrose concentration. It appears, however, that prescribed fire on our study site did not disrupt carbohydrate allocation to the roots of saplings.

Foliar N and P concentrations in 2003 and 2004 were deficient (Blevins and others 1996) regardless of treatment (table 1).

Table 1—Mean (±1 standard deviation) dormant season longleaf pine foliar nutrient concentrations in response to silvicultural treatment before (2003) and after (2004) prescribed fire

			Silvicultural treatment by year					
	Critical		2003			2004		
Nutrient	level[a]	n	B	C	N	B	C	N
N (%)	0.95	5	0.87(0.05)	0.94(0.06)	0.92(0.13)	0.85(0.08)	0.91(0.06)	0.92(0.14)
P (g/kg)	0.80	5	0.59(0.06)	0.49(0.18)	0.58(0.06)	0.66(0.06)	0.63(0.07)	0.64(0.08)
K (g/kg)	3.00	5	4.11(0.91)	3.87(1.24)	3.90(0.91)	4.93(0.79)a	3.85(0.78)b	4.08(0.45)b
Ca (g/kg)	1.00	5	1.44(0.24)	1.40(0.26)	1.94(0.53)	1.82(0.16)	1.65(0.27)	1.56(0.14)
Mg (g/kg)	0.60	5	1.06(0.17)	1.03(0.16)	0.89(0.11)	0.98(0.14)	1.18(0.29)	0.90(0.19)

Treatment B = burn; treatment C = control; treatment N = non-burned vegetation control; N = nitrogen; P = phosphorus; K = potassium; Ca = calcium; Mg = magnesium.
Means followed by different letters are significantly different using Bonferroni's pairwise comparison test with an overall P ≤ 0.05.
[a] Concentration below which the nutrient is considered deficient (Blevens and others 1996).

Although foliar N, P, Ca, and Mg concentrations were not, foliar K concentration was significantly affected by treatment ($P = 0.0010$). Foliar K concentration was greater on the B plots than on the C and N plots by 28 and 21 percent, respectively. These findings disagree with those of Boyer and Miller (1994), who found that repeated prescribed fire had no effect on the foliar K concentration of 30-year-old longleaf pine. A similar response to the B treatment was also not observed in available soil K (Personal communication. 2005. James D. Haywood. Research Forester, USDA Forest Service, Southern Research Station, 2500 Shreveport Highway, Pineville, LA 71360). Continued measurement of foliar nutrition at our study site will determine whether the effect of burning on foliar K concentration is temporary or long-term.

Annual height increment was significantly affected by treatment ($P = 0.0048$); greater growth occurred on the N plots than on the C plots (fig. 2). Between January 2003 and February 2004, longleaf pine on the N plots grew 28 percent taller than on the C plots. At the same time, those on the N plots grew 13 percent taller than on the B plots, although the difference was not statistically significant. Groundline diameter growth between January 2003 and February 2004 was also significantly affected by treatment ($P = 0.0445$); there was 32 percent more growth on the B plots than on the C plots (fig. 2). During this 1-year period, trees on the B plots had 14 percent greater diameter growth than trees on the N plots, although the difference was not statistically significant.

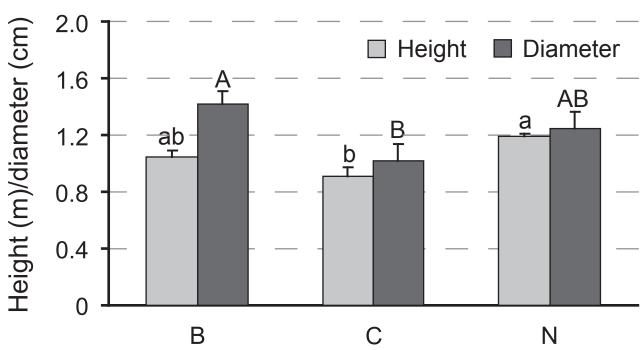

Figure 2—Annual growth increment of height (m) and groundline diameter (cm) (+1 standard error) for burn (B), control (C), and nonburned vegetation control (N) treatments. Letters above the bar indicate statistically significant differences at $P \leq 0.05$ using Tukey's Studentized Range Test.

Boyer (2000) reported that biennial prescribed fire in southwest Alabama reduced longleaf pine height and diameter at breast height over the first 24 years of stand development. Our data do not reflect those findings. Greater annual increment of groundline diameter on the B plots relative to the diameter on C plots, as well as a trend of less annual height but more annual groundline diameter growth on the B plots relative to the growth on N plots, may be a morphological response to instability. Telewski (1995) explains that trees develop shorter stems and/or greater radial growth in response to flexure stress in order to reduce wind-drag on the crown. At our study site, repeated burning removed much of the taller competing vegetation, leaving an open, parklike stand of saplings. To prevent windthrow, trees on the B plots may have allocated carbon to increase stem taper.

These data suggest that repeated prescribed fire affects the pattern of carbon allocation in young longleaf pine trees. For example, stem form may indirectly respond to fire with an increase in taper. Also, fire-induced changes in the seasonal dynamics of root carbohydrates may represent a shift in carbon allocation to restore leaf area after scorch and/or produce protective secondary metabolites such as phenolics. Research will continue in an effort to understand how carbohydrate dynamics, foliage production, and stemwood growth of longleaf pine respond to repeated use of prescribed fire. With this information, the time and intensity of prescribed fire that maximize stand growth can be defined.

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