EFFECTS OF PRESCRIBED FIRE ON PRODUCTION OF FOLIAGE BY SAPLING LONGLEAF PINE

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Abstract—We conducted an experiment that was designed to show how interaction between prescribed fire and branch phenology affects the growth of planted longleaf pine (*Pinus palustris* P. Mill.). Treatments were no control of vegetation, vegetation control by burning, and vegetation control by application of herbicides. In the plots burned in May 2003, > 50 percent of the foliage was scorched. In 2004, annual increments of biomass production were similar on the burned and herbicide plots and were greater on the burned plots than on the control plots. A larger proportion of leaf area occurred in the upper crown on the burned and herbicide plots than on the control plots, and a larger proportion of upper crown leaf area was second-flush foliage on the burned plots than on the control and herbicide plots. Results of this experiment suggest that newly established upper crown leaf area contributed to annual biomass production after burning.

INTRODUCTION

The establishment of longleaf pine (*Pinus palustris* P. Mill.) ecosystems on cutover sites requires the control of competing vegetation by burning, herbicides, or mechanical treatments. Plant and animal species common to longleaf pine ecosystems are adapted to withstand fire (Brockway and Lewis 1997, Haywood and others 2001, Landers and others 1995, Outcalt 2000). Prescribed burning limits competing vegetation in longleaf pine stands, but the benefit of this control is not consistently reflected in production. Brockway and Lewis (1997), for example, reported that the growth of longleaf pine was not adversely affected by repeated fire in winter over a 40-year period. Boyer (1983, 1987), however, found that longleaf pine production was reduced by fire after 10 years of biennial burning in winter, spring, or summer.

Inconsistency in growth responses to fire may be caused by variation in fire intensity and branch phenology at the time of burning. Past research has established the close relationship between leaf area and stand production (Albaugh and others 1998, Colbert and others 1990, Sword Sayer and others 2004, Vose and Allen 1988). Thus, fire intensities that cause severe crown scorch reduce stemwood growth (Johansen and Wade 1987). When crown scorch is not severe, stand production may depend on branch phenology and amount of stored energy at the time of the fire.

Results of a study by Weise and others (1987), who removed up to 95 percent of the foliage from 4-year-old loblolly (*P. taeda* L.) and slash pine (*P. elliottii* Engelm.) at different times of the year, suggest that the response of stem growth to fire is mediated by branch phenology. Stem growth was unaffected by defoliation in January, July, or October. When saplings were defoliated in April, however, stem growth was reduced proportionally with the amount of foliage removed. Because southern pine buds do not begin expanding until after January, defoliation before this time could not affect new foliage (Chung and Barnes 1980, Tang and others 1999). By July and October, new foliage was well developed and had undergone several months of photosynthate production and export (Chung and Barnes 1980; Dickson 1989, 1991; Tang and others 1999). In April, however, new foliage was expanding and may not have been mature enough to export photosythate to other plant components. These results suggest that the impact of fire on stand production depends on the extent and season of foliage damage.

We hypothesize that annual production of longleaf pine is maintained after scorch where regrowth of foliage at least partly restores the potential for carbon fixation. In the present study, our objectives are to (1) quantify annual aboveground biomass production and distribution of foliage by crown level and age class of sapling longleaf pine and (2) evaluate relationships between these variables in response to prescribed burning in May 2003.

MATERIALS AND METHODS

Field Sites

The field sites are located on the Kisatchie National Forest in central Louisiana. Three replications, each containing three treatment plots, are at lat. 31°1′ N, long. 92°37′ W on a gently sloping (1 to 3 percent) Beauregard silt loam and Malbis fine sandy loam complex (site 1). The Beauregard soil forms the intermound and wetter portion of the site. The Malbis soil forms slightly elevated mima or pimple mounds. Two replications, each containing three treatment plots, are at lat. 31°6′ N, long. 92°36′ W on a Ruston fine sandy loam (fine-loamy, siliceous, thermic Typic Paleudult) with some Malbis fine sandy loam and Gore very fine sandy loam with a slope of 1 to 5 percent (site 2). A mixed pine-hardwood forest originally occupied both sites. Site 1 was clearcut harvested, sheared, and windrowed in 1991 and prescribe burned in 1993 and 1996. Site 2 was clearcut harvested in 1996 and roller-drum chopped and burned in August 1997.

At each location, treatment plots (22 by 22 m; 0.048 ha) were established, and blocks were delineated based on soil drainage and topography. Three vegetation management treatments were established: (1) control (C) - no management activities after planting, (2) prescribed burning (B) - plots were burned using the strip head fire method in late spring every 2

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or 3 years, and (3) herbicides (H) - herbicides were applied after planting for herbaceous and arborescent plant control. Specifically, the H plots at site 1 were rotary tilled in December 1996 before planting in March 1997. Sethoxydim was used for postplanting grass control, and hexazinone was used for general herbaceous plant control. In May 1997 and April 1998, sethoxydim and hexazinone in aqueous solution were applied in 0.9-m bands over the rows of unshielded longleaf pine seedlings. Within the 0.9-m bands, the rate of sethoxydim application was 0.37 kg active ingredient (ai)/ha, and for hexazinone the rate was 1.12 kg ai/ha. At site 2, no tillage was necessary, and only hexazinone was banded in April 1998 and 1999 because sparse occurrence of grasses did not warrant the use of sethoxydim. For both sites, triclopyr at 0.0048 kg acid equivalent/liter was tank mixed with surfactant and water and applied as a directed foliar spray to competing arborescent vegetation in April 1998 and May 1999. Recovering brush was cut by hand in February 2001. The B plots were burned by the strip head fire method in May 1998 at site 1 and in June 2000 and May 2003 at both sites. Container-grown longleaf pine seedlings from a genetically improved, Mississippi seed source (site 1) and a Louisiana seed source (site 2) were planted at a spacing of 1.8 by 1.8 m in March 1997 and November 1997, respectively. Treatment plots contained 12 rows of 12 seedlings each. The measurement plots contained only the innermost eight rows of eight seedlings in each treatment plot.

Measurements

Fire intensity was evaluated by examining three saplings that were randomly chosen from those within 10 percent of mean height on each plot. For each of these saplings, the height of crown scorch and total tree height were measured 1 month after burning, and scorched height as a percentage of total height was estimated. Scorched height was rated 0, 1, 2, or 3 (0 = no crown scorch, 1 = < 50 percent of total height scorched, 2 = from 50 percent to < 100 percent of total height scorched, 3 = 100 percent of total height scorched).

Stand production was quantified in two ways. First, groundline diameter and total height were measured for all saplings in January 2003 and February 2004, and groundline basal area (GBA) per sapling and per ha were calculated. Second, the stem, branch, and foliage biomass per ha in January 2003 and February 2004 and annual biomass production during this period were predicted. Predictions were based on equations developed from data obtained by destructive sampling of three saplings from the outer two rows of each treatment plot in August 2003.

The three destructively sampled saplings per plot were randomly chosen from each of the three one-third percentiles of sapling total tree height on the plot. The groundline diameter and total height of each sampled sapling were measured, each sapling was felled at the groundline, and the length and midpoint of each sapling's live crown were determined. The live crown midpoint marked the point of division between the upper and lower crown sections. Branches were cut, and foliage was pulled from the stems.

Subsequently, branch foliage from the upper crown was separated from that of the lower crown. Foliage from each crown level was partitioned into four categories: (1) stem foliage and branch foliage produced in 2002, (2) first-flush foliage produced in 2003, (3) second-flush foliage produced in 2003, and (4) foliage from the third and subsequent flushes produced in 2003. Foliage, branches, and stems were dried to equilibrium at 70 °C and weighed.

Upper and lower crown peak total leaf area (TLA) were also predicted. These predictions represented peak TLA because they were based on data collected in August when leaf area was maximum. From each sample of 2002 foliage and 2003 first-flush foliage, five fascicles were subsampled. Their total or all-sided surface areas were quantified by volume displacement (Johnson 1984), and dry weights were determined after drying to equilibrium at 70 °C. For each set of 15 samples per crown level and treatment, linear equations were developed to predict peak TLA from dry weight. Equations associated with the 2002 foliage were applied to all 2002 foliage samples, and equations associated with the 2003 first-flush foliage were applied to all 2003 foliage samples. This resulted in predictions of peak TLA in the upper and lower crown for all 45 destructively sampled saplings.

Data for the destructively sampled trees were used to construct regression equations to predict stem, branch, and foliage biomass and peak TLA as functions of groundline diameter and total height. Each regression equation was developed independently of the others. To stabilize variance, a natural logarithm (ln) transformation was applied to each side of each equation. Thus, the equation form was $\ln(Y) = b_o + b_1\ln(D) + b_2\ln(H) + e$, where e represents a normal error term, D is groundline diameter, H is total height, Y is one of the biomass or peak TLA dependent variables, and the b_i are parameters to be estimated. Nested models were fitted where the parameters were common among treatments and where parameters were allowed to vary among treatments, and standard F-tests were used to compare full and reduced models and achieve a final model. Only variables that were significant at the $P = 0.05$ level were retained. The nested models were implemented by using dummy variables representing the different treatments (Weisburg 1985, p. 169-185). Potentially, one of the parameters could vary while the others were common across treatments. For some dependent variables, a common relationship was used for all treatments, and for other dependent variables, parameters were unique for each treatment.

These equations were used to predict stem and branch biomass, upper and lower crown foliage biomass, and peak TLA in 2003 and 2004 for all saplings in the measurement plots. Stem, branch, and foliage biomass were expressed as megagrams (Mg) per ha, and peak TLA was expressed as m^2 of leaf area per m^2 of measurement plot area. Foliage biomass in the upper and lower crown was summed. Annual stem, branch, and foliage biomass production was calculated as the difference between plot-level values in January 2003 and February 2004.

Statistical Analysis

Values of GBA (m^2/ha); annual production of stem, branch, and foliage biomass (Mg/ha per year); and upper and lower crown peak TLA (m^2/m^2) were transformed to their natural logarithms (ln) to establish normality. Transformed values of GBA in January 2003 and February 2004 were evaluated by analysis of variance (ANOVA) using a randomized complete block design with five blocks. With ln (GBA) in 2003 as a covariate, transformed values of annual stem, branch, and foliage biomass production and upper and lower crown peak TLA were evaluated by analysis of covariance (ANCOVA) with five blocks. Also, percentages of peak TLA in the upper and lower crown were analyzed by ANCOVA, and percentages of upper crown peak TLA in each of four age classes were evaluated by ANOVA. Mean groundline diameter was the covariate. Total leaf area data for the 45 saplings that were sampled destructively in August 2003 were used in this analysis. Main and interaction effects were considered significant at $P \leq 0.10$. Means were compared by the least significant difference test and considered significantly different at $P \leq 0.10$.

RESULTS

Prescribed burning in May 2003 resulted in a crown scorch rating of 1.5 ± 1.1 (standard deviation). This value indicates that the mean percentage of scorched sapling height was from 50 percent to < 100 percent with considerable variation.

Vegetation management treatment significantly affected GBA (table 1). In 2003 and 2004, GBA was greater in the H plots than in the C and B plots, and GBA in the C plots was similar to that in the B plots (fig. 1). Annual stem biomass and foliage biomass production, adjusted by GBA in 2003, were significantly affected by vegetation management treatment. Small but significant differences were found between adjusted annual stem production on the B plots and that on the H plots, and between adjusted annual foliage production on the C and B plots and that on the H plots. In each case, the production adjusted by the covariate was less on the H plots than on the C and B plots. Clearly, however, the H plots did not grow less stem or foliage biomass than the C and B plots (figs. 2A and 2B). Adjusted annual production of stem biomass on the B plots was similar to that on the C plots, and adjusted annual production of foliage biomass on the B plots was similar to that on the C plots (fig. 2C). Vegetation management treatment did not affect adjusted annual production of branch biomass (fig. 2C).

Upper crown peak TLA, adjusted by GBA in 2003, was significantly affected by vegetation management treatment in 2004 but not in 2003 (table 1). Adjusted upper crown peak TLA in 2003 was not significantly affected by vegetation management treatment, but there was a small but significant difference between adjusted upper crown peak TLA for B plots and that for H plots in 2004 (figs. 3A and 3B). Adjusted lower crown peak TLA was significantly affected by vegetation management treatment in 2003 and 2004. In both years, the B and H plots averaged less adjusted peak TLA in the lower crown than did the C plots (fig. 3C and 3D).

The distribution of peak TLA, adjusted by groundline diameter, between the upper and lower crown of saplings destructively sampled in August 2003 was significantly affected by vegetation management treatment (table 2). A larger percentage of

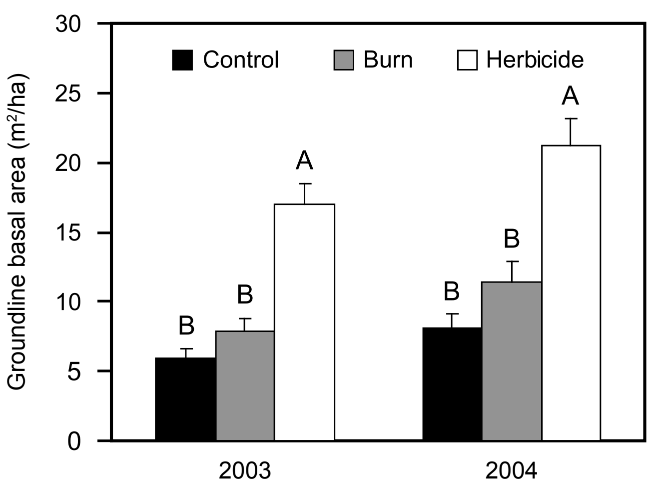

Figure 1—Groundline basal area of sapling longleaf pine in January 2003 and February 2004 in response to no vegetation management (Control), vegetation management with prescribed fire in June 2000 and May 2003 (Burn), and vegetation management by herbicide application (Herbicide). Bars represent one standard error of the mean. Means within a year associated with different upper case letters are significantly different at $P \leq 0.10$.

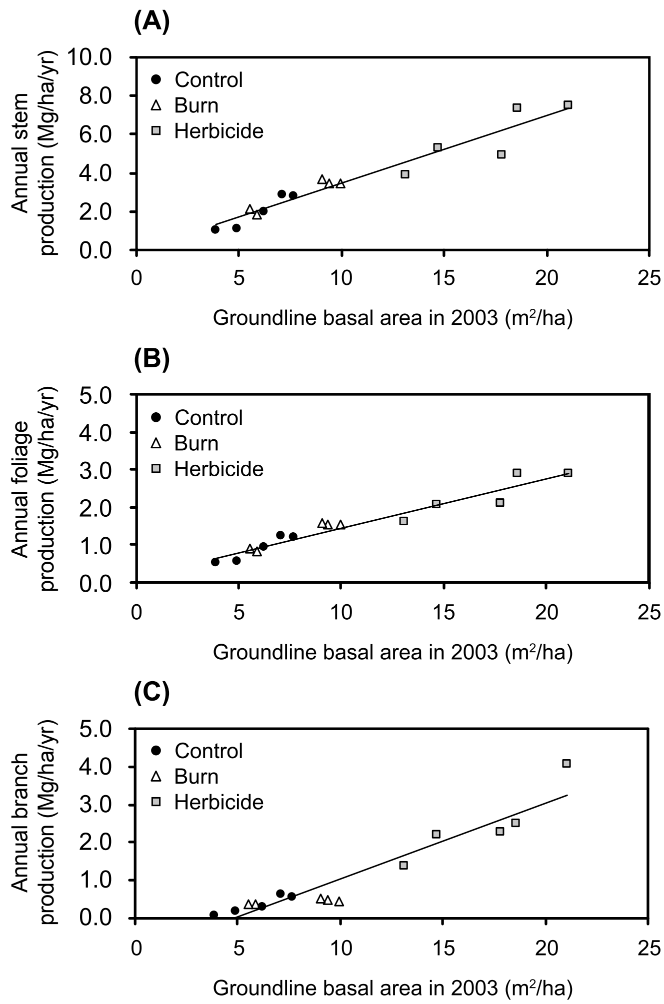

Figure 2—Relationship between groundline basal area in January 2003 and predicted annual production of stem (A), foliage (B), and branch (C) biomass between January 2003 and February 2004 of sapling longleaf pine in response to no vegetation management (Control), vegetation management with prescribed fire in June 2000 and May 2003 (Burn), and vegetation management by herbicide application (Herbicide). Lines represent regression relationships among all treatments.

Table 1—Analysis of variance of mean groundline basal area, analyses of covariance of mean annual production of stem, branch, and foliage biomass, and upper and lower crown peak total leaf area of sapling longleaf pine in response to vegetation management treatment

Variable	Source of variation	df	SS	MS	F-value	Pr > F
GBA, 2003[a]	Block	4	0.3205	0.0801	1.48	0.2937
(m^2/ha)	Treatment[b]	2	3.0581	1.5291	28.31	0.0002
	Error	8		0.0540		
GBA, 2004[a]	Block	4	0.5053	0.1263	2.14	0.1675
(m^2/ha)	Treatment	2	2.4962	1.2481	21.12	0.0006
	Error	8		0.0591		
Stem biomass	Covariate[c]	1	0.8279	0.8279	53.17	0.0002
production[a]	Block	4	0.1260	0.0315	2.02	0.1953
(Mg/ha/yr)	Treatment	2	0.1077	0.0539	3.46	0.0902
	Error	7		0.0156		
Branch biomass	Covariate	1	2.1419	2.1419	29.76	0.0010
production[a]	Block	4	0.6943	0.1736	2.41	0.1460
(Mg/ha/yr)	Treatment	2	0.0427	0.0213	0.30	0.7522
	Error	7		0.0720		
Foliage biomass	Covariate	1	0.6547	0.6547	72.02	0.0001
production[a]	Block	4	0.0700	0.0175	1.92	0.2112
(Mg/ha/yr)	Treatment	2	0.0939	0.0470	5.17	0.0419
	Error	7		0.0091		
Upper crown	Covariate	1	0.8032	0.8032	342.28	0.0001
TLA, 2003[a]	Block	4	0.0628	0.0157	6.69	0.0153
(m^2/m^2)	Treatment	2	0.0064	0.0032	1.37	0.3141
	Error	7		0.0023		
Lower crown	Covariate	1	1.3823	1.3823	127.33	0.0001
TLA, 2003[a]	Block	4	0.3658	0.0915	8.42	0.0082
(m^2/m^2)	Treatment	2	3.2503	1.6251	149.71	0.0001
	Error	7		0.0109		
Upper crown	Covariate	1	0.6935	0.6935	320.62	0.0001
TLA, 2004[a]	Block	4	0.0330	0.0083	3.82	0.0593
(m^2/m^2)	Treatment	2	0.0297	0.0143	6.86	0.0224
	Error	7		0.0022		
Lower crown	Covariate	1	1.1291	1.1291	103.45	0.0001
TLA, 2004[a]	Block	4	0.1890	0.0472	4.33	0.0447
(m^2/m^2)	Treatment	2	2.6059	1.3030	119.38	0.0001
	Error	7		0.0109		

df = degrees of freedom; SS = sum of squares; MS = mean square; Pr > F = probability of a greater F-value; GBA = groundline basal area; TLA = total leaf area.
[a] Analyses were conducted with data transformed to their natural logarithms.
[b] Treatments were no vegetation management (C), vegetation management with prescribed fire (B), and vegetation management by herbicide application (H).
[c] The covariate was groundline basal area in January 2003.

adjusted peak TLA was found in the upper crown of saplings on the B and H plots than in the upper crown of those on the C plots (fig. 4A). Consequently, a smaller percentage of adjusted peak TLA occurred in the lower crown of saplings on the B and H plots than in the lower crown of those on the C plots. Vegetation management treatment significantly affected the percentage of upper crown peak TLA that was produced in 2002, in the second flush of 2003, and in the third and subsequent flushes of 2003 (fig. 4B). Foliage produced in 2002 made up 13 percent more of peak TLA in the H plots than it did in the B and C plots. Foliage produced in the third and subsequent flushes of 2003 made up 11 percent

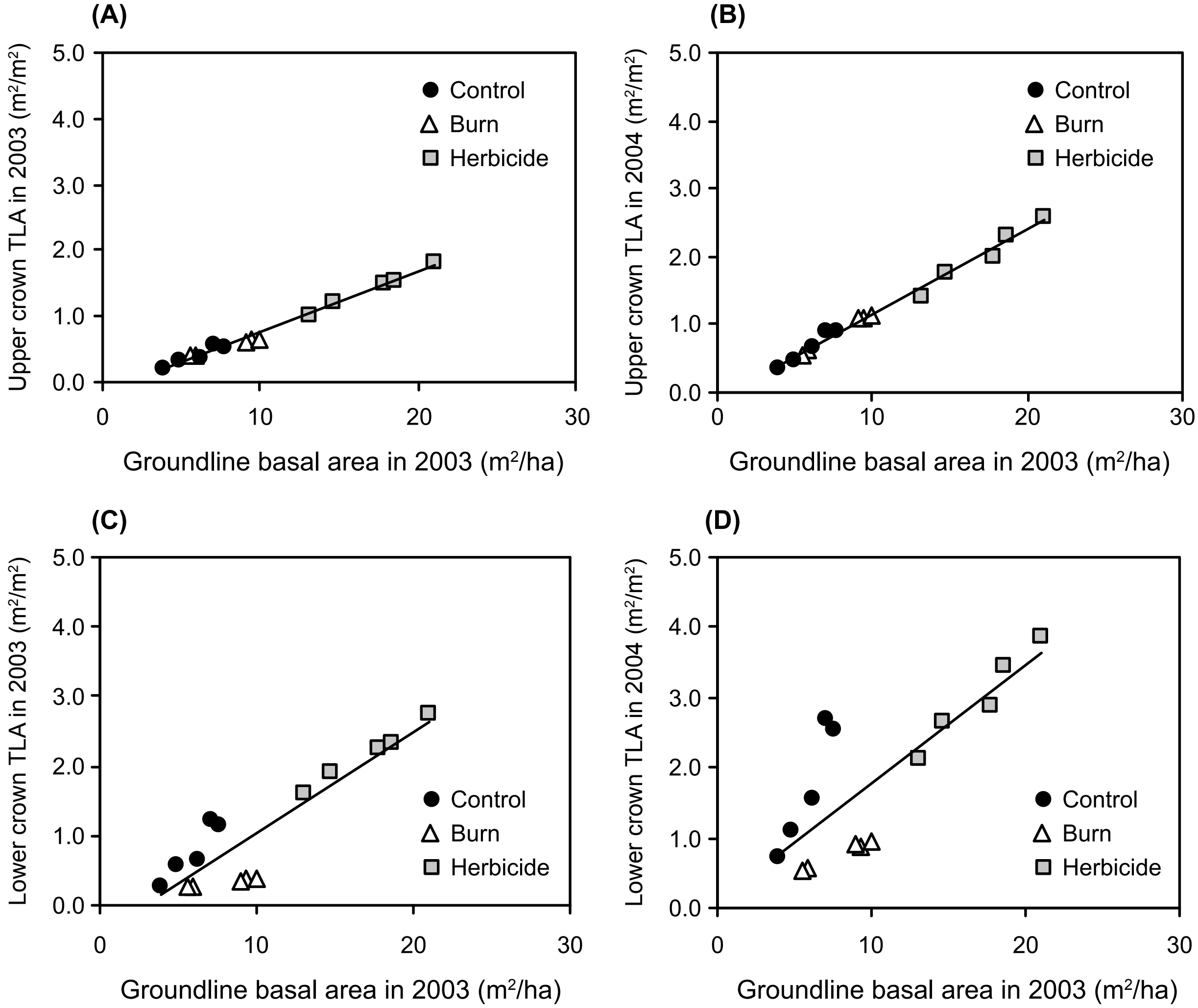

Figure 3—Relationship between groundline basal area in January 2003 and predicted peak total leaf area in the upper crown in August 2003 (A) and August 2004 (B) and in the lower crown in August 2003 (C) and August 2004 (D) of sapling longleaf pine in response to no vegetation management (Control), vegetation management with prescribed fire in June 2000 and May 2003 (Burn), and vegetation management by herbicide application (Herbicide). Lines represent simple linear regressions of all treatments combined. TLA = total leaf area.

less of peak TLA in the H plots than it did in the B and C plots. Foliage produced in the second flush of 2003 made up 10 percent more of peak TLA in the B plots than it did in the H and C plots.

DISCUSSION

Carbohydrate for the production of southern pine foliage originates from different sources. The expanding first flush is supplied with energy derived from starch stored in living parenchyma cells of branches, roots, needles, and the stem as well as current photosynthate from foliage produced in the previous year (Dickson 1989, 1991). As fascicles of the first flush reach maturity, they become a source of energy for the growth of the second flush, and surplus carbohydrate is redirected to the stem and roots. This pattern is repeated as successive flushes or cohorts of foliage develop.

The allocation of current photosynthate to growth and stored energy changes seasonally with the progression of the phenological cycle. Under normal environmental conditions, for example, current photosynthate allocated to the root system of loblolly and longleaf pine yields a pulse of fine-root production during April through July. During this time, starch reserves in the root system are mobilized to the point of near-depletion and allocated to the stem and crown (Dickson 1989, 1991; Kuehler and others 1999; Ludovici and others 2002; Sword Sayer and Haywood 2006; Sword Sayer and Tang 2004). By November, current photosynthate translocated to the root system is allocated to stored starch rather than fine-root production (Kuehler and others 1999, Ludovici and others 2002).

We suggest that both the retention of residual foliage in the crown after fire and the phenological stage of crown development at the time of fire influence postfire sapling growth. Scorch damages the lower crown more than it damages the upper crown. Thus, branch phenology in the upper crown alone may be closely tied to sapling responses to fire. Bud formation and expansion, the source-sink status of current-year fascicles, and the amount of readily accessible stored energy in longleaf pine vary seasonally (Dickson 1989, 1991; Sheffield and others 2003; Sword Sayer and Haywood 2006).

Table 2—Analyses of covariance of percentages of peak total leaf area (TLA) per sapling in the upper and lower crown, and analyses of variance of percentages of upper crown peak TLA in each of four age classes of sapling longleaf pine in August 2003 in response vegetation management treatment

Variable	Source of variation	df	SS	MS	F-value	Pr > F
Upper crown TLA (%)	Covariate[a]	1	0.0243	0.0243	10.08	0.0156
	Block	4	0.0398	0.0100	4.12	0.0499
	Treatment[b]	2	0.0350	0.0175	7.26	0.0197
	Error	7		0.0024		
Lower crown TLA (%)	Covariate	1	0.0243	0.0243	10.08	0.0156
	Block	4	0.0398	0.0100	4.12	0.0499
	Treatment	2	0.0350	0.0175	7.26	0.0197
	Error	7		0.0024		
2002–up[c] TLA (%)	Block	4	0.0037	0.0009	0.70	0.6126
	Treatment	2	0.0579	0.0289	21.97	0.0006
	Error	8		0.0013		
2003–1–up TLA (%)	Block	4	0.0118	0.0030	0.64	0.6511
	Treatment	2	0.2266	0.0113	2.43	0.1494
	Error	8		0.0047		
2003–2–up TLA (%)	Block	4	0.0033	0.0008	0.45	0.7695
	Treatment	2	0.0302	0.0151	8.16	0.0117
	Error	8		0.0019		
2003–3–up TLA (%)	Block	4	0.0138	0.0034	1.66	0.2513
	Treatment	2	0.0444	0.0222	10.65	0.0056
	Error	8		0.0021		

df = degrees of freedom; SS = sum of squares; MS = mean square; Pr > F = probability of a greater F-value; TLA = total leaf area.

[a] The covariate was mean groundline diameter in August 2003.

[b] Treatments were no vegetation management (C), vegetation management with prescribed fire (B), and vegetation management by herbicide application (H).

[c] 2002-up = upper crown foliage produced in 2002; 2003-1-up = upper crown first flush foliage produced in 2003; 2003-2-up = upper crown second flush foliage produced in 2003; 2003-3-up = upper crown third and subsequent flush foliage produced in 2003.

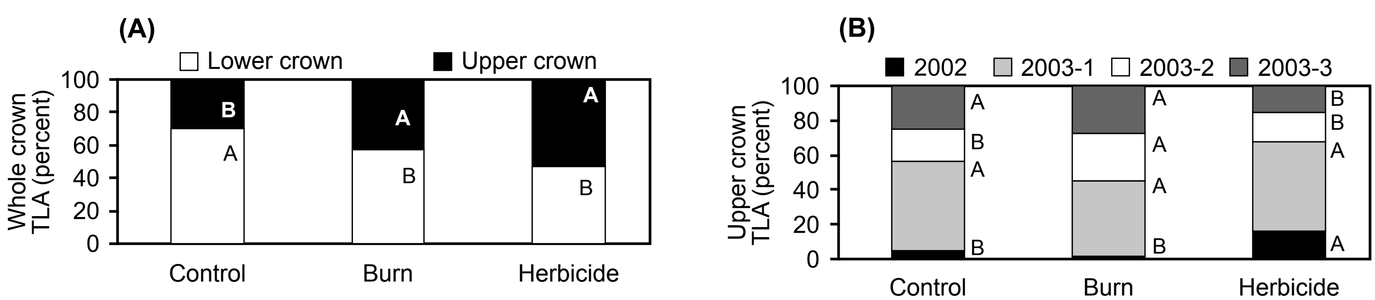

Figure 4—Distribution of predicted peak total leaf area (TLA), adjusted by groundline diameter, between the upper and lower crown (A) and distribution of TLA in the upper crown among four cohorts of foliage (B) of sapling longleaf pine in response to no vegetation management (Control), vegetation management with prescribed fire in June 2000 and May 2003 (Burn), and vegetation management by herbicide application (Herbicide). Cohorts of foliage are 2002 (stem foliage and branch foliage produced in 2002), 2003-1 (first-flush foliage produced in 2003), 2003-2 (second-flush foliage produced in 2003), and 2003-3 (foliage from the third and subsequent flushes produced in 2003). Bars represent one standard error of the mean. Means within a crown level or cohort of foliage with different upper case letters are significantly different at $P \leq 0.10$.

It is understandable, therefore, that the effects of crown scorch on stand production also vary seasonally.

Weise and others (1987) simulated crown scorch at different times of the year by removing 0, 33, 66, 95, and 100 percent of the foliage from sapling loblolly and slash pine in January, April, July, and October. When 100 percent of the foliage was removed, stemwood growth was consistently reduced regardless of month of defoliation. With 33 to 95 percent defoliation, stemwood growth was reduced only by the April defoliation. Defoliation in January did not affect new foliage because terminal buds had not yet expanded (Stenberg and others 1994). In July and October, at least two cohorts of foliage were mature or nearly mature and had been producing photosynthate and exporting it to growth and stored energy for several months (Dickson 1989, 1991; Stenberg and others 1994). It is possible that both the first and second cohorts of foliage were in the process of expanding in April and that they had not yet exported a significant amount of photosynthate (Chung and Barnes 1980; Dickson 1989, 1991; Stenberg and others 1994; Tang and others 1999). All of this work suggests that stemwood growth is more a function of sapling phenology as the growing season progresses than just a function of month of defoliation.

At our field site, prescribed fire in late May 2003 defoliated > 50 percent of the live crown length but did not reduce the annual production of stem, branch, or foliage biomass. On the basis of branch phenological measurements in June 2003 (data not shown), we estimate that upper crown first-flush internodes were fully expanded with 40 percent fascicle expansion and that second-flush internodes were 25 percent expanded with no fascicle expansion when prescribed burning took place. Unlike the first cohort of foliage, the second cohort of foliage had not begun to expand by late May and was not vulnerable to scorch.

Even though part of the upper crown was scorched in May 2003 on the B plots, upper crown peak TLA in August 2003 was similar among the B, C, and H plots. Apparently, saplings on the B plots readily re-established the upper crown leaf area that was destroyed by scorch. The contribution to upper crown peak TLA made by the second cohort of foliage was greater on the B plots than on the C and H plots, so that by August 2003, the combined contribution of the first and second cohorts of foliage to upper crown peak TLA was similar among the B, C, and H plots. Past research has shown that stored carbohydrates are used for the re-growth of leaves after defoliation (Dickson 1989, 1991). It is not surprising, therefore, that at our study site Kuehler and others (this proceedings) found a 35 percent decrease in longleaf pine root starch concentration approximately 1 month after burning on the B plots but no comparable starch drop on the C and H plots. We speculate that burning before the onset of fascicle expansion by the second cohort of needles and the availability of stored energy in roots accelerated the growth of second cohort foliage.

The retention of living foliage in the upper crown after burning, and favorable conditions of branch development and root starch concentration at the time of burning, were associated with the reestablishment of upper crown peak TLA within 3 months of scorch and no loss of annual aboveground biomass production. Because branch development and the allocation of photosynthate to starch change seasonally, similar peak TLA and annual production responses may not have occurred with burning at other times of the year. For example, peak TLA may have been more vulnerable to fire damage after fascicles of the second cohort started to expand. This vulnerability could have been increased by suboptimal starch storage in roots.

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