Fire and longleaf pine physiology-- Does timing affect response?

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ABSTRACT

Southern pines vary in their response to the loss of leaf area by crown scorch. We hypothesize that they tolerate crown scorch by at least three recovery mechanisms, but the function of these mechanisms is season-dependent. Using sapling longleaf pine as a model and experimental results from central Louisiana, U.S.A., our objective is to present examples recovery from scorch, and discuss how this may be affected by season. Results indicate that longleaf pine health and sustainability may be dependent on this species' ability to shift leaf area upward on the stem, rapidly re-establish leaf area with the mobilization of stored energy, and maintain high rates of net photosynthesis during the height of the growing season. However, the seasonal nature of carbon allocation to stored energy may interact with leaf area re-establishment to jeopardize sustained health and production.

Keywords— biennial prescribed fire, leaf area, net photosynthesis, *Pinus palustris* Mill., root starch

INTRODUCTION

Plant and animal species commonly found in longleaf pine (*Pinus palustris* Mill.) ecosystems are adapted to withstand fire and may require fire for sustainability (Brockway and Lewis 1997, Haywood and others 2001, Landers and others 1995, Outcalt 2000). Because longleaf pine is intolerant of shade, the establishment of this species on cut-over sites requires the control of competing vegetation by burning, or some other means. Prescribed fire every two to four years is commonly used for this purpose.

Carbon fixation in tree crowns controls stemwood production. Yet, although prescribed fire is often accompanied by significant crown scorch, stemwood production responses to the loss of foliage by scorch are variable. For example, Boyer (1983, 1987) assessed the absence of fire and biennial fire in winter, spring, and summer and found that after 10 years, longleaf pine production was reduced by fire regardless of season. In contrast, other studies found no effect of prescribed fire on tree growth (Brockway and Lewis 1997, Waldrop et al. 1987).

Variable effects of fire on tree crowns may be one reason why growth losses are not consistently seen in response to fire. Another explanation for inconsistent growth responses to crown scorch is that the timing of scorch rather than the extent of scorch controls the recovery of whole-crown carbon fixation and allocation. Glitzenstein et al. (1995) suggested that inconsistent growth responses to fire were attributed to interaction between branch phenology and the season of fire. Weise et al. (1987) demonstrated how the stem growth of four-year-old loblolly and slash pine was affected by defoliation in January, April, July, or October. Stem growth was reduced with defoliation in April, but was unaffected with defoliation in January, July, or October.

With the loss of leaf area, crown scorch reduces the availability of current photosynthate for growth and stored energy. The potential exists, however, for southern pine species to tolerate, and recover from the loss of leaf area. We hypothesize that longleaf pine tolerates crown scorch by recovery mechanisms, but the function of these mechanisms is season-dependent. Using sapling longleaf pine as a model and experimental results from central Louisiana, U.S.A., our objective is to present examples of recovery from scorch, and discuss how this may be affected by season.

MATERIALS AND METHODS

Study site

The study is in two locations on the Calcasieu Ranger District of the Kisatchie National Forest, Rapides Parish, Louisiana. A mixed pine-hardwood forest originally occupied both sites. Site 1 was clearcut harvested in 1996 and roller-drum chopped and burned in August 1997. Site 2 was clearcut harvested, sheared, and windrowed in 1991 and burned in 1993 and 1996. The soil at Site 1 is mostly Ruston fine sandy loam with some Gore silt loam and Malbis fine sandy loam. The soil at Site 2 is a complex of Beauregard silt loam and Malbis fine sandy loam. Soils at both sites are moderately well-drained to well-drained and have a 0 to 10 percent slope.

Treatment plots (22 x 22 m; 0.048 ha) and three vegetation management treatments were established at each site: (1) Control (C)-- no management activities after planting, (2) Prescribed burning (B)-- plots were burned every two or three years using the strip headfire method in May, and (3) Herbicides (H)--herbicides were applied after planting for herbaceous and arborescent plant control at site 1 in 1997-1999, and at site 2 in 1998-1999. Recovering brush was cut by hand in 2001. Container-grown longleaf pine seedlings from genetically improved sources (site 1: Louisiana; site 2: Mississippi) were planted at 1.8 m^2 in November 1997 at site 1 and March 1997 at site 2. Treatment plots contained 12 rows of 12 seedlings with the internal 8 rows of 8 seedlings as measurement plots. Site 2 was prescribe burned in May 1998 and both sites were prescribe burned in June 2000, and May 2003 and 2005. The study design is a randomized complete block split plot design with five blocks. Three blocks were located at site 1 and two blocks were located at site 2. The three vegetation management treatments are the whole plot effects, and site is the subplot effect. Plots at both sites were blocked by the appearance of soil drainage.

Measurements

Scorch and char. The percentage of total height with scorched foliage and bark char were calculated for each measurement tree one month after prescribed fire was applied in May 2003 and May 2005.

Temperature. Temperature sensitive paints and labels were used to monitor fire intensity around each of three permanently labeled saplings per plot. A series of five 0.5 cm wide bands of temperature sensitive Tempilaq paint (Tempil Division Big Three Industries, Inc., South Plainfield, NJ), was painted on aluminum tags (7.0 x 2.5 cm). Each band was painted with a temperature sensitive paint that volatilizes at either 93 (violet), 149 (pink), 204 (green), 260 (blue) or 316 ^{o}C (red) (200-600 ^{o}F). Four tags were wired to steel rods at either the groundline, or at a height of 0.5 m, 1.0 m, or 1.5 m. Steel rods with painted tags were pushed in the ground vertically in four cardinal directions around the crown perimeter. After the application of prescribed fire, the rods were read to determine the maximum temperature (+/- 56 ^{o}C) achieved at each height and average temperatures per height were calculated by sapling.

Temperature sensitive labels were used to monitor mid-crown temperature. Tempilabels (Series 8M, Tempil, Division Big Three Industries, Inc., South Plainfield, NJ) (1.0 x 4.0 cm) were affixed to aluminum tags (7.0 x 2.5 cm). Tags were wired with fine gauge wire to the mid-crown of three saplings per plot at four cardinal directions. Each Tempilabel contained eight white temperature rating paint chips that turned black at temperatures of: 38, 43, 49, 54, 60, and 66 ^{o}C (100-170 ^{o}F). After prescribed fire, Tempilables were read to determine the maximum temperature (+/- 5-6 ^{o}C) mid-crown foliage was exposed to.

Leaf area. In late August through September of 2003, 2004, and 2005, three healthy saplings, one randomly selected from those in each 33rd percentile of total height per plot, were destructively harvested at the groundline from the two-row buffer of each treatment plot. Total height from the groundline to the terminal tip, groundline diameter (gld), and diameter at breast height (dbh) were recorded. The live crown was separated into upper and lower halves. Branches were separated from the stem and fascicles were removed from the branches and stem, and separated by cohort and crown level. A 10-fascicle sub-sample was collected each from previous year foliage and current year first flush foliage in the upper and lower crown of each sapling. The remaining foliage, branches, and stem were dried to equilibrium at 70^{o}C and weighed. The total leaf area and dry weight of fascicle sub-samples were measured and their dry weights were added to remaining foliage dry weights. Growth and biomass data are being used in assessments of production.

For each 10-fasicicle sub-sample, total leaf area (TLA) was determined by the displaced needle volume method (Johnson 1984). Subsequently, fascicle sub-samples were dried to equilibrium at 70°C and weighed. Data from all three years were combined and linear equations were developed to predict the TLA of previous and current year foliage of saplings destructively harvested from the B, C, and H plots. These equations were used to estimate the TLA of the upper, lower, and total crown of the destructively harvested saplings. Fractions of total leaf area by upper and lower crown level were determined.

Net photosynthesis. In winter of 2002 (site 1 only), 2003, 2004, and 2005 three saplings of average height per plot were randomly selected and permanently labeled. Fascicle gas exchange was measured during a three day period of sequential sunny days between February 2002 and October 2005 (February and April 2002 (site 1 only); May, July, and September of 2003; April and July of 2004; May, July, and October of 2005). Two blocks were measured on each of the first two days and the fifth block was measured on the third day.

On each day, six series of measurements in the lower and upper one-half of the live crown were conducted with three series in the morning (0900-1230) and three series in the afternoon (1300-1530). On each day, the first morning and the first afternoon measurements were done in a randomly selected plot on a pre-selected seedling that was randomly chosen without replacement. After the first series of morning and afternoon measurements, subsequent measurements on pre-selected seedlings, randomly chosen without replacement, were done in the order of consecutive plots to be measured that day. To minimize diurnal effects, the second and third series of measurements in the morning and afternoon were done in the reverse order of consecutive plots to be measured that day.

Within two minutes of sampling from the south side of saplings, light saturated net photosynthesis (A_{sat}) was measured on detached fascicles with a portable photosynthesis system (Model 6400, Li-Cor, Inc. Lincoln, NE) and a standard needle chamber equipped with a LED light source (Model 6400-02B, Li-Cor, Inc. Lincoln, NE). After the placement of two fascicles in the leaf chamber and a one- to two-minute equilibration period, recorded measurements were an average of point measurements taken each second over a 20 second period. All measurements were conducted at a photosynthetically active radiation of 1400 umol/m^2/s. After each measurement, fascicles were stored in plastic bags on ice and surface areas in the leaf chamber were determined by the displaced needle volume method (Johnson 1984). Values of A_{max} were expressed on a total leaf surface area basis as µmol CO$_2$/m^2/s.

Root starch. Between May 2003 and April 2006, three to five coarse longleaf pine roots (2-5 mm diameter) were collected from each sapling used for fascicle physiology measurements. Roots were sampled within 0.5 m of the bole with a garden trowel, washed within 30 minutes of collection with ice-cold water to remove excess soil, placed into a labeled paper bag, and set on ice until they arrive at the laboratory. Roots were pooled by plot, lyophilized, and ground through a 20-mesh screen. Ground root samples were analyzed for total starch content by Dairyland Laboratories, Inc. (Arcadia, WI) using a modified Back Knudsen enzymatic assay

(Hall 2009). Root starch was expressed as percentage of dry weight. Using an established seasonal pattern of root starch for southern pines (Sword et al. 2000, Sword Sayer and Haywood 2006), periods of peak (i.e., February through April 2003-2006) and depleted (i.e., August 2005) root starch were identified, and data were partitioned into these two periods. The rate of starch depletion from small woody roots was calculated as the difference in starch concentration before (i.e., early May) and after (i.e., June) prescribed fires in 2003 and 2005.

Statistical analyses

Means and standard errors of crown scorch, stem char, air temperatures, and crown temperatures after prescribed fires in May 2003 and May 2005 were calculated. All other data were transformed to square root or natural logarithm values as needed to establish normally distributed experimental errors. Plot means were calculated. Fractions of leaf area in the upper and lower crown of destructively harvested saplings, and TLA of the destructively harvested saplings by crown level and foliage age (i.e., produced in the previous or current year) were evaluated by analyses of covariance using a randomized complete block split plot in time design with five blocks. Mean gld was the covariate. Vegetation management treatment was the whole plot effect and year was the subplot effect. Values of A_{max} by crown level and diurnal period (i.e., 0900-1230 or 1300-1530) and small woody root starch concentration at peak and depleted levels were evaluated by analyses of variance using a randomized complete block split plot in time design with five blocks. Vegetation management treatment was the whole plot effect and measurement period was the subplot effect. Effects were considered significant at $P \leq 0.05$. Means were compared by the Tukey test and considered significantly different at $P \leq 0.05$.

RESULTS

Prescribed fire intensity. Crown scorch after prescribed fires in May 2003 and May 2005 averaged 60±7 and 90±1 percent, respectively. Average bole char was 26±2 percent in 2003 and 37±4 percent in 2005. Average minimum air temperatures at the groundline, and at 0.5, 1.0, and 1.5 m heights during prescribed fire in May 2003 were 262, 173, 137, and 128 °C. Corresponding average minimum air temperatures in May 2005 were 312, 206, 163, and 133 °C. During prescribed fire in May 2003, average maximum mid-crown air temperature was 55 °C. In May 2005, all mid-crown air temperatures exceeded 77 °C which was the highest temperature detectable by the Tempilables used.

Leaf area. The fraction of sapling TLA, adjusted by gld, in the upper crown was significantly greater on the B plots compared to the C plots in 2003 and 2005 (Figure 1a). In 2005, the fraction of TLA in the upper crown was also significantly greater on the H plots compared to the C plots. In 2004, the fraction of TLA in the upper crown was not significantly different among the treatments. In 2005, the fraction of TLA in the lower crown was significantly lower on the B plots compared to the C plots (Figure 1b). In 2003 and 2004, the fraction of TLA in the lower crown did not differ by treatment.

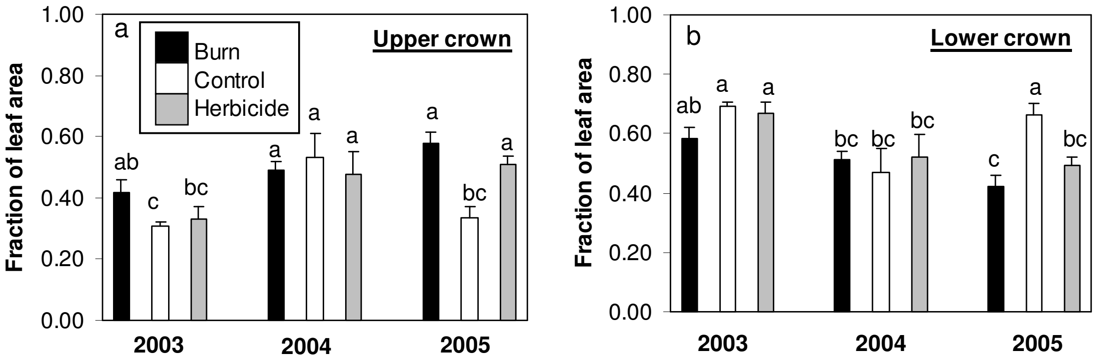

Figure 1. Fraction of total leaf area, adjusted by gld, in the upper crown (a) and lower crown (b) of destructively harvested longleaf pine saplings in late August through September of 2003, 2004, and 2005. Prescribed fire was applied in May 2003 and May 2005. Bars represent one standard error of the mean. Means within a crown level with a different lower case letter are significantly different at $P \leq 0.05$ by the Tukey test.

Across the three years, the TLA, adjusted by gld, of foliage produced in the previous year was significantly lower on the B plots compared to the C and H plots (Figure 2), and that produced in the current year was not significantly affected by treatment. Total foliage TLA across the three years on the B plots was significantly less than that on the H plots but was statistically similar to that on the C plots.

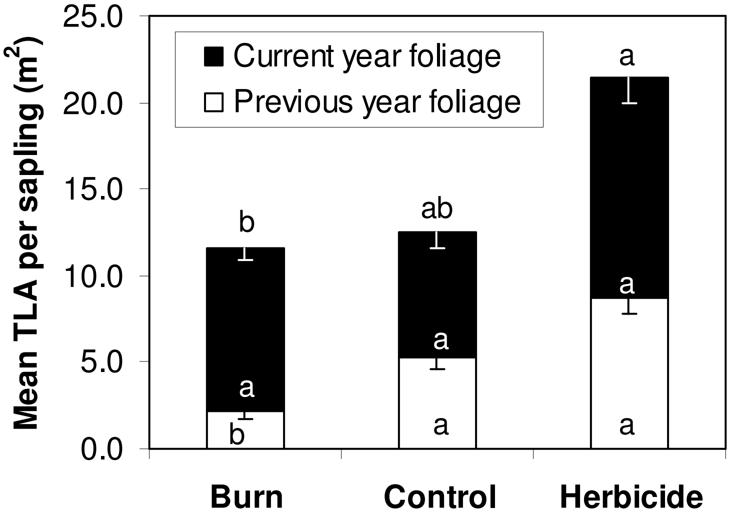

Figure 2. Total surface area of foliage (TLA), adjusted by sapling groundline diameter, from destructively harvested longleaf pine saplings in late August through September of 2003, 2004, and 2005. Means represent the TLA of foliage produced in the previous and current year and the sum of these age classes of foliage. Prescribed fire was applied in May 2003 and May 2005. Bars represent one standard error of the mean. Means of TLA by foliage age class and means of total TLA with a different lower case letter are significantly different at $P \leq 0.05$ by the Tukey test.

Net photosynthesis. Mean A_{max} across ten measurement periods during 2002 through 2005 was significantly affected by vegetation management treatment. While A_{max} in the upper crown was not significantly affected by treatment in the morning (i.e., 0900-1230) (Figure 3a), upper crown A_{max} was significantly greater on the B plots compared to the C and H plots in the afternoon (1300-1530) (Figure 3b). Upper crown A_{max} was also significantly greater on the C plots compared to the H plots in the afternoon. In the lower crown, A_{max} was significantly greater on the B plots compared to both the C and H plots in the morning (Figure 3c) and the afternoon (Figure 3d).

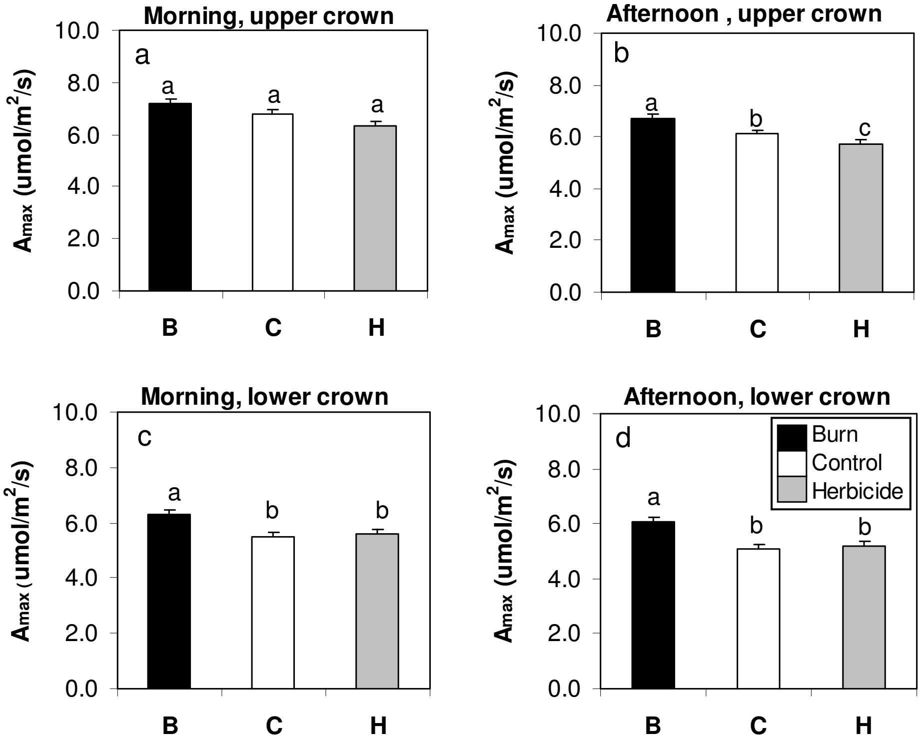

Figure 3. Morning (a and c) and afternoon (b and d) net photosynthesis rate (A_{max}) of sapling longleaf pine in the upper (a and b) and lower crown (c and d) across ten measurement periods during 2002 through 2005 in response to three vegetation management treatments. Bars represent one standard error of the mean. Means within a crown level and diurnal period with a different lower case letter are significantly different at $P \leq 0.05$ by the Tukey test.

Root starch. Peak root starch concentration was significantly affected by year; whereas, depleted root starch concentration was significantly affected by treatment. Peak root starch concentration in 2003 (35.3±1.9%) was significantly greater than that in 2004 (29.8±1.8%), 2005 (30.3±0.7%), and 2006 (23.4±2.2%), peak root starch in 2004 and 2005 was significantly greater than that in 2006. In 2003 and 2005, depleted root starch concentration was significantly greater on the H plots compared to the B plots, and that on the C plots was statistically similar to that on both the B and H plots (Figure 4a). The rate of starch depletion after prescribed fires in 2003 and 2005 was significantly greater on the B plots compared to the C and H plots (Figure 4b).

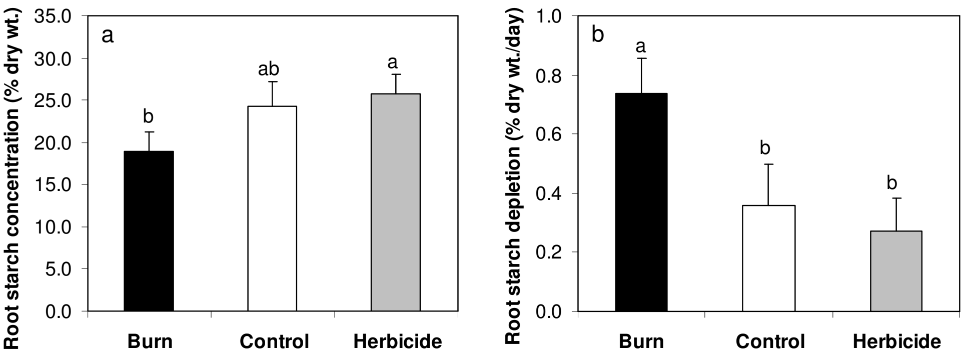

Figure 4. Small woody root starch concentration during its seasonal minimum in 2005 (a) and the rate of depletion of starch from small woody roots immediately after prescribed fire in 2003 and 2005 (b) in response to vegetation management treatment. Bars represent one standard error of the mean. Means with a different lower case letter are significantly different at $P \leq 0.05$ by the Tukey test.

DISCUSSION

Our results demonstrate three potential mechanisms of recovery after crown scorch. First, a larger fraction of TLA was found in the upper crown of saplings on the B plots compared to saplings on the C plots. This was observed in 2003 and 2005 when prescribed fire was applied in May, but not in 2004 when no fire was applied (Figure 1). In 2005, saplings on the B plots contained a smaller fraction of TLA in the lower crown compared to saplings on the C plots. These observations suggest that fire changes the allocation of carbon among the branches in favor of the upper crown. This may arise from the pruning of or damage to lower crown branches during fire. However, as saplings grow in height and the number of branch whorls increases, this effect appears to be lost in non-burn years. Whole crown carbon fixation may benefit from concentration of new foliage in the upper crown because available light is generally higher in the upper crown compared to the lower crown. Also, upper crown foliage is less vulnerable than lower crown foliage to crown scorch as a result of the next application of prescribed fire. These benefits may accelerate the potential for fascicle-level carbon fixation in the upper crown, and minimize the potential for future damage to foliage by fire.

It is not surprising that the TLA of foliage produced in the previous year was less on the B plots compared to the C and H plots (Figure 2). This simply reflects the destructive effect of prescribed fires in 2003 and 2005 on mature and expanding immature foliage. It is intriguing, however, that values of TLA attributed to foliage produced in the current year were similar among treatments, and that this corresponded to similar whole crown TLA values on the B and C plots. This suggests that even though 60 and 90 percent of the crowns were scorched on the B plots in May 2003 and May 2005 causing significant loss of the previous year foliage and the first flush of the current year, a large portion of TLA was re-established by late summer.

Efficient re-establishment of damaged foliage represents a potential mechanism of recovery after crown scorch. However, if prescribed fire scorches a significant portion of the crown so that current photosynthate is limiting, the re-establishment of damaged foliage may depend on the mobilization of stored starch in roots and other plant tissues. Starch storage in roots is seasonal with an accumulation period between November and March, and a depletion period between

May through August (Sword et al. 2000, Sword Sayer and Haywood 2006). We determined that peak starch storage in small woody roots during February through April was unaffected by treatment. This indicates that carbon fixation during winter and early spring is adequate to supply carbohydrate for root starch storage. Although year-to-year variation in climate may affect root starch accumulation, silvicultural treatments that maintain normal leaf areas are not likely to affect root starch accumulation. In contrast, root starch concentration at the point of near depletion in August was lower on the B plots compared to the H plots. It appears as though the demand for root starch was greater on the B plots than on the H plots. Therefore, silvicultural treatments have the potential to affect root starch mobilization and use. In support, we found that the rate of root starch depletion immediately after prescribed fires in May 2003 and May 2005 was greater on the B plots compared to the C and H plots (Figure 4).

Our results indicate that although longleaf pines are capable of re-establishing leaf area after crown scorch, this process may depend on the availability of root starch as an energy source. Two conditions, however, jeopardize this recovery mechanism. First, climate conditions that lower the availability of root starch during its peak concentration may indirectly affect the re-establishment of leaf area if photosynthate from existing foliage is limiting. In a previous study, we found that a three-year period of prolonged drought coincided with a significant drop in root starch accumulation by mature longleaf pine in central Louisiana (Sword Sayer and Haywood 2006). This information as well as the significant effect of year on peak root starch accumulation in the present study suggests that further research is needed to understand how interaction between severe drought and prescribed fire affects carbon allocation to the roots and foliage of southern pines.

The second condition that jeopardizes the role of root starch in leaf area re-establishment is the occurrence of crown scorch at a time when root starch is naturally depleted. If prescribed fire causes severe crown scorch at a time of year when root starch is seasonally low, leaf area re-establishment may not be achieved. Moreover, the leaf area that does re-establish may not adequately supply carbohydrate for the accumulation and mobilization of root starch in the subsequent year. A reduction in pine root starch concentration in response to crown scorch or defoliation has been reported elsewhere (Sword and Haywood 1999, Guo et al. 2004). Perhaps absence of root starch contributed to the reduced stemwood growth of scorched slash pine (*Pinus elliottii* Engelm.) for two years after burning (Johansen and Wade 1987).

In addition to shifting leaf area upward on the stem, and rapid re-establishment of leaf area, longleaf pine that were prescribe burned in May 2003 and May 2005 maintained higher rates of lower crown and afternoon A_{max} compared to saplings on the C and H plots. This was true across the ten measurement periods between 2002 and 2005. Further, analyses will resolve seasonal and annual differences among the treatments. Available water and soil fertility are primary drivers of carbon fixation and stand production by southern pines, and water availability may limit carbon fixation during the height of the growing season in the western Gulf region (Allen 1987, Tang et al. 2004). In our study, sapling leaf area had re-established three to four months after burning. However, during this three to four month period, TLA results suggest that transpiration rates of the B saplings were lower than those of the C and H saplings. During periods of water limitation, this may have allowed the B saplings to maintain higher A_{max} for a longer period during the day. Our results suggest that the B saplings benefited from higher A_{max}

in the lower crown in the morning and afternoon and in the upper crown in the afternoon (Figure 3).

By themselves, these three potential mechanisms of recovery from scorch are not likely to sustain production when severe scorch occurs at a frequent interval (Haywood 2009). Together, however, they may help to sustain high levels of production in frequently burned stands. The seasonal pattern of root starch accumulation and mobilization and the apparent demand for this energy source during the re-establishment of leaf areas after scorch advises that the contribution of leaf area re-establishment to sustained production may be limited by season. Research will continue in an effort to identify the seasonal window in which prescribed fire and crown scorch have a minimum negative effect on longleaf pine production and health.

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