OPTIMUM PRESCRIBED FIRE CONDITIONS FOR FOLIAGE REGROWTH AMONG LONGLEAF PINE SEEDLINGS

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Abstract—We synthesized experimental observations in central Louisiana to estimate the season and precipitation conditions for optimal post-scorch foliage regrowth among longleaf pine (*Pinus palustris* Mill.) seedlings. After severe crown scorch, starch reserves support foliage regrowth and are at their maximum concentration in March through May. When sustained longleaf pine seedling vigor is desired, prescribed fire in March through May is optimal if seedlings have not experienced prolonged drought. We observed that 2 sequential years of severe drought reduced peak starch for 2 years after drought ended. Therefore, when high seedling vigor is desired and prolonged drought has occurred, a prescribed fire delay or other means of vegetation control may be needed until foliage mass and peak starch levels are restored. Furthermore, when seedling development has advanced beyond the grass stage, prescribed fire should be applied during the period of peak starch concentration, but before or after there is a high risk of terminal bud mortality.

INTRODUCTION

By the mid-20th century, longleaf pine (*Pinus palustris* Mill.) shifted from being a major to a minor *Pinus* species in the Southeastern United States (Frost 2006). Research has since resolved many of the problems that contributed to the loss of this fire-climax species (Barnett 2002, Boyer 1993, Brockway and Lewis 1997, Croker and Boyer 1975, Kush and others 1996, Palik and others 1997). At present, restoration of longleaf pine ecosystems is an ongoing emphasis among Federal, State, and private agencies that manage forested land in the Southeastern United States (America's Longleaf 2009).

Longleaf pine requires full sunlight to survive and become dominant in a forest stand (Brockway and others 2006). Once longleaf pine is established, repeated fire not only sustains longleaf pine ecosystem structure, but also reduces competition for light between longleaf pine seedlings and competing vegetation (Haywood 2015, Haywood and others 2001, Mitchell and others 2009). Where aggressive competition for light is anticipated between seedlings of longleaf and other southern pines, the early introduction of prescribed fire may be warranted. Since the average duration of the longleaf pine "grass" stage is 2 to 5 years (Brockway and others 2006, Haywood 2007), it may be necessary to prescribe burn longleaf pine seedlings while they are in this stage of development (Longleaf Alliance 2009). However, it is anticipated that longleaf pine seedlings in the grass or "hardy growing" stages of development (Wahlenberg 1946) will experience complete crown scorch during prescribed fire.

Will this loss of crown prove to be a problem? Southern pine production is closely related to canopy leaf area by the direct relationship between leaf area and photosynthesis in tree crowns (Jokela and others 2004, Vose and Allen 1988). Longleaf pine sustainability also relies on crown health and function regardless of developmental stage (Gonzalez-Benecke and others 2014, Mitchell and others 2009). For mature longleaf pines, a lag in foliage re-establishment after crown scorch was implicated as the cause of low current annual stem increment in the year of prescribed fire (Ford and others 2010). Past research has also shown correlation between stemwood growth loss and poor foliage regrowth after defoliation among other southern pine species (Boyer 2000, Haywood 2009, Johansen and Wade 1987, Weise and others 1987). Among grass stage longleaf pine seedlings, root collar diameter growth was reduced after fire, and it was suggested this was due to prioritization of carbohydrate allocation to needle production (Knapp and others 2018).

The regrowth of scorched longleaf pine foliage is possible by the end of the growing season after prescribed fire (Sayer and others 2018, Sword Sayer and Haywood 2006). Two mechanisms of this response are current photosynthate produced by non-scorched

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foliage and starch stored in parenchyma cells (Chung and Barnes 1980, Klein and Hoch 2015). Complete crown scorch eliminates current photosynthate as a mechanism of foliage regrowth, and new foliage growth depends on stored starch. Similar to other southern pines (Adams and others 1986, Gholz and Cropper 1991, Ludovici and others 2002), longleaf pine starch reserves are characterized by a distinct seasonal pattern of availability (Sayer and others 2018, Sword Sayer and Haywood 2006). Our objective is to synthesize this published information with corresponding patterns of annual precipitation to describe the seasonal window and precipitation conditions when post-scorch foliage regrowth is optimum among longleaf pine seedlings.

MATERIALS AND METHODS

Mature Tree Woody Root Starch

Seasonal woody root starch concentrations of mature longleaf pines were quantified in two experiments in central Louisiana on the Calcasieu Ranger District of the U.S. Department of Agriculture, Forest Service, Kisatchie National Forest, Rapides Parish, LA. In study 1, 65-year-old longleaf pines were severely crown scorched or were not crown scorched during a September 1996 prescribed fire. Starch concentrations of woody roots, 2 to 5 mm in diameter, were evaluated at a 1- to 2-month interval between May 1997 and May 1998 (Sword and Haywood 1999). In this study, small woody root starch concentration was reduced for 17 months after severe crown scorch. In study 2, small woody root starch concentrations were measured among 45- to 50-year-old longleaf pines at a monthly interval between March 1998 and April 2001 (Sword Sayer and Haywood 2006). Treatments were 24 biennial or triennial prescribed fires in March, May, or July (Haywood and others 2001). Prescribed fires in 1998 did not scorch tree crowns, and leaf area indices were similar among the three prescribed fire treatments. In studies 1 and 2, small woody roots were frozen, freeze-dried, and ground to pass a 1-mm^2 mesh sieve. Starch concentrations of dried and ground root samples were quantified by a modification of the procedure of Jones and others (1977).

For the present evaluation, average starch concentrations of small woody roots in two replications that were not scorched in study 1 were calculated by sampling interval and year. Similarly, average starch concentrations of small woody roots in two replications that were prescribed burned but not crown scorched in March, May, or July in study 2 were calculated by month and year. Coefficients of variation were calculated by monthly interval.

Sapling Taproot Starch

Seasonal taproot starch concentrations of sapling longleaf pines were measured in central Louisiana on the Winn Ranger District of the U.S. Department of Agriculture, Forest Service, Kisatchie National Forest, Rapides Parish, LA. This study assessed the physiological and growth responses of longleaf pine saplings to (1) no prescribed fire or (2) application of prescribed fire in May 2011 or October 2012 (Sayer and others 2018). Taproot starch concentration was reduced by prescribed fire in May or October. The May response was correlated with foliage regrowth after crown scorch; whereas, the October response represented a void of normal starch accumulation that was likely due to allocation of fixed carbon to foliage regrowth after crown scorch. In this study, taproots of 6- to 8-year-old saplings that were or were not prescribed burned were sampled in February, March, May, June, July, September, and October of 2011, 2012, and 2013. Taproot tissues were frozen, freeze-dried, ground to pass a 1-mm^2 mesh sieve, and analyzed for starch concentration by Dairyland Laboratories, Inc. (Arcadia, WI) using the acid hydrolysis method (Vidal and others 2009).

For the present evaluation, taproot starch concentration was averaged among three saplings by non-burned treatment plot and sampling interval. Subsequently, mean taproot starch concentrations among three replications were averaged by sampling interval.

Precipitation Estimates

Monthly precipitation near mature longleaf pine studies 1 and 2 in 1997 through 2001 was estimated by two sources. In 1997 and 2001, precipitation was monitored by an electronic weather station in an open field approximately 20 and 16 km from studies 1 and 2, respectively. Similarly, in 1998, 1999, and 2000, precipitation was monitored approximately 10 and 6 km from studies 1 and 2, respectively. Mean monthly precipitation over the 30-year period between 1971 and 2000 was estimated by long-term data from two locations near Alexandria, LA (NOAA 2019).

At the sapling longleaf pine study, a centrally located electronic weather station recorded precipitation in 2011 through 2013. Mean monthly precipitation in 2010 and over the 25-year period between 1988 and 2013 was estimated by long-term data from two locations near Winnfield, LA (NOAA 2019).

RESULTS AND DISCUSSION

Seasonal Starch Availability

Under most circumstances, bud scales and a dense accumulation of fascicles around the buds of longleaf pine seedlings insulate buds from heat damage by fire (Brockway and others 2006, Komarek 1974). While terminal buds are insulated from fire, the stature of longleaf pine seedlings predisposes foliage to crown scorch by prescribed fire. This loss of mature foliage interrupts photosynthesis and allocation of recently fixed carbon to regrow scorched foliage. The regrowth of scorched foliage among longleaf pine seedlings, therefore, depends on stored carbohydrate until new foliage matures and exports current photosynthate.

Starch reserves are important to foliage regrowth after defoliation (Bond and Midgley 2001, Climent and others 2004, Galiano and others 2011, Wigley and others 2009). Furthermore, starch is the primary source of stored carbohydrate in *Pinus* (Gower and others 1995). Across three studies, we observed that mature trees and saplings of longleaf pine exhibited similar seasonal patterns of starch accumulation and mobilization (Sayer and others 2018, Sword and Haywood 1999, Sword Sayer and Haywood 2006). Among mature trees, starch accumulation occurred between November and March with maximum starch concentrations in March through May and starch mobilization in May through July (fig. 1A). Sapling starch exhibited a similar annual pattern (fig. 1B). Monthly coefficients of variation associated with the starch concentration of mature longleaf pine small woody roots indicated that starch variation was greater during June through January compared to February through May (table 1). These observations suggest that the availability of starch to regrow scorched longleaf pine foliage among seedlings is at its maximum in March through May. While starch may be available after May for post-scorch foliage regrowth, factors that affect seedling carbon physiology during the growing season influence starch availability on a year-to-year basis.

Drought Effects on Available Starch

Environmental conditions that reduce carbon fixation in November through March have the potential to reduce maximum starch concentrations attained in March through May. Similarly, factors that accelerate starch mobilization in May through July reduce the duration of starch availability for post-scorch foliage regrowth after May. For mature trees and saplings, year-to-year differences were apparent in starch concentration during its peak in March through May and as it was mobilized

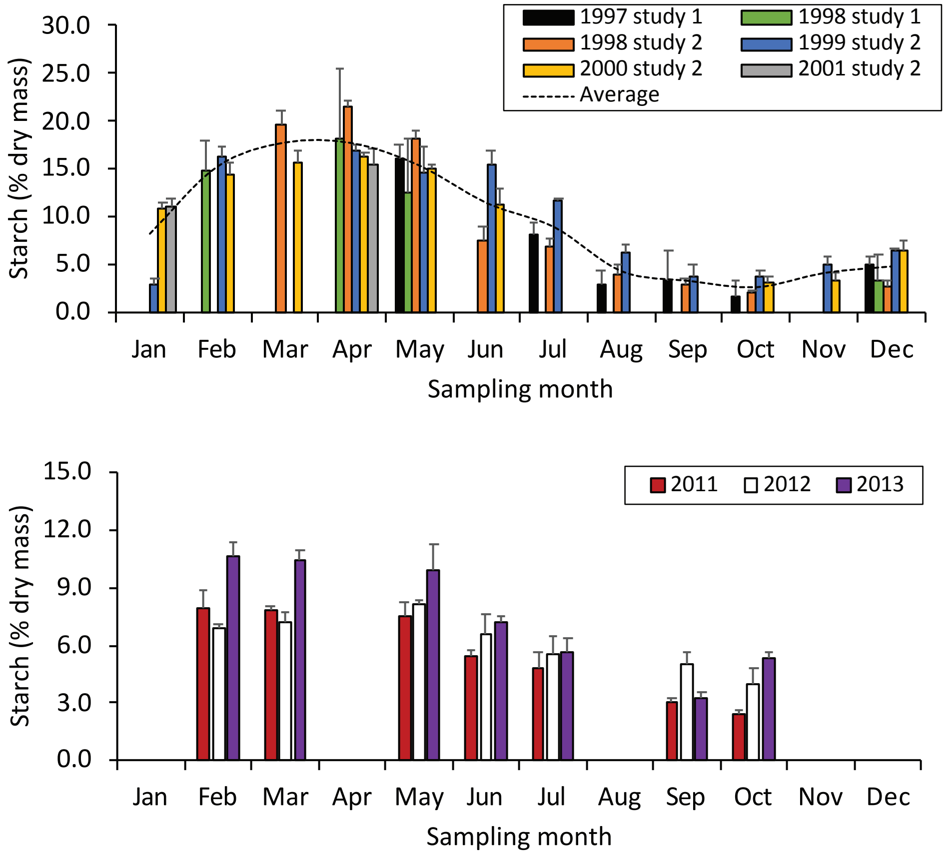

Figure 1—Small woody root starch concentrations of mature longleaf pines (A) or taproot starch concentrations of longleaf pine saplings (B) by sampling month in central Louisiana. Mature tree values are the mean of two replications in study 1 that were not prescribed burned in 1996 (Sword and Haywood 1999) or the mean of two replications that did not exhibit crown scorch after plots were prescribed burned in 1998 (Sword Sayer and Haywood 2006). Sapling values are the mean of three replications that were not prescribed burned in 2011 or 2012 (Sayer and others 2018). Sampling months are January (Jan), February (Feb), March (Mar), April (Apr), May, June (Jun), July (Jul), August (Aug), September (Sep), October (Oct), November (Nov), and December (Dec). Starch concentrations are expressed as a percentage of root dry mass, and bars represent one standard error of the mean. The magnitude of y-axes differs between figures.

in May through July (fig. 1A and 1B). In study 2, a reduced level of peak starch concentration in mature longleaf pine woody roots was associated with periodic drought in 1998, 1999, and 2000 (Sword Sayer and Haywood 2006).

During our sapling study, annual precipitation in 2010 and 2011 was 44 and 54 percent less, respectively, than the 30-year average between 1988 and 2013 (fig. 2A). Quarterly precipitation in January–March and April–June of 2010 and 2011 and in July–September and October–December of 2011 was more than 40 percent less than normal (fig. 2B). In contrast, annual precipitation in 2012 and 2013 was 19 and 22 greater, respectively, than the 30-year average between 1988 and 2013. A comparison of mean peak starch levels of saplings between 2011 and 2013 (8.5 mg g^{-1}), mature trees in studies 1 and 2 (17.7 mg g^{-1}), and 5-year-old longleaf pine saplings in

Table 1—Coefficients of variation for monthly values of small woody root starch concentration as determined by two or more annual means across two studies of mature longleaf pine between 1997 and 2001

	Month											
Variable	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
n	3	3	2	5	5	3	3	3	3	3	2	5
CV	56.1	6.4	15.5	13.3	13.1	34.1	27.3	39.4	11.9	34.7	25.8	35.2

Jan = January; Feb = February; Mar = March; Apr = April; Jun = June; Jul = July; Aug = August; Sep = September; Oct = October; Nov = November; Dec = December.

n = number of annual means used to calculate coefficients of variation.

CV = coefficient of variation.

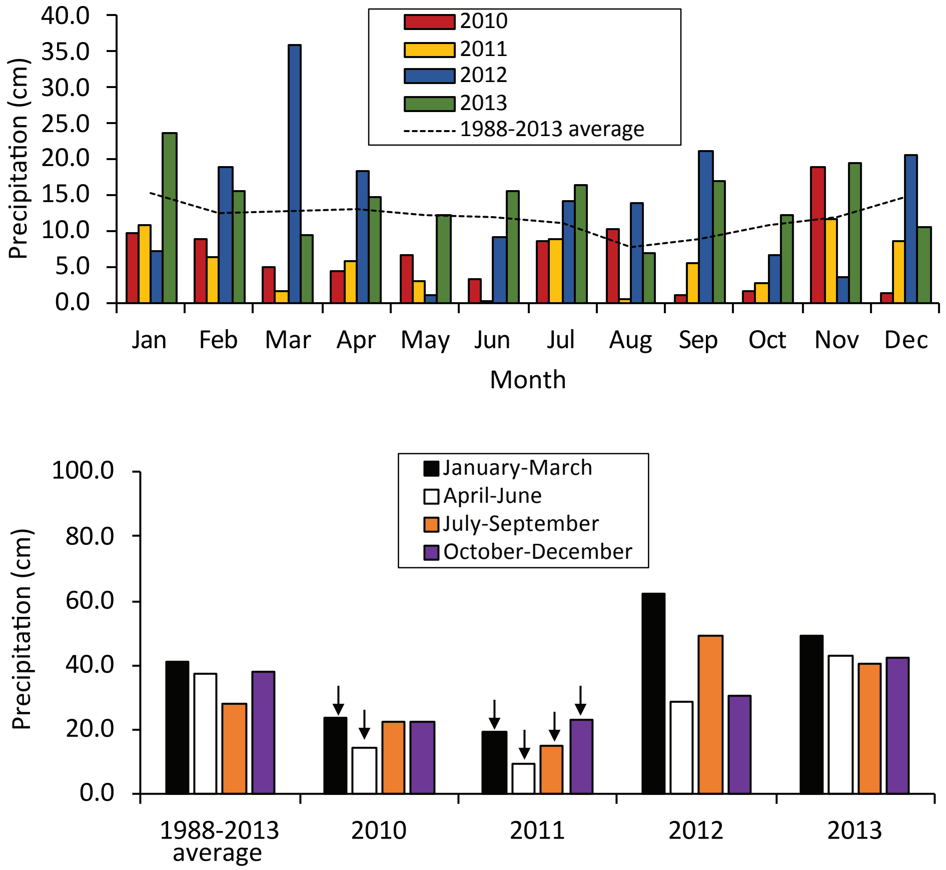

Figure 2—Monthly (A) and quarterly (B) precipitation among experimental longleaf pine saplings in 2011, 2012, and 2013 and estimates of monthly and quarterly precipitation near Winnfield, LA, in 2010 and averaged for 30 years between 1988 and 2013 (dashed line). Arrows indicate annual quarters in which precipitation was at least 40 percent less than the 30-year average.

the absence of prolonged drought (25 mg g^{-1}) (Kuehler and others 2006) suggests that water deficit over 2 years negatively affected sapling starch accumulation in 2011 through 2013. We do not attribute the range in magnitude of these observations to differences in woody root type because starch levels are comparable between the taproot and woody lateral root tissues of longleaf pine (Aubrey and Teskey 2018). Furthermore, it is unlikely that variation in starch analyses was responsible for differences in peak starch concentration because similar minimum values of starch were observed in August through November regardless of methodology.

Prolonged drought has the potential to affect longleaf pine carbon allocation to starch in at least two ways. First, the net photosynthesis of longleaf pine is sensitive to water deficit (Addington and others 2006, Jose and others 2003). Second, under prolonged drought, premature fascicle senescence and carbon limitations to *Pinus* foliage growth reduce total foliage mass (Pallardy and others 1995, Schoettle and Fahey 1994). In association with drought relief in 2012 and 2013, peak starch concentration among saplings in 2013 was 40 percent greater than in 2011 and 2012 but was more than 40 percent less than values reported for mature longleaf pines (Sword Sayer and Haywood 2006) and 5-year-old longleaf pines (Kuehler and others 2006). We propose these losses of starch storage between 2011 and 2013 were due, in part, to the negative effect of drought on gas exchange during starch accumulation in January through March 2011 and the overlapping negative effect of prolonged drought in 2010 and 2011 on total sapling foliage mass in 2011 through 2013. Fascicle-level gas exchange rates may have responded positively to drought relief in 2012 and 2013 leading to a relative increase in peak starch by early 2013. However, we did not observe recovery of normal peak starch levels during 2012 and 2013 after the prolonged drought in 2010 through 2011 ended in 2012.

SUMMARY

Starch is the primary source of carbohydrate to regrow the scorched foliage of longleaf pine seedlings and young saplings. Starch availability is greatest in March through May and may also be adequate to regrow scorched foliage for a limited period after May. At this point, however, starch availability is subject to annual variation. Severe drought for 2 years not only reduced but delayed the recovery of peak starch levels in longleaf pine saplings. When sustained longleaf pine seedling vigor is desired but drought has reduced foliage mass, a delay in prescribed fire application or other means of vegetation control should be considered until foliage mass and peak starch levels are restored. These guidelines apply to seedlings in the grass stage of development and, with one exception, to individuals that have initiated height growth. Longleaf pine terminal bud expansion generally begins in late February and continues through mid-April (Sung and others 2013). During this window of time, elongating terminal buds are vulnerable to heat damage. However, with continued development, they escape mortality by a combination of favorable fire intensity, distance from lethal temperatures, and insulation due to newly emerged fascicles. Therefore, when there is a risk of fire damage to expanding terminal buds, prescribed fire should be applied during the period of peak starch concentration but before or after the risk of terminal bud mortality.

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