New Forests (2018) 49:851–869
https://doi.org/10.1007/s11056-018-9674-0

CrossMark

Foliage re-establishment of *Pinus palustris* Mill. saplings after spring or fall prescribed fire

Mary Anne S. Sayer[1] · **Michael C. Tyree**[2] · **Dylan N. Dillaway**[3] · **Brian M. Rudd**[4]

Received: 21 November 2017 / Accepted: 18 August 2018 / Published online: 23 August 2018

Abstract

Repeated fire is key to the viability of longleaf pine (*Pinus palustris* Mill.) ecosystems, but its acceptance as a management tool may depend on satisfactory longleaf pine growth. This is because longleaf pine establishment often has the dual-purpose of ecosystem restoration and stemwood production. Timely recovery of scorched foliage among longleaf pine seedlings and saplings supports maximum juvenile growth. We identified two means of foliage re-establishment in the growing season after prescribed fire regardless of the season of fire application. New foliage growth after spring or fall fire was correlated with un-scorched foliage biomass and the presence of lateral branches. After prescribed fire in spring, foliage biomass recovery also appeared to benefit from the mobilization of starch. The high carbon demand of foliage recovery after fall prescribed fire was associated with interruption of seasonal starch accumulation in the stem and taproot. The implication of low starch accumulation in stem and taproot tissues during the growing season after fall prescribed fire is unknown and warrants further investigation. Our results demonstrate a positive influence of residual foliage, lateral branches, and stored starch on timely foliage recovery of young longleaf pines after fire. Together with knowledge of longleaf pine development and fuel and climate conditions at the time of prescribed fire, this information will aid prescribed fire practitioners charged with maintaining longleaf pine stands of high vigor.

Keywords Grass stage · Scorch · Lateral branches · Longleaf pine · Prescribed burn · Stored starch

✉ Mary Anne S. Sayer
msword@fs.fed.us

[1] RWU-4158 Restoring and Managing Longleaf Pine Ecosystems, United States Department of Agriculture, Forest Service, Southern Research Station, Alexandria Forestry Center, 2500 Shreveport Highway, Pineville, LA 71360, USA

[2] Department of Biology, Indiana University of Pennsylvania, Indiana, PA 15705, USA

[3] School of Environmental Citizenship, Unity College, Unity, ME 04988, USA

[4] United States Department of Agriculture, Kisatchie National Forest, Winn Ranger District, Winnfield, LA 71483, USA

Introduction

By the middle of the twentieth century, a convergence of economic and social conditions reduced the 37 million hectare expanse of native longleaf pine (*Pinus palustris* Mill.) ecosystems in the southeastern United States by 98% (America's Longleaf 2009; Jose et al. 2006). The stately longleaf pines of these forests were replaced by plantations of loblolly (*Pinus taeda* L.) and slash pines (*Pinus elliottii* Engelm.), and the periodic occurrence of uniform, low intensity fire that once perpetuated the former longleaf pine forests was suppressed. Without frequent fire, dense understory vegetation prevented sunlight from filtering to the forest floor, which threatened the diversity of ground-layer plants and animals unique to longleaf pine ecosystems (Peet 2006).

Awareness of the negative trajectory facing several species such as the red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot 1809) that occur naturally in longleaf pine forests was evident by the mid-1990s. At this time, forestry research was actively addressing many of the early challenges of longleaf pine establishment success (Barnett 2002; Dumroese et al. 2013), and an era of fire suppression in the southeastern United States was replaced by prescribed fire recommendations to benefit wildlife habitat and reduce hazardous fuel loads (Stanturf et al. 2002). The Range-wide Conservation Plan for Longleaf Pine released in 2009 (America's Longleaf 2009) united advocates of longleaf pine restoration and strengthened their resolve by a collective mission to increase longleaf pine forest land from 1.4 to 3.2 million hectares by 2024. Government conservation directives have led to high traction of longleaf pine restoration on public land; but the momentum of longleaf pine restoration on private land is occurring at a slower pace (America's Longleaf 2018). Because the majority of land potentially available for longleaf pine restoration is owned by the private sector (America's Longleaf 2009), efforts to garner interest in longleaf pine restoration among private landowners are warranted.

Key to longleaf pine ecosystem function is the frequent occurrence of uniform, low intensity fire that depends on a well-developed grass-sedge component of the ground-layer (Peet 2006). While in the grass stage of development, stem elongation is absent and the terminal bud of longleaf pine seedlings is insulated from fire by a mass of bud scales and a dense tuft of fascicles (Brockway et al. 2006; Komarek 1974). Bud anatomy and insulation by adjacent foliage is a fire tolerance strategy among several *Pinus* species (Fernandes et al. 2008; Stephens and Finney 2002). Also similar to other fire-tolerant *Pinus* species, the stem vascular cambium of longleaf pine in all stages of development is protected from fire by thick bark (Brockway et al. 2006; Eberhardt 2013). This species is most vulnerable to fire after stem elongation initiates and seedling or sapling stature is below the flame height. During this period, there is a high risk of fire damage to terminal and lateral buds but this risk is tempered if buds are dormant and therefore protected by bud scales (Brockway et al. 2006). While one fire adaptation among some *Pinus s*pecies is emergence of epicormics shoots from the root collar and stem after terminal and lateral shoot consumption (Bradley et al. 2016; Fernandes et al. 2008; Climent et al. 2004), this occurrence is uncommon in longleaf pine after height growth is initiated (Farrar 1975).

Once longleaf pine achieves a stature above the flame height of prescribed fire, the risk of mortality diminishes. While the potential for prescribed fire to reduce stem growth remains, this impact is variable and seems to depend on tree vigor and acclimation to repeated fire as well as fire season, frequency, and intensity (Ames et al. 2015; Boyer 1987; Haywood 2002; Johansen and Wade 1987; Valor et al. 2015; Varner et al. 2009). When fire-induced growth loss occurs in longleaf pines that are acclimated to frequent fire, it is often correlated with the amount of foliage consumed by the fire which creates shortfalls in crown function and carbon allocation to the stem (Boyer 1987; Ford et al. 2010; Glitzenstein et al. 1995; Haywood 2009; Zahner 1989).

In addition to the direct effect fire may have on crown function, it may diminish long-term stemwood production by reducing survival and growth before saplings have grown above the flame height. This risk is heightened by an inherently high variation in grass stage duration among longleaf pine individuals. By the end of the third growing season after planting, for example, the frequency of grass stage seedlings may range between 10 and 70% (Haywood 2007, 2012). This phenomenon which is attributed to interaction between genotype and environment, contributes to an equally high variation in total height among juvenile longleaf pines (Nelson et al. 1994).

Among longleaf pine grass stage seedlings, saplings, and mature trees, production losses are minimized by the regrowth of scorched foliage so that pre-fire levels of carbon fixation and allocation can be achieved as soon as possible (Sword Sayer et al. 2006). The availability of carbon for foliage regrowth after crown scorch may differ by the season when fire is applied. This premise is supported by Weise et al. (1987) in their assessment of the stemwood growth of 4-year-old loblolly and slash pines that were manually defoliated at different times of the year. For both species, removal of more than 95% of the foliage in April reduced subsequent diameter growth rates for only 1 year; whereas, similar defoliations in October had a negative effect on diameter growth rates over multiple years.

Past research has shown that the magnitude of reserve starch in plant tissues may be an index of recovery potential after damage or environmental stress (Bond and Midgley 2001; Galiano et al. 2011). In their study of *Pinus canariensis* C. Sm. adaptation to fire, Climent et al. (2004) attributed post-fire sprouting of epicormics buds to high concentrations of starch in sapwood (Climent et al. 1998). A similar relationship may exist between post-fire foliage regrowth and reserve starch in longleaf pine. However, because reserve starch is seasonally dynamic among *Pinus* (Adams et al. 1986; Klein and Hoch 2015; Sword Sayer and Haywood 2006), its mobilization in response to a critical demand may depend on seasonal availability.

Longleaf pine restoration on private land will benefit from management activities that promote the stemwood growth of this species, and knowledge of how to maximize post-fire foliage regrowth among juvenile longleaf pines advances this effort. Our objectives are to quantify the foliage regrowth of sapling longleaf pines one growing season after crown scorch by spring or fall prescribed fires, and assess corresponding relationships between foliage regrowth and taproot and stem starch concentrations. We hypothesize that foliage is re-established by the end of the growing season after spring but not fall prescribed fire, and that after spring prescribed fire this process is correlated with taproot and stem starch dynamics. Our results will provide guidelines about season and intensity of prescribed fire to landowners who desire maximum rates of post-scorch foliage regrowth to support the juvenile stemwood production of longleaf pine.

Materials and methods

Study site

The study was located in central Louisiana on the Winn Ranger District of the Kisatchie National Forest, Winn Parish, Louisiana, USA (32°3′10.345′N, 92°51′20.279″W). Between

January of 2011 and 2014, this region had average annual summer and winter air temperatures of 26 °C and 10 °C, respectively, and annual precipitation averaged 143 cm with the majority of precipitation in December through May (National Oceanic and Atmospheric Administration 2017). The soil at the study site is Sacul fine sandy loam (fine, mixed, active, thermic Aquic Hapludults) with a slope of 0–20% (National Cooperative Soil Survey 2015). After a stand of loblolly pine was harvested in 2003, the area was site prepared by chopping and burning and planted with container-grown longleaf pine seedlings (International Forest Co.; Moultrie, GA) in November 2004 at a spacing of 1.8 by 2.7 m^2 for 327 trees ha^{-1}. The planted area was operationally prescribed burned in April 2008.

Experimental design and treatments

In fall 2010, the study was established within a 24-ha area of the longleaf pine plantation using a randomized complete block experimental design with three blocks. Blocks were contiguous and ranged between 5.6 and 8.8 ha. Blocking was based on topographic orientation and proximity to roads. Three plots per block were randomly assigned one of three treatments [no burn (CON), and prescribed fire applied in spring (SPB) or fall (FAB)]. Treatment plots were 1.4–4.3 ha in size and were partitioned by roads and plowed lanes that served as fire breaks. Also at this time, three 0.02-ha permanent, circular measurement subplots were randomly established within each treatment plot to collect fuel consumption and taproot and stem starch data. In January 2011, the 7-year-old longleaf pines in each subplot that had initiated height growth (i.e., ≥ 12 cm) were permanently tagged. This resulted in 21 and 45 permanently identified saplings per subplot and represented an average stocking of 1747 trees ha^{-1}. Both prescribed fire treatments were backfires with the spring fire on May 16, 2011, and the fall fire on October 23, 2012. Visual observations 1 month after prescribed fires indicated that 80% or more of sapling crowns were scorched. A moderate to exceptional drought occurred in Winn Parish between May 2010 and January 2012 (National Drought Mitigation Center 2017). The May 16, 2011, prescribed fire was conducted in a short window of time that was locally within prescription. Drought caused a 1-year delay of the fall prescribed fire planned for October 2011. No drought existed at the study site on October 23, 2012 when the fall prescribed fire was conducted.

Fuel consumption

Within each of the 0.02-ha subplots in each spring and fall prescribed burned treatment plot, three randomly located fuel-monitoring subplots, 0.22 m^2 in area, were harvested before and after prescribed fires. Vegetation was sampled as described by Haywood (2009). For the spring burn treatment, pre and post-burn samples were collected on May 12th and 16th, 2011, respectively. Similarly, pre and post-burn samples were collected for the fall burn treatment on September 18th and November 1st, 2012, respectively. All combustible material was oven-dried at 70 °C to equilibrium and weighed to the nearest 0.001 kg. Fuel consumed was calculated by the difference of subplot values before and after prescribed fires.

Total sapling height and aboveground biomass

Dormant season total height among permanently identified longleaf pine saplings in the measurement subplots was quantified before the start of the 2011 and 2013 growing seasons by a height pole to the nearest 1 cm as the distance between the stem at ground-line and the apex of the terminal bud before bud expansion. Because stands of juvenile longleaf pine are highly variable in stature (Nelson et al. 1994), we identified saplings for aboveground biomass analyses from among the range of sapling heights in each subplot. This insured that individuals chosen for aboveground biomass sampling were representative of the natural size distribution of sapling longleaf pines at our study site. Means and standard deviations of total sapling height by quartile in January 2011 (Fig. 1a) and by quintile in January 2013 (Fig. 1b) were calculated. The range of total height between two standard deviation below and above the means was determined by 2011 quartile and 2013 quintile resulting in four total height classes in 2011 and five total height classes in 2013.

On CON and SPB treatment plots excluding 0.02-ha measurement subplots, one sapling in each of the four 2011 total height classes was chosen for destructive harvest in September of 2011 and 2012. Similarly, on FAB treatment plots, one sapling in each of the five 2013 total height classes was randomly chosen for destructive harvest in September 2013. Also in September 2013, one sapling in each of the two largest 2013 total height classes on each CON and SPB treatment plot was randomly chosen for destructive harvest.

At peak leaf area, longleaf pine contains foliage produced in the previous and current years. The annual senescence of most previous year foliage occurs in fall, and current year foliage growth lags behind bud expansion that begins in March (Sheffield et al. 2003). In our study, saplings were felled before the peak period of previous year foliage senescence. The timing of destructive harvests in 2011 and 2013 allowed separation of un-scorched, previous year foliage retained after prescribed fire (old foliage) and current year foliage produced after prescribed fire (new foliage). Once felled at the ground-line, destructively harvested saplings were separated into foliage produced in the previous (old foliage) or current year (new foliage), branches, and stem. Tissues were oven-dried to equilibrium at

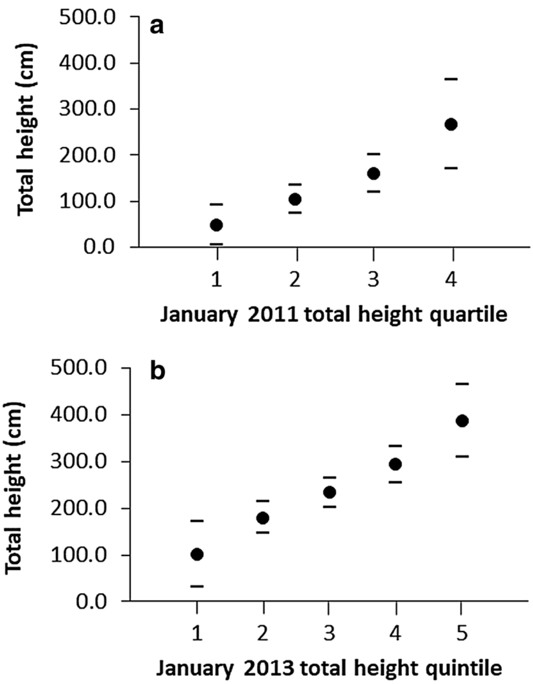

Fig. 1 Range among longleaf pine total height quartiles at the start of the 2011 growing season (**a**), and total height quintiles at the start of the 2013 growing season (**b**). Circle symbols represent quartile or quintile means and line symbols represent two standard deviations above and below the means

70 °C and weighed to the nearest 0.1 g. The sum of total foliage dry mass and percentages of total foliage dry mass occurring as old and new foliage were calculated.

Taproot and stem starch

Approximately monthly between February 2011 and October 2013, one longleaf pine sapling from each 0.02-ha subplot of selected treatment plots was felled at its root collar and the upper portion of the taproot was excavated by hand tools. Felled saplings appeared healthy and represented mean sapling size by visual comparison among saplings in the vicinity of the subplot. Segments of the taproot and stem adjacent to the root collar and approximately 13 cm in length were excised, put in a plastic bag, and placed in an ice chest containing ice. Taproot and stem samples were stored at −20 °C for up to 12 h after saplings were felled, and then transferred to paper bags, frozen at −20 °C, freeze-dried for 72 h, and finely ground to pass a 1-mm^2 sieve. Taproot and stem starch concentrations were determined by Dairyland Laboratories, Inc. (Arcadia, WI) using the acid hydrolysis method (Vidal et al. 2009).

Statistical analysis

Sapling biomass data and percentages of new and old foliage biomass quantified annually were evaluated by analyses of variance using a randomized complete block split-plot design with three blocks. The whole plot effect was prescribed fire treatment and the subplot effect was sapling size represented by four 2011 total height classes or five 2013 total height classes.

On CON and SPB treatment plots in September 2013, the harvest was limited to two saplings representing the two largest 2013 total height classes. To retain sapling size as a subplot effect in the 2013 analyses of variance, we supplemented the CON and SPB biomass data collected in 2013 with that collected in 2012. Specifically, total heights of the four CON and SPB saplings harvested by treatment plot in September 2012 were compared to the three smallest 2013 total height classes. Among the saplings harvested from each treatment plot in 2012, three were chosen as being representative of the three smallest 2013 total height classes. Biomass data from these three saplings was combined with biomass data from the two saplings harvested in September 2013.

We justify combining CON and SPB sapling biomass data collected in 2012 and 2013 for two reasons. Carbon dynamics among CON and SPB saplings in 2012 and 2013 were comparable because water, nutrition, and light availabilities at this young age were uniform between the 2 years (Jose et al. 2003). Second, the effect of May prescribed fire on sapling biomass variables was no longer apparent in September 2012 (Table 1). As a result, aboveground morphologies of longleaf pine saplings in September 2012 and 2013 were similar.

Starch concentrations among three subplot saplings were averaged by tissue, treatment plot, and sampling date. Taproot and stem starch means by sampling date were evaluated by analyses of variance using a randomized complete block design with three blocks. Between February 2011 and June 2012, treatments were CON or SPB. Between July 2012 and October 2013, treatments were CON or FAB.

Two series of ordinary least squares regressions were used to evaluate relationships between new and old foliage biomass among CON and SPB saplings in September 2011 and 2012, and among CON and FAB saplings in September 2013. The first series of regressions were conducted among all saplings with and without branch biomass. The second

Table 1 Probabilities of a greater *F*-value among aboveground biomass variables of sapling longleaf pines in response to total height class and season of prescribed fire

Source of variation	Aboveground biomass variable					
	df[a]	Old foliage	New foliage	Total foliage	Branches[b]	Stem[b]
2011						
Total height class (H)[c]	3	0.0011	0.0001	0.0001	0.0001	0.0001
Prescribed fire (F)[d]	1	0.0327	0.0360	0.8147	0.0476	0.2238
F × H	3	0.0144	0.0072	0.5123	0.0068	0.0546
2012						
H[c]	3	0.0005	0.0056	0.0005	0.0019	0.0001
F[d]	1	0.1419	0.9698	0.1831	0.1600	0.0951
F × H	3	0.2147	0.7694	0.3210	0.1374	0.2557
2013						
H[c]	4	0.0001	0.0001	0.0001	0.0001	0.0001
F[e]	2	0.0294	0.0509	0.3623	0.7882	0.4738
F × H	8	0.0072	0.0005	0.0011	0.0021	0.0076

[a]Degrees of freedom

[b]Data were transformed to natural logarithm values to establish normally distributed experimental errors

[c]In 2011 and 2012, H corresponded to four total height ranges defined as two standard deviations less than or greater than 2011 quartile total height means. In 2013, H corresponded to five total height ranges defined as two standard deviations less than or greater than 2013 quintile total height means

[d]Prescribed fire occurred on May 23, 2011

[e]Prescribed fire occurred on May 23, 2011, or October 16, 2012

series of regressions excluded saplings without branch biomass. Levene's test was used to evaluate the homogeneity of mean square errors (s^2) of pairs of regression lines (Snedecor and Cochran 1980). The slope and Y-intercept of pairs of lines with similar s^2 were further evaluated by the general linear test approach and *F* statistic (Neter and Wasserman 1974).

Before analyses of variance, data were transformed as needed to square root or natural logarithm values to establish normally distributed experimental errors. The *F* statistics in all analyses were considered significant at an α-level of 0.05 unless otherwise indicated. Means were compared by the Tukey–Kramer test and considered significantly different at an α-level of 0.05.

Results

The dry mass of fuel at the time of the spring prescribed fire on May 23, 2011 averaged 7383 kg ha^{-1}, and at the time of the fall prescribed fire on October 16, 2012 averaged 4916 kg ha^{-1} (Table 2). Fuel loss by fire was similar between the two prescribed fires and averaged 87% and 82% after spring and fall prescribed fires, respectively.

Prescribed fire treatment significantly affected percentages of total foliage biomass as old foliage biomass that was un-scorched and retained after prescribed fire and new foliage biomass produced in the growing season after prescribed fire in 2011 ($P = 0.0090$) or 2013 ($P = 0.0224$), but not in 2012 ($P = 0.0770$) (Fig. 2). Total height class and its interaction with prescribed fire treatment did not significantly affect the percentages of

Table 2 Mean fuel load and percent loss by prescribed fire in spring on May 23, 2011 or in fall on October 16, 2012. Values in parentheses are the standard deviation of the measurment plot mean

Season of prescribed fire	n	Mean fuel load (kg ha^{-1})[a]		Fuel loss by fire (%)
		Before prescribed fire	After prescribed fire	
Spring	9	7383 (846)	800 (221)	87.0 (4.0)
Fall	9	4916 (808)	641 (95)	82.0 (5.0)

[a]Values are an average of nine measurement plot means each determined by three subplot values

total foliage biomass distributed between old and new foliage in any year. In September 2011, total foliage biomass was composed of 47 percentage points more new foliage for SPB saplings compared to CON saplings. In September 2013, total foliage biomass was composed of 29 percentage points more new foliage for FAB saplings compared to CON saplings.

All aboveground biomass variables were significantly affected by sapling size in 2011, 2012, and 2013 (Table 1). The dry mass of all aboveground components increased as 2011 and 2013 total height classes increased (Data not shown). Old and new foliage biomass were affected by significant interaction between total height class and prescribed fire treatment in September 2011 and 2013. Among the largest total height class of saplings harvested in September 2011, old foliage biomass was greater and new foliage biomass was less for the CON saplings compared to the SPB saplings (Table 3). Among the second largest total height class of saplings harvested in September 2013, old foliage biomass was greater for the CON saplings compared to the SPB and FAB saplings, and among the largest total height class of saplings harvested in September 2013, new foliage biomass was lower for the CON saplings compared to the SPB and FAB saplings.

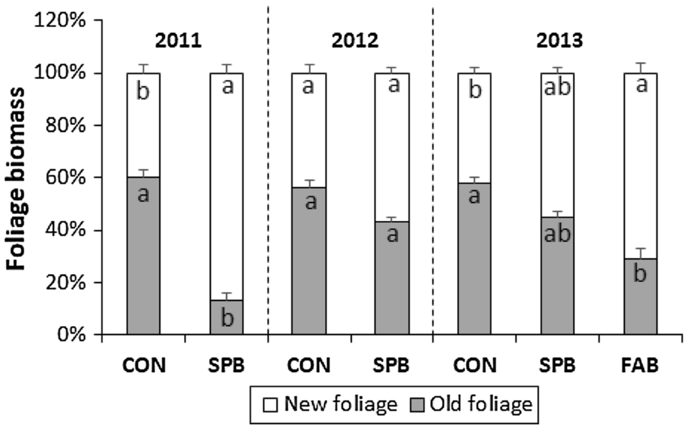

Fig. 2 Mean percentages of new and old foliage biomass among longleaf pine saplings (CON: Non-burned control, SPB: prescribed burned on May 23, 2011, FAB: prescribed burned on October 16, 2012) in September 2011, 2012, and 2013. Bars represent one standard error of the mean. Means by year and foliage class associated with a different lower case letter are significantly different by the Tukey–Kramer test at the 0.05 level

Table 3 Mean (standard error) of longleaf pine sapling old and new foliage biomass by prescribed fire treatment among four total height classes in September 2011 and among five total height classes in September 2013

Treatment	Total height class[a]	Year and foliage biomass variable			
		2011		2013	
		Old	New	Old	New
CON[c]	1	47 (18) b[b]	28 (4) b	143 (31) de	118 (6) ef
	2	126 (40) b	107 (36) b	279 (71) de	155 (44) def
	3	128 (26) b	72 (3) b	273 (42) cde	289 (14) cdef
	4	342 (75) a	181 (15) b	708 (25) a	340 (19) cde
	5	–	–	474 (125) abcd	372 (65) cd
SPB	1	11 (5) b	93 (13) b	73 (15) e	103 (6) f
	2	15 (7) b	122 (29) b	190 (45) de	184 (45) def
	3	56 (34) b	209 (16) b	182 (35) de	237 (23) def
	4	66 (47) b	502 (97) a	306 (110) bcde	335 (30) cde
	5	–	–	642 (59) ab	736 (90) a
FAB	1	–	–	74 (39) e	128 (20) ef
	2	–	–	26 (10) e	187 (84) def
	3	–	–	98 (45) e	227 (47) def
	4	–	–	185 (85) de	508 (65) bc
	5	–	–	562 (130) ab	712 (3) ab

[a]In 2011, total height class corresponded to four total height ranges defined as two standard deviations less than or greater than 2011 quartile total height means. In 2013, total height class corresponded to five total height ranges defined as two standard deviations less than or greater than 2013 quintile total height means

[b]Means within a year and foliage biomass variable followed by different lower case letter letters are significantly different by the Tukey–Kramer test at the 0.05 level

[c]CON: Non-burned control, SPB: prescribed burned on May 23, 2011, FAB: prescribed burned on October 16, 2012

Branch biomass in September 2011 and 2013 was affected by significant interaction between total height class and prescribed fire treatment (Table 1). Among the largest total height class of saplings harvested in September 2011, branch biomass was smaller for CON saplings (21 g) compared to SPB saplings (111 g). Similarly in September 2013, branch biomass of the largest total height class was smaller for CON saplings compared to SPB saplings (Fig. 3b). Total stem and foliage biomass in September 2013 were also affected by significant interaction between sapling total height class and prescribed fire treatment. In the largest total height class, stem biomass of CON saplings was smaller than that of FAB saplings (Fig. 3a). Among saplings of the third largest total height class, the foliage biomass of FAB saplings was smaller than that of CON saplings (Fig. 3c).

Linear regressions between new foliage biomass produced in the growing season after prescribed fire and old foliage biomass that was un-scorched and retained after prescribed fire were significant for CON saplings ($P = 0.0002$, $r^2 = 0.7696$) and SPB saplings ($P = 0.0248$, $r^2 = 0.4103$) in September 2011 (Fig. 4a), CON saplings ($P = 0.0361$, $r^2 = 0.3693$) and SPB saplings ($P = 0.0004$, $r^2 = 0.7264$) in September 2012 (Fig. 4b), and CON saplings ($P = 0.0013$, $r^2 = 0.5606$) and FAB saplings ($P = 0.0010$, $r^2 = 0.5778$) in September 2013 (Fig. 4c). Dissimilar mean square errors (s^2) of the relationship

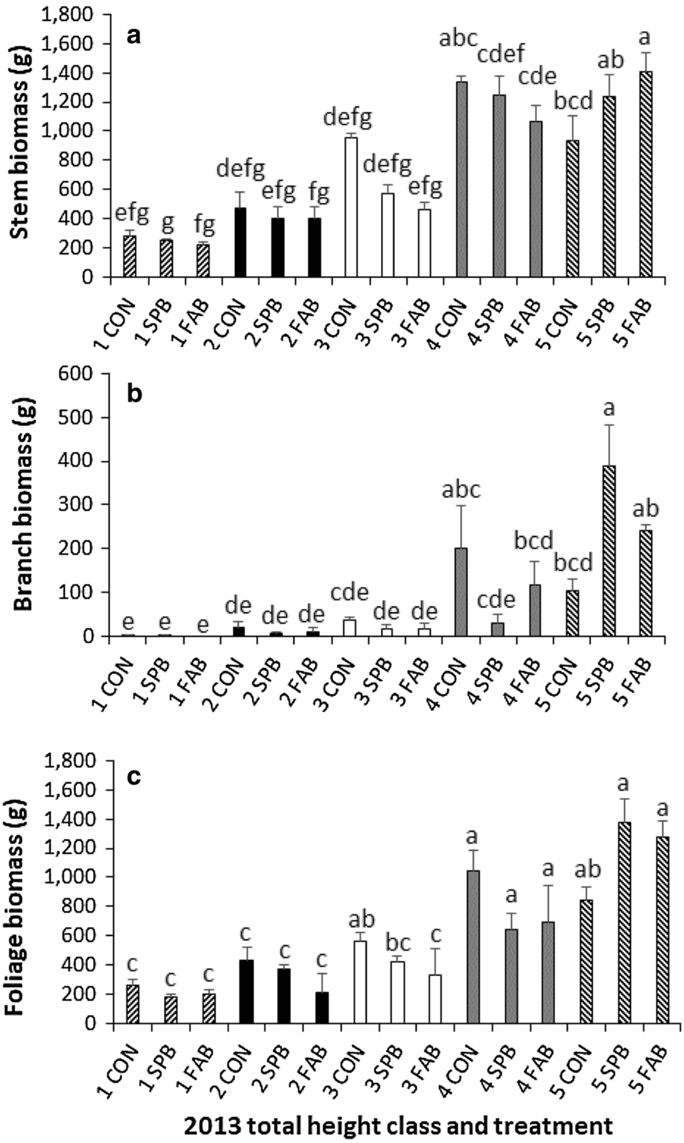

Fig. 3 Mean stem (**a**), branch (**b**), and foliage (**c**) biomass in September 2013 by 2013 total height class and prescribed fire treatment (CON: Non-burned control, SPB: prescribed burned on May 23, 2011, FAB: prescribed burned on October 16, 2012). Bars represent one standard error of the mean. Means associated with a different lower case letter are significantly different by the Tukey–Kramer test at the 0.05 level

between new and old foliage biomass for CON ($s^2=1078$ g) and SPB ($s^2=22{,}371$ g) saplings in September 2011, and CON ($s^2=6511$ g) and FAB ($s^2=26{,}742$ g) saplings in September 2013 prevented evaluation of regression parameters. Relationships between new and old foliage biomass for CON ($s^2=5506$ g) and SPB ($s^2=1360$ g) saplings in September 2012 were characterized by homogenous s^2. Slopes ($P=0.2598$) and

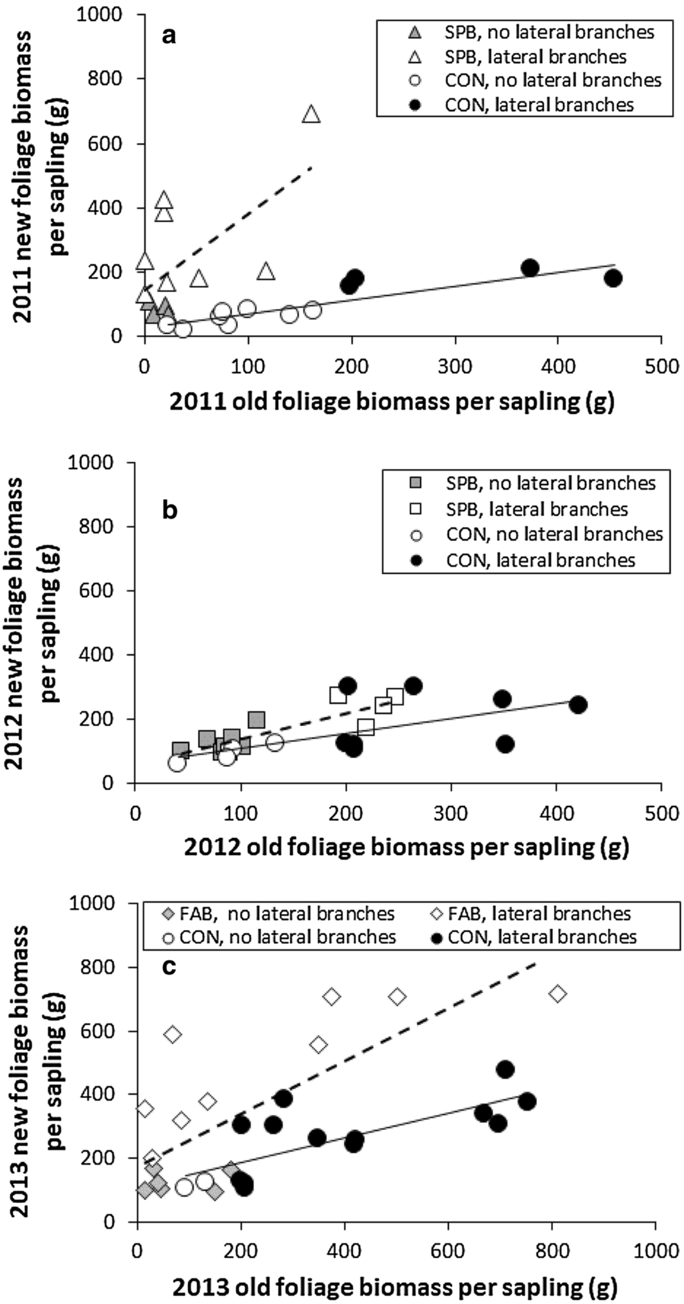

Fig. 4 Relationships between new foliage biomass produced in the growing season after prescribed fire and old foliage biomass that was un-scorched and retained after prescribed fire. New and old foliage biomass are shown among longleaf pine saplings with and without lateral branches in September 2011 (**a**), 2012 (**b**), and 2013 (**c**) and in response to prescribed fire treatment (CON: Non-burned control, SPB: prescribed burned on May 23, 2011, FAB: prescribed burned on October 16, 2012)

y-intercepts ($P = 0.9261$) of these September 2012 regressions were not significantly different.

Among harvested longleaf pine saplings, the percentage of those without lateral branches decreased as sapling total height class increased (Table 4). When saplings having no lateral branches were excluded from the September 2011 linear regressions between new and old foliage biomass per sapling, coefficients of determination for the CON and SPB saplings were not significant (CON: $n = 4$, $P = 0.4448$; SPB: $n = 8$, $P = 0.1274$). Exclusion of saplings without lateral branches from the September 2013 linear regressions resulted in homogenous s^2 (CON: 7275 g; FAB: 15,840 g), and coefficients of determination were significant for CON ($n = 13$, $P = 0.0113$, $r^2 = 0.4559$) and FAB saplings with lateral branches ($n = 9$, $P = 0.0103$, $r^2 = 0.6337$). A subsequent evaluation of regression parameters indicated that slopes of the CON and FAB relationships in September 2013 were not significantly different ($P = 0.2418$), but the y-intercept of the FAB relationship was significantly greater than that of the CON relationship ($P = 0.0142$).

Taproot and stem starch concentrations were significantly affected by prescribed fire treatment in the first and second months after application of prescribed fire in May 2011, respectively (taproot: $P = 0.0434$; stem: $P = 0.0709$). Taproot starch concentration was 35% lower among SPB saplings in late May 2011 (Fig. 5a), and stem starch concentration was 46% lower among SPB saplings in June 2011 compared to CON saplings (Fig. 5b). Significantly lower taproot and stem starch concentrations among prescribed burned saplings were also observed on five of seven dates between February and October 2013 after

Table 4 Percentages of harvested longleaf pine saplings in September 2011, 2012, and 2013 with and without lateral branch biomass

Total height class[a]	n[b]	With lateral branch biomass (%)	Without lateral branch biomass (%)
Age 8 years in 2011			
1	6	17	83
2	6	50	50
3	6	50	50
4	6	100	0
Age 9 years in 2012			
1	6	0	100
2	6	50	50
3	6	83	17
4	6	83	17
Age years 10 in 2013			
1	9	22	78
2	9	67	33
3	9	78	22
4	9	100	0
5	9	100	0

[a]In 2011, total height class corresponded to four total height ranges defined as two standard deviations less than or greater than 2011 quartile total height means. In 2013, total height class corresponded to five total height ranges defined as two standard deviations less than or greater than 2013 quintile total height means

[b]Number of saplings harvested

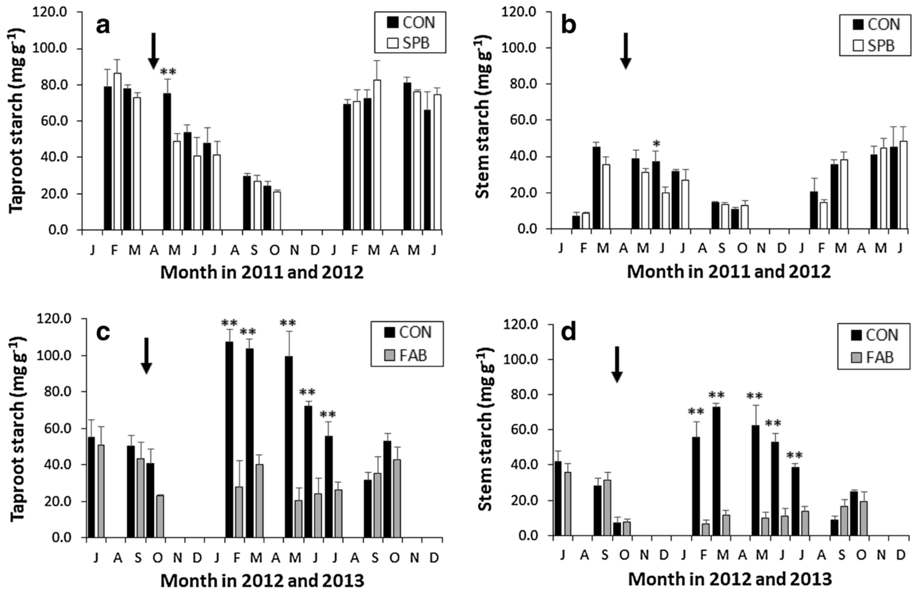

Fig. 5 Mean taproot and stem starch concentrations of sapling longleaf pine before and after prescribed fire in spring (**a** taproot, **b** stem) or fall (**c** taproot; **d** stem) (CON: Non-burned control, SPB: prescribed burned on May 23, 2011, FAB: prescribed burned on October 16, 2012). Error bars represent one standard error of the mean and bold arrows represent the time of prescribed fire application. Means by month associated with a single or double asterisk are significantly different by the Tukey–Kramer test at the 0.10 or 0.05 level, respectively

prescribed fire in October 2012 (Fig. 5c–d). Between February and July after October prescribed fire, average starch concentrations were reduced by 67% and 80% in taproot and stem tissues, respectively.

Discussion

Amounts of available fuel in our study represent typical conditions in young longleaf pine stands across the western range of this species. Similar values were reported by Haywood (2010) for longleaf pine shelterwood, clearcut, and small pole stands in central Louisiana, USA, before application of prescribed fires on three occasions. In another study by Haywood (2009), fuel loads before four biennial prescribed fires in March, May, or July 1999–2005 averaged 5565 kg ha^{-1}, 6852 kg ha^{-1}, and 5665 kg ha^{-1}, respectively.

We anticipated the observed spatial variability in fuel amounts in our study because vegetation in young stands of planted longleaf pine is naturally patchy (Haywood 2012). One reason for fuel patchiness is poor advancement of grasses and forbs under low light conditions caused by woody shrubs and small trees (Gonzales-Benecke et al. 2015). Also, while litterfall serves as a means of advancing fire through areas of low fuel (Mitchell et al. 2009), it is not uniformly distributed in stands of young longleaf pine (Brockway and Outcalt 1998). Despite the high variability of fuel levels across our study site, percentages of fuel consumed by prescribed fire in May 2011 and October 2012 were similar and averaged 85%. Furthermore, variation in fuel loss by prescribed fire in May 2011 and October 2012 was relatively low. These observations indicate fuel and weather conditions in May 2011 and October 2012 compensated for vegetation patchiness to produce relatively uniform prescribed fires.

Four months after May prescribed fire under fuel conditions typical of young longleaf pine stands in the bluestem-pine woodlands, we found equivalent amounts of total foliage biomass between CON and SPB saplings across all total height classes. Significant interaction between total height class and prescribed fire treatment in September 2013 indicated a comparable response was observed among most, but not all total height classes of CON and FAB saplings 11 months after prescribed fire application in October. Sword Sayer et al. (2006) also observed this response in sapling longleaf pines 4 months after May prescribed fire and attributed post-fire leaf area regrowth to accelerated growth of second flush foliage. After significant crown scorch, the timely recovery of normal foliage mass is essential to sustain overall tree vigor. Conversely, fire damage to the stem vascular cambium may slow foliage growth, delay restoration of longleaf pine's normal carbon allocation pattern, and cause a stemwood growth loss in the year of fire application (Ford et al. 2010).

Across all total height classes in 2011 and 2013, we observed an acceleration of relative foliage growth during the growing season after prescribed fire with total foliage biomass composed of 87% and 71% new foliage produced in the growing season after prescribed fires that occurred 4 and 11 months earlier in May and October, respectively. In contrast, an average of only 48% of total foliage biomass was new foliage in the absence of prescribed fire. These observations demonstrate the potential of new foliage to counteract foliage loss by crown scorch in young stands of longleaf pine.

Actual values of new and old foliage biomass by total height class provide additional insight about the potential for foliage recovery after crown scorch. Interactions between prescribed fire treatment and total height class revealed that greater absolute amounts of new foliage biomass occurred exclusively in the largest total height classes. Compared to the largest total height class of CON saplings, the largest total height class of SPB and FAB saplings had more new foliage biomass one growing season after prescribed fire application. A similar but nonsignificant trend was observed among most of the smaller total height classes. One factor limiting our ability to detect significant differences in new foliage biomass among smaller total height classes was variability in sapling size. For example, coefficients of variation in total height for the smallest total height class in 2011 and 2013 were 44% and 34%; whereas, those averaged across all other total height classes in 2011 and 2013 were 15% and 9%, respectively.

Another observation in our study supports the premise that after prescribed fire, the presence of live lateral branches expedited foliage recovery. Among the total height classes in 2011 and 2013, detection of significant prescribed fire effects on new foliage biomass only occurred when all saplings in a total height class had branch biomass. Linear relationships between new and old foliage biomass among FAB saplings in September 2013 also demonstrated how the presence of lateral branches fostered a stronger relationship between foliage that survived prescribed fire and foliage that emerged in the next growing season. By excluding six saplings without branch biomass from the FAB regression, we explained a larger amount of the variation in new foliage biomass among the FAB saplings in September 2013 (saplings with and without branch biomass: $n=15$, $r^2=0.5778$; saplings with branch biomass: $n=9$, $r^2=0.6337$). Once saplings without branch biomass were excluded from the 2013 CON and FAB linear regressions, we found that the FAB s^2 decreased 41% and homogeneity of s^2 was achieved between the FAB and CON regressions of new and old foliage biomass.

The relationship between new and old foliage biomass by sapling was more variable among SPB saplings in September 2011 compared to FAB saplings in September 2013 (SPB: $r^2=0.4103$; FAB: $r^2=0.5778$). We attribute this difference to another factor that may have affected new foliage growth in the early part of the growing season after prescribed fire in May but not October. Mobilization of starch stored in parenchyma cells throughout organs of *Pinus* provides a portion of the carbohydrate needed for sustained vigor (Blanche et al. 1992; Chung and Barnes 1980). Past research has shown that *Pinus* starch storage reaches a maximum in early spring and then declines to a minimum level by late summer (Adams et al. 1986; Gholz and Cropper 1991; Ludovici et al. 2002; Sword Sayer and Haywood 2006). A similar modal pattern of starch concentration was observed in longleaf pine taproot and stem tissues of the CON saplings during 2011, 2012, and 2013. Our May prescribed fire was applied when starch storage was relatively high. Subsequently, during a 1 month period after burning, natural mobilization of starch occurred more rapidly in SPB saplings compared to CON saplings. We propose that foliage re-growth after prescribed fire in May was achieved by both the mobilization of starch reserves stored in the taproot and stem and photosynthesis in old foliage biomass.

In longleaf pine, prolonged drought has the potential to decrease peak starch levels that accumulate in the dormant season and are mobilized in spring and summer to support growth. This response is consistent with some but not all *Pinus* species (Adams et al. 2013; Klein et al. 2014; Piper et al. 2017). Sword Sayer and Haywood (2006) found that the peak starch concentration of longleaf pine woody roots was 30% lower than normal across a 3-year span of consecutive drought and a normal level of peak starch accumulation lagged by 1 year after drought lifted. In the present study, we observed similar responses in taproot and stem starch. Compared to values in 2013—a year of normal precipitation, peak levels of CON sapling taproot and stem starch were 26% and 38% lower, respectively, in 2011—a year of prolonged extreme and exceptional drought. Furthermore, a 1-year, post-drought lag in normal levels of peak starch concentration were observed with 30% and 52% lower starch concentrations in taproot and stem tissues, respectively, in 2012 compared to 2013. In assessments of the nonstructural carbohydrate dynamics of mature *Pinus sylvestris* L. under drought, it has been suggested that whole-tree leaf area rather than gas exchange rates control carbohydrate dynamics (Galiano et al. 2011; Schönbeck et al. 2018). In our study, the time required to establish a normal amount of whole-crown leaf area after extreme drought may have led to the 1-year, post-drought lag in reserve starch levels among the CON saplings. While conclusions about how drought-starch interactions affect post-scorch foliage regrowth cannot be made by our study, we propose that a more robust mobilization of taproot and stem starch may have occurred in the spring of 2011 and 2012 if saplings had not been under extreme drought conditions in 2010 and 2011.

The regrowth of longleaf pine foliage biomass within one growing season of May prescribed fire supports our initial hypothesis, and validates similar observations in sapling longleaf pine (Sword Sayer et al. 2006). Contrary to our initial hypothesis, however, we observed that foliage mass per sapling was also restored by September 2013 after prescribed fire application in October 2012. It is unlikely that mobilized starch contributed significantly to the growth of new foliage biomass because longleaf pine starch reserves are nearly depleted in late summer and fall (Sword Sayer and Haywood 2006). In large part, we attribute the recovery of foliage biomass during the 11-month period after prescribed fire in October to photosynthate produced by un-scorched foliage biomass.

Among the southern pines, dormant season photosynthesis appears to contribute substantially to whole tree carbon fixation (Henderson and Grissino-Mayer 2009; Tang et al. 2003). It is not surprising, therefore, that immediately after prescribed fire in October, un-scorched foliage was a strong support to foliage recovery. At the same time, we note that this positive response to October prescribed fire coincided with disruption of normal taproot and stem starch accumulation over multiple months during the 2013 growing season. This indicates a temporary disruption of normal carbon dynamics may be the cost of foliage biomass recovery after heavy crown scorch late in the growing season.

A linkage exists between stored starch and intrinsic pools of non-structural carbon in *Pinus* (Klein and Hoch 2015). For example, Blanche et al. (1992) observed a negative correlation between the oleoresin yield and starch concentration of mature loblolly pine stems. At present, the consequence of low starch storage on the production of oleoresin and other defense chemicals in our study is unknown. Further research is needed to evaluate how a temporary reduction in starch storage affects both constitutive and inducible defense mechanisms among longleaf pine and other *Pinus* species potentially managed by late growing season prescribed fire.

We observed an effect of prescribed fire on organ biomass accumulation four times during this study, but we attribute this to natural variation in the grass stage duration of longleaf pine seedlings and the subsequent high degree of variation in longleaf pine sapling stature and morphology (Haywood 2007; Nelson et al. 1994). For example, the effect of fall prescribed fire on the sapling foliage biomass of the third largest total height class harvested in September 2013 was influenced by the presence of lateral branches. This is because one of the three harvested CON saplings had no lateral branch biomass. As a result, accumulation of foliage biomass was not only influenced by prescribed fire treatment, but also by the potential to grow foliage among lateral branches. A similar effect of variable sapling stature on stem biomass was observed in the largest total height class harvested in September 2013. At this time, one harvested CON sapling had a total height less than the midpoint of the 2012 total height class range of 3.1–4.6 m, while all other harvested CON and FAB saplings had total heights above this value. Finally, in response to spring prescribed fire in 2011, branch biomass values among the largest total height classes in 2011 and 2013 were larger for SPB saplings compared to CON saplings. However, considerable variation in the size of CON and SPB saplings harvested in September 2011, and absence of this effect in September 2012, again suggest that prescribed fire effects on branch biomass were due to high variability in sapling stature.

Summary and conclusions

Our findings inform the prescribed fire practitioner about mechanisms of sustained vigor in young longleaf pine despite severe crown scorch in spring or fall. This information also provides an awareness about physiological adaptations to fire that may sustain *Pinus* vigor where prescribed fire is or may become a valuable fuel reduction tool (Fernandes 2015). Because tree vigor is highly dependent on whole-crown carbon fixation, timely re-growth of scorched foliage biomass minimizes the impact of fire on carbon endpoints such as stemwood growth and the production of defense chemicals. In our study, the pathway to restoring foliage biomass was dependent on un-scorched foliage and lateral branches in the growing season after fire. The positive role of un-scorched foliage on foliage recovery was observed after early and late growing season prescribed fire, and absence of lateral branches created an impasse to this mechanism. A second means of foliage recovery after early growing season prescribed fire was observed by starch mobilization when fire was applied at the time of peak starch storage.

Longleaf pine seedlings tolerate fire during the grass stage of development if they have grown thick bark and an insulated bud (Brockway et al. 2006; Longleaf Alliance 2009). Because foliage scorch among grass stage seedlings is high, there will be little un-scorched foliage to support foliage biomass recovery after prescribed fire. As such, the replacement of scorched foliage among grass stage longleaf pine may be expedited if fire is applied in spring when starch reserves are high.

Once height growth is initiated, prescribed fire can be applied when terminal buds are dormant and insulated from heat damage, or when actively elongating terminal buds are above the zone of heat damage (Longleaf Alliance 2009). These stipulations safeguard the landowner from high sapling mortality under normal stand conditions. Of equal importance in some situations is early longleaf pine growth. If prescribed fire is applied in young stands with few lateral branches, then the timely recovery of foliage biomass may be delayed because new foliage growth is restricted to the terminal shoot. The same outcome is possible if prescribed fire causes a large portion of lateral branches to be pruned from the sapling stem. These scenarios warrant the attention of prescribed fire practitioners with a duel interest in restoring longleaf pine ecosystems and maximizing early longleaf pine stemwood growth.

Acknowledgements The authors gratefully acknowledge the Kisatchie National Forest, Winn Ranger District's Fire Management Officer, Larry Kile, and Assistant Fire Management Officer, Dustin Dill, for conducting the prescribed fire treatments in this study.

References

Adams MB, Allen HL, Davey CB (1986) Accumulation of starch in roots and foliage of loblolly pine (*Pinus taeda* L.): effects of season, site and fertilization. Tree Physiol 2:35–46

Adams HD, Germino MJ, Breshears DD, Barron-Gafford GA, Guardiola-Claramonte M, Zou CB, Huxman TE (2013) Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. New Phytol 197:1142–1151

America's Longleaf (2009) Range-wide conservation plan for longleaf pine. America's Longleaf, 52 p

America's Longleaf (2018) 2017 Range-wide accomplishment report. America's Longleaf, 14 p

Ames GM, Vineyard DL, Anderson SM, Wright JP (2015) Annual growth on longleaf (*Pinus palustris*) and pond pine (*P. serotina*) in the Sandhills of North Carolina is driven by interactions between fire and climate. For Ecol Manag 340:1–8

Barnett JP (2002) Longleaf pine: why plant it? Why use containers? In: Barnett JP, Dumroese RK, Moorhead DJ (eds) Proceedings of workshops on growing longleaf pine in containers—1999 and 2001. Gen Tech Rep SRS-56. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 5–7

Blanche CA, Lorio PL Jr, Sommers RA, Hodges JD, Nebeker TE (1992) Seasonal cambial growth and development of loblolly pine: xylem formation, inner bark chemistry, resin ducts, and resin flow. For Ecol Manag 49:151–165

Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51

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

Bradley JC, Will RE, Stewart JF, Nelson CD, Guldin JM (2016) Post-fire resprouting of shortleaf pine is facilitated by a morphological trait but fire eliminates shortleaf x loblolly pine hybrid seedlings. For Ecol Manag 379:146–152

Brockway DG, Outcalt KW (1998) Gap-phase regeneration in longleaf pine wiregrass ecosystems. For Ecol Manag 106:125–139

Brockway DG, Outcalt KW, Boyer WD (2006) Longleaf pine regeneration ecology and methods. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem, ecology, silviculture, and restoration. Springer, New York, pp 95–133

Chung H-H, Barnes RL (1980) Photosynthate allocation in *Pinus taeda*. III. Photosynthate economy: its production, consumption and balance in shoots during the growing season. Can J For Res 10:348–356

Climent J, Gil L, Pardos A (1998) Xylem anatomical traits related to resinous heartwood formation in *Pinus canariensis* Sm. Trees 12:139–145

Climent J, Tapias R, Pardos JA, Gil L (2004) Fire adaptations in the Canary Islands pine (*Pinus canariensis*). Plant Ecol 171:185–190

Dumroese RK, Barnett JP, Jackson DP, Hainds MJ (2013) 2008 interim guidelines for growing longleaf pine seedlings in container nurseries. In: Guldin JM (ed) Proceedings of the 15th Biennial southern silvicultural research conference e-Gen Tech Rep SRS-GTR-175. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 141–148

Eberhardt TL (2013) Longleaf pine inner bark and outer bark thicknesses: measurement and relevance. South J Appl For 37:177–180

Farrar RM Jr (1975) Sprouting ability of longleaf pine. For Sci 21:189–190

Fernandes PM (2015) Empirical support for the use of prescribed burning as a fuel treatment. Curr For Rep 1:118–127

Fernandes PM, Vega JA, Jiménez W, Rigolot E (2008) Fire resistance of European pines. For Ecol Manag 256:246–255

Ford CR, Minor ES, Fox GA (2010) Long-term effects of fire and fire-return interval on population structure and growth of longleaf pine (*Pinus palustris*). Can J For Res 40:1410–1420

Galiano L, Martínez-Vilata J, Lloret F (2011) Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. New Phytol 190:750–759

Gholz HL, Cropper WP Jr (1991) Carbohydrate dynamics in mature *Pinus elliottii* var. *elliottii* trees. Can J For Res 21:1742–1747

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

Gonzales-Benecke CA, Samuelson LJ, Stokes TA, Cropper WP Jr, Martin TA, Johnsen KH (2015) Understory plant biomass dynamics of prescribed burned *Pinus palustris* stands. For Ecol Manag 344:84–94

Haywood JD (2002) Delayed prescribed burning in a seedling and sapling plantation in Louisiana. In: Outcalt KW (ed) Proceedings of the 11th biennial southern silvicultural research conference Gen Tech Rep SRS-48. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 103–108

Haywood JD (2007) Influence of herbicides and felling, fertilization, and prescribed fire on longleaf pine establishment and growth through six growing seasons. New For 33:257–279

Haywood JD (2009) Eight years of seasonal burning and herbicidal brush control influence sapling longleaf pine growth, understory vegetation, and the outcome of an ensuing wildfire. For Ecol Manag 258:295–305

Haywood JD (2010) Effects of prescribed fire on vegetation and fuel loads in longleaf pine stands in the bluestem range. In: Stanturf JA (ed) Proceedings of the 14th biennial southern silvicultural research conference Gen Tech Rep SRS-121. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 213–217

Haywood JD (2012) Frequency and season of prescribed fire affect understory plant communities in longleaf pine stands. In: Butnor JR (ed) Proceedings of the 16th biennial southern silvicultural research conference Gen Tech Rep SRS-156. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 137–143

Henderson JP, Grissino-Mayer HD (2009) Climate-tree growth relationships of longleaf pine (*Pinus palustris* Mill.) in the Southeastern Coastal Plain, USA. Dendrochronologia 27:31–43

Johansen RW, Wade DD (1987) Effect of crown scorch on survival and diameter growth of slash pines. South J Appl For 11:180–184

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

Jose S, Jokela EJ, Miller DL (2006) The longleaf pine ecosystem: an overview. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem, ecology, silviculture, and restoration. Springer, New York, pp 3–8

Klein T, Hoch G (2015) Tree carbon allocation dynamics determined using a carbon mass balance approach. New Phytol 205:147–159

Klein T, Hock G, Yakir D, Körner C (2014) Drought stress, growth and nonstructural carbohydrate dynamics of pine trees in a semi-arid forest. Tree Physiol 34:981–992

Komarek EV (1974) Effects of fire on temperate forests and related ecosystems: Southeastern United States. In: Kozlowski TT, Ahlgren CE (eds) Fire and ecosystems. Academic Press Inc., New York, pp 251–278

Longleaf Alliance (2009) The pine that fire built, burning young longleaf. Longleaf alliance note no 9. The Longleaf Alliance, Andalusia, p 9
Ludovici KH, Allen HL, Albaugh TJ, Dougherty PM (2002) The influence of nutrient and water availability on carbohydrate storage in loblolly pine. For Ecol Manag 159:261–270
Mitchell RJ, Hiers JK, O'Brien J, Starr G (2009) Ecological forestry in the southeast: understanding the ecology of fuels. J For 107:391–397
National Cooperative Soil Survey (2015) Official series description- Sacul Series. U.S. Department of Agriculture, Natural Resource Conservation Service. https://soilseries.sc.egov.usda.gov/OSD_Docs/S/SACUL.html. Accessed 26 Oct 2017
National Drought Mitigation Center (2017) Statistics by threshold. University of Nebraska, Lincoln, NE. http://droughtmonitor.unl.edu/Data/DataDownload/StatisticsbyThreshold.aspx. Accessed 26 Oct 2017
National Oceanic and Atmospheric Administration (2017) National Centers for Environmental Information Climate Data Online. https://www.ncdc.noaa.gov/cdo-web/. Accessed 26 Oct 2017
Nelson CD, Kubisiak TL, Stine M, Nance WL (1994) A genetic linkage map of longleaf pine (*Pinus palustris* Mill.) based on random amplified polymorphic DNAs. J Hered 85:433–439
Neter J, Wasserman W (1974) Applied linear statistical models regression, analyses of variance, and experimental design. Richard D Irwin Inc, Homewood, p 842
Peet RK (2006) Ecological classification of longleaf pine woodlands. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem, ecology, silviculture, and restoration. Springer, New York, pp 51–93
Piper FI, Fajardo A, Hoch G (2017) Single-provenance mature conifers show higher non-structural carbohydrate storage and reduced growth in a drier location. Tree Physiol 37:1001–1010
Schönbeck L, Gessler A, Hoch G, McDowell NG, Ringling A, Schaub M (2018) Homeostatic levels of nonstructural carbohydrates after 13 yr of drought and irrigation in *Pinus sylvestris*. New Phytol Early View. https://doi.org/10.1111/nph.15224
Sheffield MCP, Gagnon JL, Jack SB, McConville DJ (2003) Phenological patterns of mature longleaf pine (*Pinus palustris* Miller) under two different soil moisture regimes. For Ecol Manag 179:157–167
Snedecor GW, Cochran WG (1980) Statistical methods, 7th edn. The Iowa State University Press, Ames, p 507
Stanturf JA, Wade DD, Waldrop TA, Kennard DK, Achtemeier GL (2002) Background paper: fire in southern forest landscapes. In: Wear DN, Greis JG (eds) Southern forest resource assessment Gen Tech Rep SRS-53. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, pp 607–630
Stephens SL, Finney MA (2002) Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For Ecol Manag 162:261–271
Sword Sayer MA, Haywood JD (2006) Fie root production and carbohydrate concentrations of mature longleaf pine (*Pinus palustris* P. Mill.) as affected by season of prescribed fire and drought. Trees 20:165–175
Sword Sayer MA, Goelz JCG, Haywood JD (2006) Effects of prescribed fire on production of foliage by sapling longleaf pine. In: Connor KF (ed) Proceedings of the 13th biennial southern silvicultural research conference Gen Tech Rep SRS-92. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 478–485
Tang Z, Chambers JL, Sword Sayer MA, Barnett JP (2003) Seasonal photosynthesis and water relations of juvenile loblolly pine relative to stand density and canopy position. Trees 17:424–430
Valor T, González-Olabarria JR, Piqué M (2015) Assessing the impact of prescribed burning on the growth of European pines. For Ecol Manag 343:101–109
Varner JM, Putz FE, O'Brien JJ, Mitchell RJ, Gordon DR (2009) Post-fire tree stress and growth following smoldering duff fires. For Ecol Manag 258:2467–2474
Vidal BC Jr, Rausch KD, Tumbleson ME, Singh V (2009) Determining corn germ and pericarp residual starch by acid hydrolysis. Cereal Chem 86:133–135
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. US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station Asheville, NC, 4 p
Zahner R (1989) Tree-ring series related to stand and environmental factors in south Alabama longleaf pine stands. In: Miller JH (ed) Proceedings of the 5th biennial southern silvicultural research conference Gen Tech Rep SO-50. US Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA, pp 193–197