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Fire effects on a fire-adapted species: response of grass stage longleaf pine seedlings to experimental burning

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Abstract

Background: Longleaf pine (*Pinus palustris* Mill.) seedlings have a morphological "grass stage" that is considered to be an adaptation to frequent surface fire regimes. However, fire can kill longleaf pine seedlings and thus may play an important role in longleaf pine regeneration dynamics. We used a prescribed burn simulation tool designed to treat individual grass stage longleaf pine seedlings with controlled delivery of fire treatments and then measured survival and growth responses through two growing seasons. Naturally regenerated grass stage longleaf pine seedlings were randomly selected from three size classes and each assigned one of four treatments (Control, no treatment; Clip, mechanical needle removal; LB, a low-temperature burn treatment; or HB, a high-temperature burn treatment) in both the dormant season (January) and the growing season (May).

Results: Seedlings greater than 15 mm root collar diameter had greater than 0.5 probability of survival after the first growing season in the HB treatment, regardless of the season of treatment application, and seedlings across all sizes had greater than 0.6 probability of survival in the LB treatment after the first growing season. The growing season treatment application resulted in additional mortality during the second growing season, across all seedling size classes, which was not observed in the dormant season application. Burning reduced root collar growth through two growing seasons, likely due to needle mortality and the subsequent prioritization of growth to needle production rather than to root or stem growth.

Conclusions: Our results suggest that the interplay between seedling size and fire intensity likely contributes to the success of longleaf pine natural regeneration and that seedling size should be considered when scheduling the first burn following planting of longleaf pine seedlings.

Keywords: Fire adaptation, Longleaf pine, *Pinus palustris*, Prescribed burn simulation tool, Prescribed fire, Southeastern USA, Thermocouple

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Resumen

Antecedentes: Las plántulas del pino de hoja larga (*Pinus palustris* Mill.) tienen un estadio morfológico del tipo "pasto" que es considerado como una adaptación a un régimen frecuente de fuegos de superficie. Sin embargo, el fuego puede matar plántulas de pino de hoja larga, y por lo tanto jugar un rol importante en la dinámica de su regeneración. Usamos una herramienta de simulación de quema prescripta para tratar plántulas individuales de este pino en estado de pasto, mediante la aplicación controlada de un tratamiento de quema, y dos temporadas post-tratamiento medimos las respuestas a la supervivencia y el crecimiento. Tres clases de edad de regeneración natural de plántulas de pino de hoja larga en estado de pasto fueron seleccionadas al azar y expuestas cada una a cuatro tratamientos (Control, o no tratado; Cortado, mediante el cual las hojas se removían mecánicamente; Quema a baja temperatura o LB; y Quema a alta temperatura o HB), tanto durante la estación de dormición (enero) como en la de crecimiento (mayo).

Resultados: Las plántulas mayores a 15 mm de diámetro en la base de la altura del cuello tienen una probabilidad de más del 0,5 de sobrevivir después la primera estación de crecimiento en el tratamiento HB, independientemente de la estación de aplicación del tratamiento, y las plántulas de todos los tamaños tienen un 0,6 o más de probabilidad de sobrevivir en el tratamiento LB después de la primera estación de crecimiento. La estación de aplicación de los tratamientos resultó en una mortalidad adicional durante la estación de crecimiento (mayo) para todas las clases de edad de las plántulas, lo que no fue observado cuando la aplicación fue realizada en la estación de dormición (enero). La quema redujo el crecimiento a la altura del cuello durante las dos estaciones de crecimiento, debido probablemente a la mortalidad de acículas y la subsiguiente priorización del crecimiento de las acículas por sobre la raíz o el tallo.

Conclusiones: Nuestros resultados sugieren que la interrelación entre el tamaño de las plántulas y la intensidad del fuego probablemente contribuya al éxito en la regeneración natural del pino de hoja larga, y que el tamaño de las plántulas debe ser considerado cuando se planea la primera quema posterior a la plantación de plántulas de pino de hoja larga.

Background

During the past few decades, forest managers have increasingly attempted to incorporate patterns of natural disturbance regimes into forest management practice (Attiwill 1994, Franklin *et al.* 2002, Palik *et al.* 2002), with particular interest in understanding the effects of fire regimes on forested ecosystems in both ecological and management contexts. In North America, longleaf pine (*Pinus palustris* Mill.) ecosystems of the southeastern United States exemplify the tight coupling of ecosystem function and fire regime (Van Lear *et al.* 2005, Mitchell *et al.* 2006). Much of the southeastern Coastal Plain region was historically dominated by longleaf pine ecosystems that were maintained with fire return intervals generally < 5 yr (Frost 2006, Huffman 2006, Stambaugh *et al.* 2011). In these ecosystems, frequent fire generates a positive feedback among vegetation, fuels, and fire (O'Brien *et al.* 2008, Mitchell *et al.* 2009). The combination of long, resinous pine needles shed from the canopy trees and herbaceous ground-layer vegetation creates a fuelbed that ignites easily and burns quickly along the forest floor. Consumption of the forest floor creates space for regenerating individuals of the characteristically species-rich ground flora (Hiers *et al.* 2007, Veldman *et al.* 2014) and germination sites for longleaf pine seed (Croker and Boyer 1975, Brockway *et al.* 2006). Longleaf pines are shade intolerant and poor competitors compared to faster-growing tree species (Boyer 1990). Frequent fires inhibit the development of other woody vegetation (Glitzenstein *et al.* 1995, Brockway and Lewis 1997, Addington *et al.* 2015) that would displace longleaf pine regeneration and the herbaceous ground flora. Without fire, longleaf pine ecosystems can quickly transition to alternative states and may be difficult to re-establish without intensive treatments (Martin and Kirkman 2009).

Longleaf pines have a seedling morphology described as a "grass stage," which is also expressed by other pine species that occur within frequent-fire ecosystems across the world (*e.g., Pinus merkusii* Jungh. & Vriese ex Vriese, *P. montezumae* Lamb, *P. michoacana* Lindl.; Koskela 2000, Keeley 2012). Following germination, grass stage seedlings allocate growth to root and needle production rather to than stem elongation (Brockway *et al.* 2006, O'Brien *et al.* 2008). During this stage, the terminal bud is located near the ground surface and is surrounded by a dense tuft of needles that may be consumed by fire but protects the terminal bud from damage (Wahlenberg 1946, O'Brien *et al.* 2008, Keeley 2012). Although generally considered to be resistant to fire, grass stage longleaf pine seedlings have also been documented to sprout following top-kill, providing an additional mechanism for survival with frequent fire (Farrar 1975). For longleaf pine, seedlings emerge from the grass stage and begin stem elongation when the root collar diameter is approximately 25 mm (Boyer 1990, Ramsey *et al.* 2003, Knapp *et al.* 2006), and the thick bark of saplings provides protection from fire during tree recruitment (Schafer *et al.* 2015).

The grass stage is widely accepted as an adaptation to frequent fire (Brockway *et al.* 2006, Keeley 2012), yet several studies have reported high mortality rates of small grass stage seedlings following fire (Croker and Boyer 1975, Grace and Platt 1995a, Moule 2013). Brockway *et al.* (2006) suggested a threshold root collar diameter of 13 mm for increasing the probability of survival from surface fire, although seedling mortality has also been shown to increase with fire intensity (Jack *et al.* 2010). Observations of seedling aggregation within canopy openings in naturally regenerated longleaf pine stands may be related to fire-induced mortality of longleaf pine seedlings beneath canopy pines (Grace and Platt 1995a, Avery *et al.* 2004). However, effects of seedling size and fire intensity on mortality are difficult to separate in observational studies because greater canopy densities often correspond to greater competition (*i.e.,* smaller longleaf pine seedlings) and greater fuel loads from needlefall (*i.e.,* greater fire intensity).

Fire adaptation of longleaf pine seedlings is often associated with traits that allow for survival, whereas the impacts of fire on seedling growth have not been well documented. The consumption of foliage by fire would necessitate the allocation of stored carbohydrate to replace needles and restore pre-burn photosynthetic capacity. Long-term experimental studies have reported growth reductions of longleaf pine saplings following repeated prescribed burning (Boyer 1987). However, the release of nutrients following burning and the consumption of competing vegetation may also provide opportunities for increased growth of survivors (Brockway *et al.* 2006). Grelen (1978) reported that prescribed burning increased the proportion of seedlings that had emerged from the grass stage in a four-year study in Louisiana, USA. It is not clear to what degree burning alone, in the absence of indirect effects such as changes in resource availability, affects longleaf pine seedling growth responses.

Previous studies have shown season of burn to be an important ecological driver within frequent-fire ecosystems, although effects vary across taxa and by response variable (Platt *et al.* 1988a, Streng *et al.* 1993, Hiers *et al.* 2000). Generally, burning within the growing season has been reported as more effective at killing small hardwood trees than burning in the dormant season (Waldrop *et al.* 1992, Brose *et al.* 1999). Seasonal effects of burning on trees and shrubs have been attributed to differences in fire intensity due to differences in weather conditions during burns, as well as to differences in plant physiology at the time of burning (Glitzenstein *et al.* 1995, Drewa *et al.* 2002). Although previous studies have reported no effects of season of burn on longleaf pine survival (Glitzenstein *et al.* 1995, Jack *et al.* 2010), these studies either considered trees that were out of the grass stage, or grouped grass stage seedlings as a single size class.

This study was designed to examine the direct effects of fire on grass stage longleaf pine seedlings in a controlled field experiment. Whereas previous experimental studies have manipulated fire intensities in longleaf pine ecosystems by removing or adding fuels during burns (*e.g.,* Thaxton and Platt 2006, Jack *et al.* 2010), we used a prescribed burn simulation tool (PBST) to deliver controlled fire treatments to individual longleaf pine seedlings. We used thermocouple (TC) temperatures as a surrogate of fire intensity. Our specific objectives were to determine: 1) effects of seedling size, fire intensity (measured as TC temperature), and season of treatment application on longleaf pine seedling survival and growth; 2) the contribution of sprouting to longleaf pine seedling survival following burning; and 3) impacts of fire on the initiation of height growth. We hypothesized that: 1) seedling size is positively related to post-fire survival while fire intensity is negatively related to post-fire survival; 2) direct effects of fire on longleaf pine seedlings result in short-term growth reductions; and 3) season of burn would not affect longleaf pine growth or survival, similar to results reported from previous studies.

Methods

Study sites

This study was conducted in an approximately 6 ha longleaf pine stand located at Norfolk Southern Corporation's 5830 ha Brosnan Forest property in Dorchester County, South Carolina, USA (33°5'9.24"N, 80°15'26.28"W). Soils throughout the stand were somewhat poorly drained Albany sands, a deep Atlantic Coast Flatwoods soil formed from marine or eolian deposits. For the 50-year period prior to study initiation, mean annual temperature at a weather station near the study location (33°2'11.76"N, 80°13'57.00"W) was 16.1 °C, and mean annual precipitation was 125.1 cm. During the growing season (April to August), the mean 50-year precipitation was 65.8 cm, whereas growing season precipitation amounts were 106.3 cm and 45.0 cm during 2013 and 2014, respectively. The stand had basal area of 11.7 m^2 ha^{-1} and mean diameter at breast height (DBH) of 41.4 cm and had not been harvested recently. Prescribed fire is commonly used in longleaf pine forests at Brosnan Forest, and the stand had been previously burned in spring 2011.

Experimental design

This study used a completely randomized design with four treatments and a sample population of naturally regenerated, grass stage longleaf pine seedlings. We conducted an inventory of all seedlings within the central 1 ha of the stand and stratified seedlings into three classes of root collar diameter (RCD): Small (6.4 to 13.0 mm), Medium (13.1 to 19.0 mm), and Large (19.1 to 25.4 mm). Seedlings with obvious damage (*e.g.,* brown-spot needle blight [caused by *Mycosphaerella dearnessii* Barr]) were removed from consideration for the study, as were seedlings located within 5 m of canopy trees or within 1 m of other seedlings. Seedlings in each size class were then randomly assigned to one of four treatments, including an untreated control (Control), a high-temperature burn treatment (HB; maximum [recorded on 1 s intervals] TC temperature ~ 425 °C), a low-temperature burn treatment (LB; maximum [recorded on 1 s intervals] TC temperature ~ 225 °C), and mechanical removal of foliage (Clip). Study treatments were applied in January and in May 2013 to compare the effects of dormant and growing season application on response variables. The sample population for the dormant season application was 12 seedlings for each seedling size × treatment combination ($n = 144$), and the sample population for the growing season application was 10 seedlings per combination ($n = 120$).

Although the PBST may not be able to completely create the conditions of wildland prescribed fire (Kral *et al.* 2015), the burn treatments used in this study were designed based on data from fires in longleaf pine ecosystems. We considered three primary sources of information for developing the burn treatments. First, we reviewed the published literature for reports of data on fire behavior in longleaf pine ecosystems and found that the reported maximum temperatures derived from measuring devices (*e.g.,* TCs or pyrometers) commonly ranged from < 100 to ~ 600 °C (Gibson *et al.* 1990, Kennard *et al.* 2005, Wally *et al.* 2006, Ellair and Platt 2013), with “cooler” prescribed burns reaching maximum temperatures around 200 °C (Olson and Platt 1995, Thaxton and Platt 2006) and “hotter” fires reaching maximum temperatures closer to 500 °C (Olson and Platt 1995, Drewa *et al.* 2002, Hiers *et al.* 2009, Jack *et al.* 2010). Because burn conditions and temperature measuring devices affect reported fire temperatures, we also referred to data collected with the same TCs that we used in our study. Our second source of information was a fire temperature dataset collected during experimental prescribed burns between February and April 2008 at Carolina Sandhills National Wildlife Refuge in Chesterfield County, South Carolina, USA. These data describe fire behavior using TCs within fuel types that were dominated by longleaf pine needles, wiregrass (*Aristida stricta* Michx.), or turkey oak (*Quercus laevis* Walter) leaf litter (Wenk *et al.* 2011) and generally indicate that “hotter” burns reached peak temperatures between 400 and 500 °C ,and “cooler” burns reached peak temperatures around 200 °C (Fig. 1). Finally, we conducted a series of small-area (< 100 m^2) test fires at our study location to describe the time–temperature curves generated by TCs at the time of treatment application, and we found that peak temperatures of the TCs in the test burns were close to 200 °C but reached temperatures of approximately 400 °C with addition of pine needle fuels (Fig. 1).

Treatment application

The HB and LB treatments were applied with a PBST that allowed us to control the time–temperature curves of TCs placed at each seedling’s terminal bud (Fig. 2). The PBST was designed as a 21 cm diameter furnace mounted to a tripod and positioned directly above each target seedling. Two opposite sides of the furnace were each connected to a propane tank with oxygen-acetylene hosing. During treatment application, propane was delivered to the furnace, lit, and then the furnace was lowered onto each target seedling individually. Prior to treatment application, all vegetation and the forest floor were removed in a 1.0 m radius around each target seedling. We positioned four Type-K thermocouples probes (4.8 mm thickness), one at each cardinal direction, at least 1 cm above the soil surface and within 2 cm of the terminal bud of each seedling. Each burn treatment was applied by slowly lowering the lit furnace onto the target seedling, monitoring temperatures of the TCs using a laptop computer installed with LoggerNet 4.1 software (Campbell Scientific, Inc., Logan, Utah, USA), and raising the furnace to control maximum temperature of the TCs during application. After several calibration burns, we determined that a small amount of pine needle fuel (within a 15 cm radius of each seedling) at the base of each seedling better simulated the shape of the time–temperature curves of our test fires (Fig. 1). The Clip treatment was applied by removing all foliage to within 2.5 cm of the fascicle sheath with garden pruners. The dormant-season treatment was applied 9–14 January 2013, and the growing season treatment was applied 20–24 May 2013.

Data collection

We recorded RCD (mm) and height from the root collar to the top of the terminal bud (cm) of each seedling prior to treatment. For each treatment burn, we recorded the ambient air temperature (°C), relative humidity (%), and wind speed (m s^{-1}) using a Kestrel 3000 portable weather station (Nielsen-Kellerman Co., Boothwyn, Pennsylvannia, USA). During the burns, TC temperatures (°C) were recorded every second. In August 2013 and 2014, we surveyed seedling survival

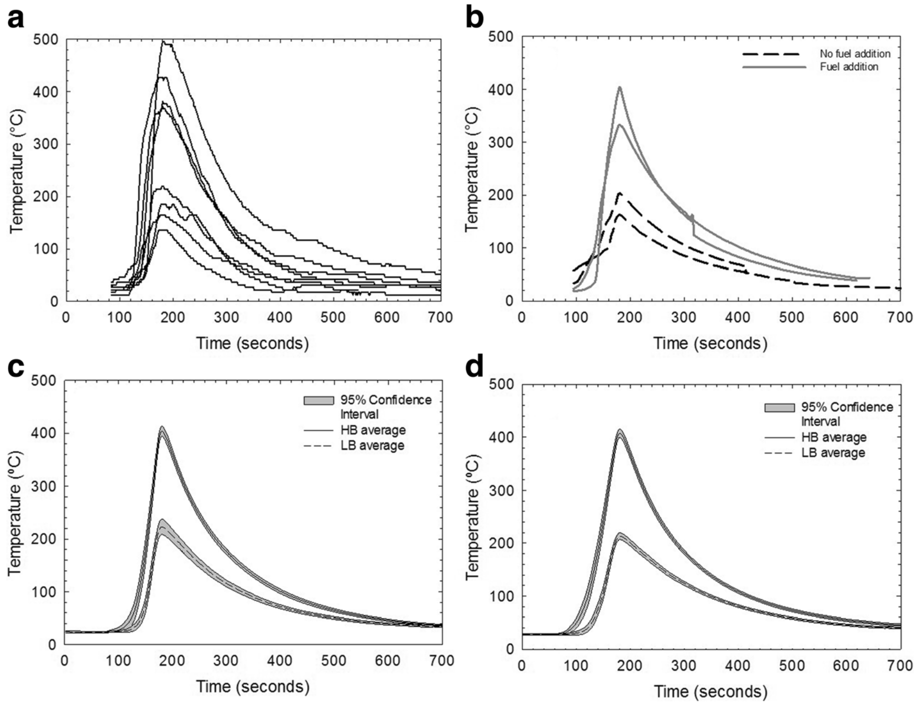

Fig. 1 Time–temperature curves for (**a**) prescribed burns from Carolina Sandhills National Wildlife Refuge (February – April 2008) used as reference for treatment development; (**b**) test fires with and without fuel additions conducted at our study site (January 2013); and mean and 95% confidence intervals for (**c**) the January (*n* = 36 seedlings per treatment) and (**d**) the May (*n* = 30 seedlings per treatment) treatment applications. All curves were created by aligning the maximum temperature for each time–temperature curve with 180 s to standardize display

and recorded the RCD and height of every seedling. Thus, seedling data were collected prior to treatment application and 8 and 20 months following treatment for the January application, and 4 and 16 months following treatment for the May application. In August 2014, each seedling was carefully excavated from the soil to preserve as much of the root system as possible and returned to the laboratory to determine biomass. Each seedling was separated into needles, stem, and roots, and each section was oven-dried at 80 °C to a constant mass and weighed to determine biomass (g).

Data analyses

We tested the assumption that the PBST allowed repeatable, controlled treatment application to each seedling by using Analysis of Variance (ANOVA) to test for effects of the month of burn application (January or May), the burn treatment (HB or LB), seedling size (Small, Medium, or Large), and all possible interactions on response variables related to the burning environment. We tested for differences among these variables as indication of consistent conditions during treatment application. Response variables included ambient air temperature, relative humidity, and wind speed at the time of treatment, as well as maximum TC temperature (°C; Max), the area under the TC temperature curve above a threshold of 60 °C (Area60), and the duration (number of seconds) TC temperature remained above a threshold of 60 °C (Dur60). The threshold of 60 °C is the temperature at which cellular necrosis occurs (Stephan *et al.* 2010), and previous fire effects studies commonly include area under the temperature curve and duration as important variables to describe fire effects (Kennard *et al.* 2005, Wally *et al.* 2006).

We classified each seedling from the initial seedling population as alive or dead in August 2013 and August 2014. We used contingency tables with the Mantel-Haenszel chi-square test to determine treatment effects on survival for each size class and month of burn application. Similarly, we tested for effects of month of application on survival for each treatment and each seedling size class. For significant treatment effects, pair-wise comparisons were made using chi-square tests on each pair of treatments, and *P*-values were adjusted using the Bonferroni adjustment.

We used logistic regression to model the probability of seedling survival in August 2013 (after one growing season) and in August 2014 (after two growing seasons). We modeled survival probability of all seedlings based on treatment (Control, Clip, HB, LB), initial (pre treatment) RCD, and application month. In the absence of a significant effect of application month, data were combined

Fig. 2 Photographs of (**a**) the prescribed burn simulation tool, (**b**) a burn treatment being applied to a longleaf pine seedling in 2013, (**c**) a seedling and thermocouples immediately post burn (HB treatment), and (**d**) seedling recovered by sprouting in South Carolina, USA, in August 2014

across months. We also used an information-theoretic approach to determine the best model for predicting survival of burned seedlings (*i.e.,* only HB and LB seedlings) based on initial RCD, season of application, and three different fire variables (Max, Area60, Dur60). Candidate models included a null (intercept only); four models with intercept plus one variable (initial RCD, Max, Area60, or Dur60); four models of intercept, initial RCD, plus one variable (application season, Max, Area60, or Dur60); thee models of intercept, application month, plus one variable (Max, Area60, or Dur60); and three models of intercept, initial RCD, application season, plus one variable (Max, Area60, or Dur60). We used Akaike Information Criterion (AIC_c) for small sample size to calculate ΔAIC_c and Akaike weights (w_i) for each model. Lower AIC_c scores and greater w_i values indicated better models for the data (Burnham and Anderson 2003). In the case of significant initial RCD, results are presented by seedling size class (Small, Medium, Large).

To quantify growth, we first calculated the root collar area (RCA; mm^2) for the initial measurement period (at the time of treatment application) and for the August 2014 measurement period. We then calculated the RCA increment as the difference between root collar area in August 2014 and the initial RCA for each seedling. We used ANOVA to test for effects of study treatment, seedling size class, and the interaction of treatment and size class on RCA increment and on root biomass, stem biomass, needle biomass, and total biomass of seedlings destructively sampled in August 2014. In the case of significant effects, we used Tukey's Honestly Significant Difference adjustment to test for differences in pair-wise comparisons. Analyses for RCA increment and biomass were conducted separately for each month of treatment application because the seedling populations in each application month experienced different growing period lengths during the study duration. We used $\alpha = 0.05$ to determine statistical significance for all analyses.

Results

Application of burn treatment

Air temperature, relative humidity, and wind speed did not differ between burn treatments or among seedling size classes (Table 1). Air temperature and relative humidity were greater in May than in January, and wind speed was greater in January than in May. Time−temperature curves indicated similar maximum temperatures for each month of application, with low variability within each treatment level (Fig. 1). As intended, Max was significantly different between treatment levels but did not differ by month of burn application or seedling size class (Table 2). Mean Area60 and Dur60 were each greater in the May burn application than in the January application and were each greater for Large seedlings than for Small seedlings.

Survival

For Control and Clip treatments, there were no differences in survival between the January and the May applications (Fig. 3). Survival in August 2014 was high for Controls (≥ 90%) for all seedling sizes and both months of burn application. The LB treatment had lower survival than Control ($\chi^2 = 8.14$, $P = 0.004$) and Clip ($\chi^2 = 8.14$, $P = 0.004$) for only Small seedlings treated in May. Small seedlings treated with HB had significantly lower survival than all other treatments in the January application (Control $\chi^2 = 19.46$, $P < 0.001$; Clip $\chi^2 = 15.97$, $P < 0.001$; LB $\chi^2 = 13.03$, $P < 0.001$) and significantly lower survival than Control ($\chi^2 = 8.14$, $P = 0.004$) and Clip ($\chi^2 = 8.14$, $P = 0.004$) treatments in the May application. The Medium seedlings treated with HB in May had significantly lower survival than all other treatments (Control $\chi^2 = 7.13$, $P = 0.008$; Clip $\chi^2 = 4.80$, $P = 0.029$; LB $\chi^2 = 7.13$, $P = 0.008$). Survival differences between months of application were found in two cases: Medium seedlings in the HB treatment ($\chi^2 = 4.25$, $P = 0.039$) and Small seedlings in the LB treatment ($\chi^2 = 4.23$, $P = 0.040$), with January treatment survival exceeding May treatment survival in both cases.

Table 2 Heat delivery during burn treatment application by month, treatment, and longleaf pine seedling size class in South Carolina, USA, in 2013. There were no significant interactions among any of the independent variables in the model; the same superscript letter within a column and effect indicates no significant difference; HB = high-intensity burn; LB = low-intensity burn treatment; Max = peak temperature during burn application; Area60 = area above 60 °C within the time–temperature curve; Dur60 = duration (s) with temperature above 60 °C

		Max (°C)		Area60		Dur60 (s)	
Effect	Level	Mean	SE	Mean	SE	Mean	SE
Month	January	315	11	52 951^{b}	2001	348^{b}	7
	May	310	12	60 276^{a}	2428	408^{a}	9
	P-value	0.364		< 0.001		< 0.001	
Treatment	HB	405^{a}	2	72 183^{a}	1207	423^{a}	7
	LB	220^{b}	3	40 378^{b}	897	327^{b}	6
	P-value	< 0.001		< 0.001		< 0.001	
Size class	Large	306	16	58 961^{a}	3069	394^{a}	11
	Medium	314	14	55 191^{ab}	2641	369^{b}	12
	Small	317	14	54 689^{b}	2475	363^{b}	9
	P-value	0.144		0.016		0.002	

There was no effect of application month on the probability of survival after one growing season ($F_{1,\ 255} = 0.93$, $P = 0.335$), with the probability of survival positively related to initial seedling size for LB and HB treatments but not for Clip or Control (Fig. 4a). The probability of survival after two growing seasons was significantly

Table 1 Weather conditions during burn treatment application by month, treatment, and longleaf pine seedling size class in South Carolina, USA, in 2013. There were no significant interactions among any of the independent variables in the model; the same superscript letter within a column and effect indicates no significant difference; HB = high-intensity burn; LB = low-intensity burn treatment

		Air temperature (°C)		Relative humidity (%)		Wind speed (m s^{-1})	
Effect	Level	Mean	SE	Mean	SE	Mean	SE
Month	January	26.0^{b}	0.2	61.0^{b}	1.0	2.8^{a}	0.4
	May	28.9^{a}	0.6	67.9^{a}	1.3	1.6^{b}	0.1
	P-value	< 0.001		< 0.001		< 0.001	
Treatment	HB	27.8	0.5	63.3	1.1	2.2	0.4
	LB	26.9	0.4	64.9	1.3	2.3	0.3
	P-value	0.074		0.290		0.793	
Size class	Large	28.1	0.6	64.8	1.2	2.0	0.2
	Medium	27.5	0.6	64.0	1.5	2.3	0.5
	Small	26.6	0.4	63.6	1.7	2.4	0.5
	P-value	0.089		0.820		0.144	

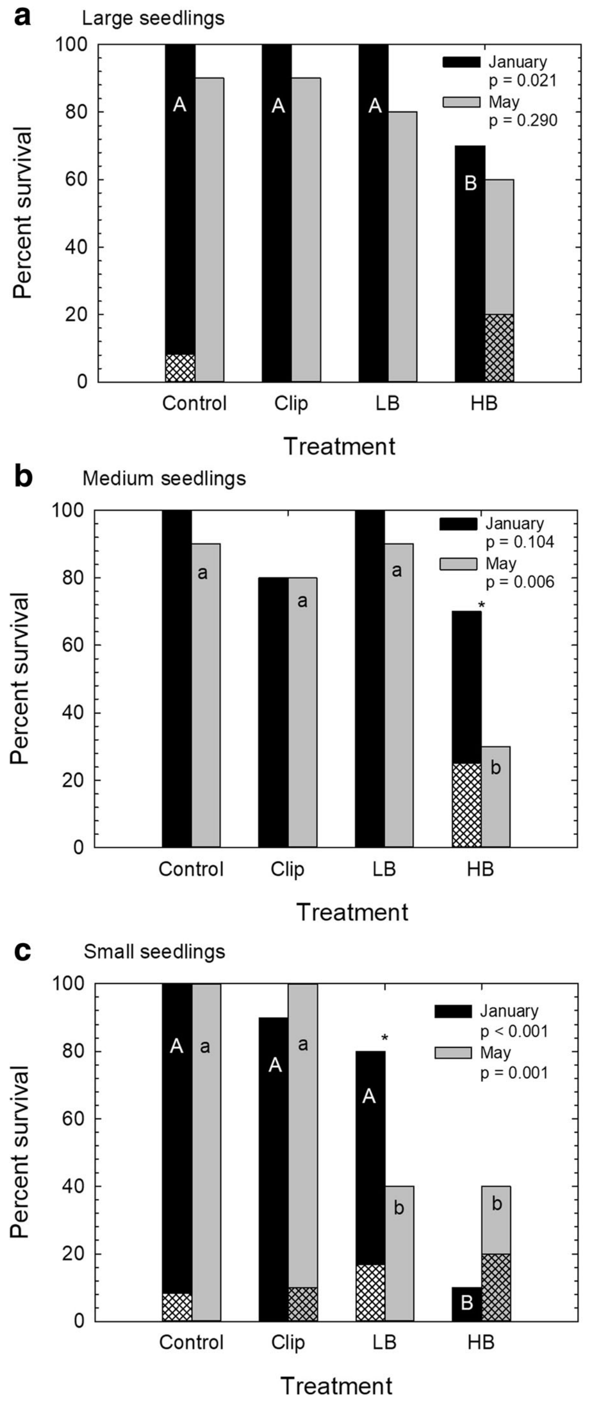

Fig. 3 Survival by treatment near the end of the second growing season (August 2014) after treatment application for (**a**) Large, (**b**) Medium, and (**c**) Small longleaf pine seedlings treated in South Carolina, USA, in January and May 2013. The *P*-values indicate significance from the Mantel-Haenszel test for treatment effect, and the same letter within an application month indicates no significant difference in Pearson chi-square pair-wise comparisons. An asterisk (*) indicates a significant difference in survival between the January and May treatment applications by treatment and seedling size class. Cross hatching on bars illustrates the percentage of the original seedlings that survived by sprouting

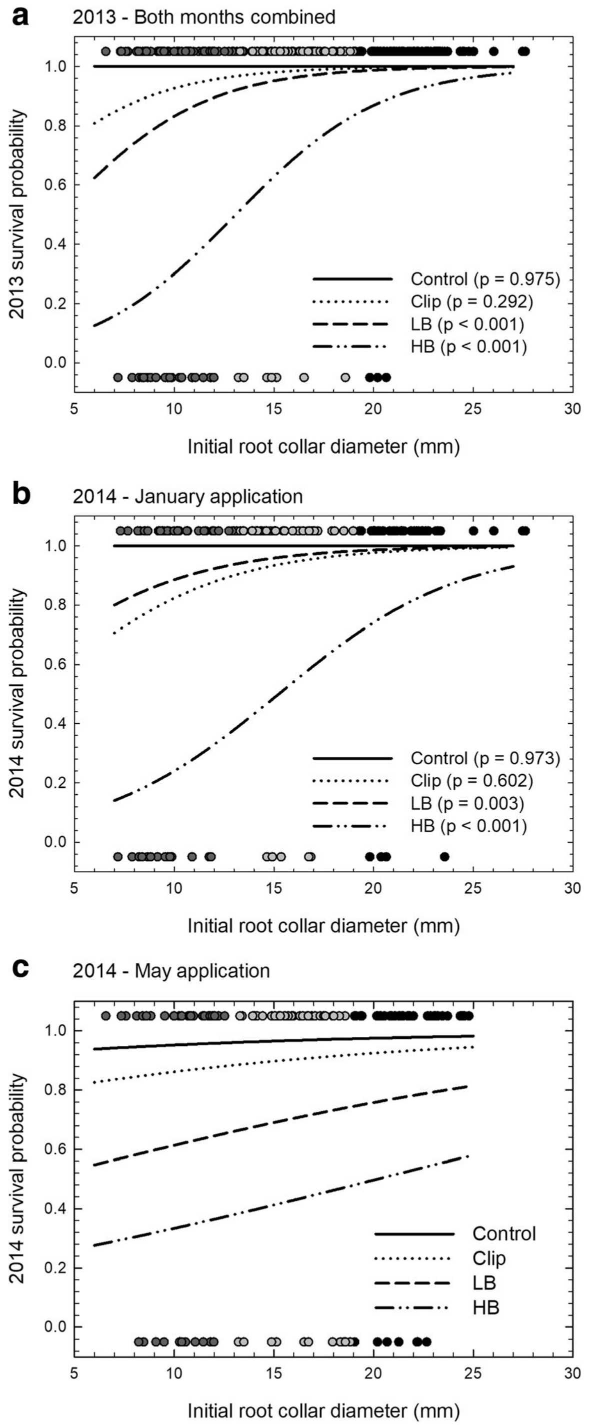

Fig. 4 Probability of longleaf pine seedling survival in **a**) August 2013 (the first growing season) and in **b**) and **c**) August 2014 (the second growing season) in relation to initial RCD (mm) by treatment in South Carolina, USA. The logistic regression model indicated that month of application significantly affected 2014 survival but not 2013 survival. Initial root collar diameter did not significantly affect probability of survival in 2014 for the May application. Data points in each figure represent Small (dark grey), Medium (light grey), and Large (black) seedlings, with seedlings that survived at the top of the figure and seedlings that died at the bottom

affected by month of application ($F_{1,\ 257} = 5.33$, $P = 0.022$). Seedlings treated in January had survival models that appeared similar to those from the first growing season, with the probability of survival positively related to initial seedling size for LB and HB (Fig. 4b). For seedlings treated in May, initial seedling RCD was not significantly related to the probability of survival after two growing seasons ($F_{1,\ 114} = 1.93$, $P = 0.168$; Fig. 4c), although survival was significantly lower for HB than for Control based on non-overlapping 95% confidence intervals of parameter estimates. Among the burned seedlings, the best model of the probability of first-year survival included initial RCD and Area60, whereas the best model of the probability of survival after two growing seasons included initial RCD, application month, and Max (Table 3, Fig. 5).

By the end of the study period, a portion of the seedling population had survived by sprouting in all treatments, including two seedlings in the Control treatment groups (Fig. 3). In the Medium and Large size classes, treated seedlings in only the HB treatment had sprouted. Sprouting contributed to survival of half the Small seedlings remaining at the end of the study from the May application of the HB treatment.

Table 3 Akaike Information Criterion values for each candidate model for the probability of seedling survival in 2013 and in 2014 following burn treatments applied to longleaf pine seedlings in South Carolina, USA, in 2013. Lower AIC_c values and higher w_i values indicate better models for the data, and the best model for each year is shown in boldface; RCD = root collar diameter, Max = peak temperature during burn application; Area60 = area above 60 °C within the time–temperature curve; Dur60 = duration (s) with temperature above 60 °C; Month = month of treatment application (January or May)

	2013 survival			2014 survival		
Model	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i
Null (intercept only)	143.01	49.63	0.00	172.71	36.18	0.00
Initial RCD	118.70	25.33	0.00	163.25	26.73	0.00
Max	123.84	30.47	0.00	150.89	14.36	0.00
Area60	132.10	38.73	0.00	155.43	18.90	0.00
Dur60	139.65	46.28	0.00	162.36	25.83	0.00
Initial RCD; Month	120.07	26.70	0.00	160.65	24.12	0.00
Initial RCD; Max	94.58	1.21	0.25	140.54	4.01	0.07
Initial RCD; Area60	**93.37**	**0.00**	**0.45**	138.27	1.74	0.22
Initial RCD; Dur60	103.44	10.07	0.00	143.22	6.69	0.02
Month; Max	134.14	40.77	0.00	148.35	11.83	0.00
Month; Area60	134.14	40.77	0.00	156.31	19.79	0.00
Month; Dur60	141.53	48.16	0.00	164.20	27.67	0.00
Initial RCD; Month; Max	95.71	2.33	0.14	**136.53**	**0.00**	**0.51**
Initial RCD; Month; Area60	95.43	2.06	0.16	138.69	2.16	0.17
Initial RCD; Month; Dur60	104.64	11.27	0.00	145.22	8.69	0.01

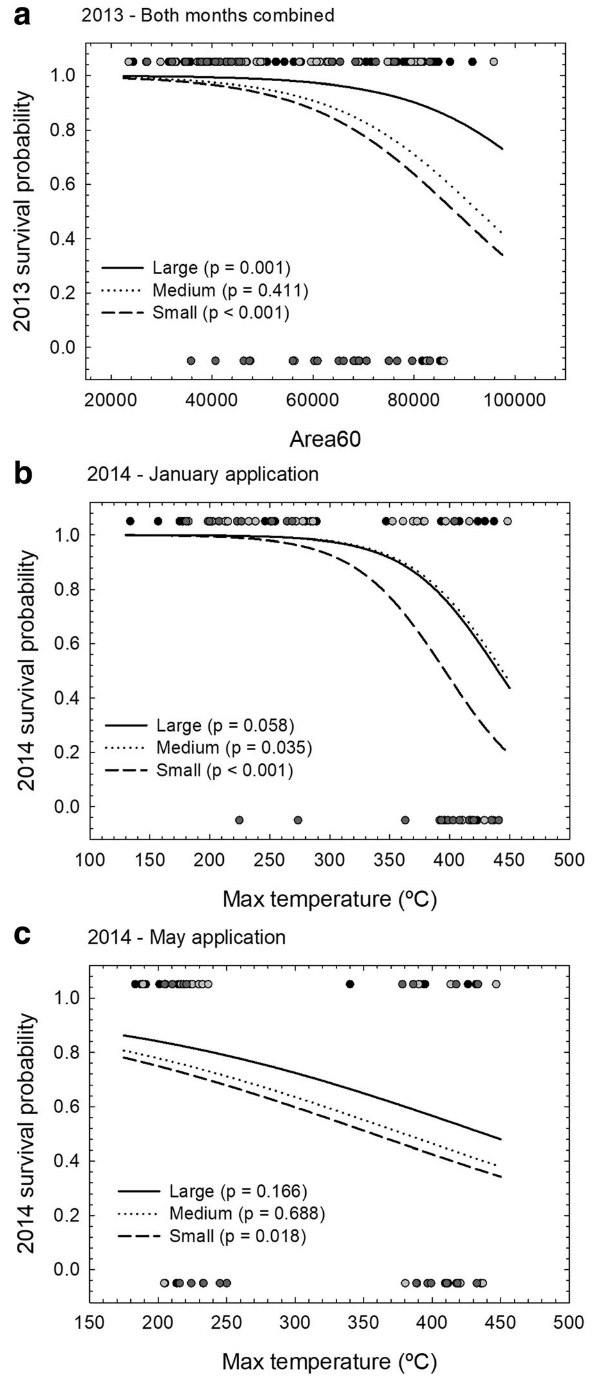

Fig. 5 Probability of longleaf pine seedling survival in (**a**) August 2013 in relation to Area60 for both application months combined, and probability of seedling survival in August 2014 in relation to Max temperature for (**b**) the January application and (**c**) the May application from logistic regression by size class. Data points in each figure represent Small (dark grey), Medium (light grey) and Large (black) seedlings, with seedlings that survived at the top of the figure and seedlings that died at the bottom

Growth and biomass

There was no significant interaction between treatment and seedling size class for RCA increment for either application month (January $F_{6,\ 109} = 0.97$, $P = 0.451$; May $F_{6,\ 77} = 1.12$, $P = 0.360$). Treatment did not significantly affect the RCA increment for the May application but was significant for the January application (Fig. 6a). Seedlings in the Control treatment grew an average of 104 mm^2 from January 2013 through August 2014, which was significantly greater than seedlings from any other treatment (Clip $F_{1,\ 109} = 27.14$, $P < 0.001$; LB $F_{1,\ 109} = 10.69$, $P = 0.001$; HB $F_{1,\ 109} = 7.08$, $P = 0.044$; Fig. 6a). Mean RCA increment of seedlings from the Clip, LB, and HB were not different from each other. Seedling size class did not significantly affect RCA increment for the May application but was significant for the January application (Fig. 6b).

There were no significant interaction effects between seedling size and treatment on total ($F_{6,\ 105} = 1.33$, $P = 0.250$), root ($F_{6,\ 105} = 1.48$, $P = 0.194$), stem ($F_{6,\ 104} = 2.14$, $P = 0.060$), and needle ($F_{6,\ 105} = 0.87$, $P = 0.517$) biomass for the January application. Total seedling biomass was greater for seedlings in the Control treatment than in Clip ($F_{1,\ 105} = 20.61$, $P < 0.001$) or HB ($F_{1,\ 105} = 7.24$, $P < 0.041$) treatments, and stem and root biomass were each greater for seedlings in the Control treatment than in the Clip treatment (stem $F_{1,\ 105} = 22.47$, $P < 0.001$; root $F_{1,\ 105} = 22.77$, $P < 0.001$; Fig. 7a). Needle biomass did not differ among treatments. In the May application, we found no significant interaction effects between seedling size and treatment on total biomass ($F_{6,\ 67} = 1.13$, $P = 0.355$) or any of the biomass components (roots $F_{6,\ 67} = 1.34$, $P = 0.252$; stem $F_{6,\ 67} = 0.97$, $P = 0.450$; needles $F_{6,\ 68} = 0.68$, $P = 0.666$). Of the component seedling biomass, only root biomass was different among treatments, with greater biomass for seedlings in the Control treatment than in the LB treatment ($F_{1,\ 105} = 9.06$, $P = 0.019$; Fig. 7b).

For each seedling, we plotted RCD and height from the final measurement period (Fig. 8). Using a threshold of 15 cm height as an indicator of grass stage emergence

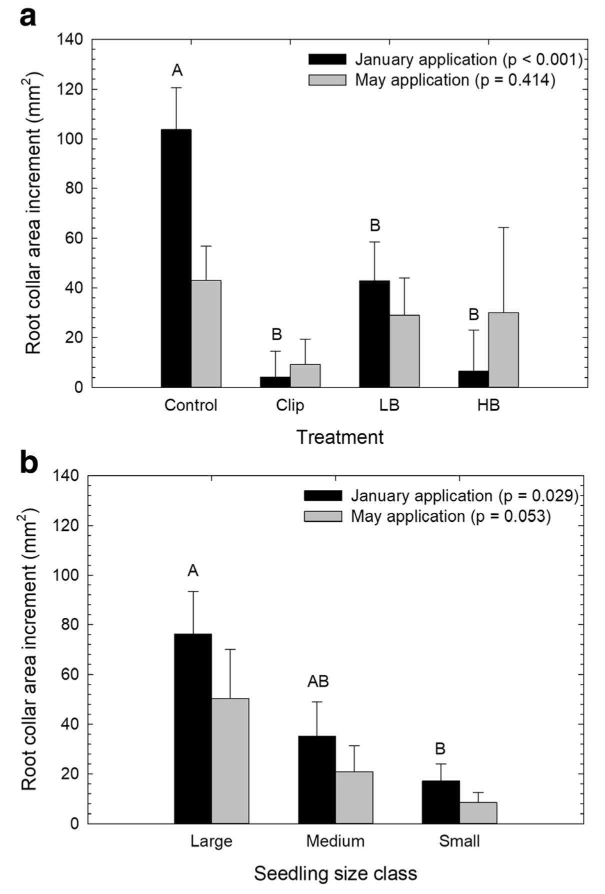

Fig. 6 Root collar area increment (mm^2) from pre treatment through August 2014 for the January and May applications by (**a**) study treatment and (**b**) longleaf pine seedling size class from South Carolina, USA. The same letter within an application month indicates no statistical difference from pair-wise comparisons

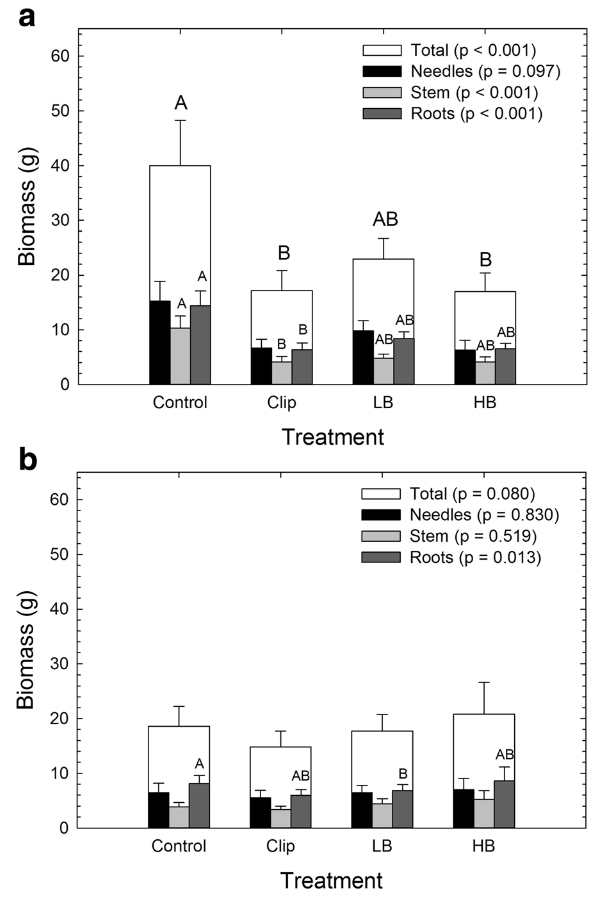

Fig. 7 Biomass of needles, stems, roots, and total seedlings from the (**a**) January application and (**b**) May application after destructive sampling of longleaf pine seedlings in South Carolina, USA, in August 2014

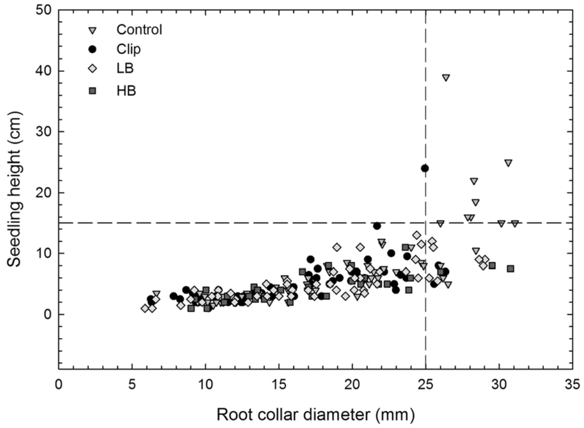

Fig. 8 Relationship between root collar diameter (mm) and height (cm) in August 2014 by treatment, for each longleaf pine seedling measured in South Carolina, USA. The horizontal dashed line at 15 cm height represents the threshold for height growth, and the vertical dashed line is at 25 mm, which is the rule-of-thumb root collar diameter for emergence from the grass stage

(*e.g.,* Nelson *et al.* 1985, Knapp *et al.* 2013), there were 10 seedlings that had emerged from the grass stage in August 2014, nine of which were from the Control treatment and one of which was from the Clip treatment. The nine seedlings from the Control treatment each had RCD > 25 mm.

Discussion

With historical fire return intervals reported to have been as frequent as 1 to 3 years (Frost 2006, Huffman 2006, Stambaugh *et al.* 2011), longleaf pine must be able to survive fire during the seedling stage for successful regeneration to occur. Similar to previous studies, our results provide evidence that longleaf pine seedlings are fire resistant but not fireproof, and that seedling size and fire intensity each affect seedling survival (Hypothesis 1). In a prescribed fire study of *in situ* longleaf pines that ranged in size from grass stage seedlings to saplings, Jack *et al.* (2010) found that grass stage seedlings (defined as < 0.2 m tall) had greater mortality than larger seedlings and saplings. Results from our study demonstrate that the size of seedlings within the grass stage also affects the probability of survival. Previous studies have reported a range of root collar diameter thresholds for fire resistance. Bruce (1951) reported that all grass stage seedlings with root collar diameters greater than 5.1 mm survived a winter burn in Mississippi, USA; Croker and Boyer (1975) cite 7.6 mm as the threshold for fire resistance; and Brockway *et al.* (2006) cited a threshold of 13.0 mm. Generally, our results suggest that the probability of seedling survival one year after fire exceeds 50% for seedlings with root collar diameters greater than 15 mm for the high-temperature burn treatment. Our results indicate that the low-temperature burn treatment had little effect on seedling mortality. However, reduced survival of small seedlings after the second growing season, even in the low-temperature burn treatment, demonstrates the potential importance of the interaction between seedling size and fire intensity for grass stage seedling mortality.

The best models for seedling survival (of only burned seedlings) differed for survival near the end of the first (August 2013) and second (August 2014) growing seasons, although initial seedling size was included in both models. In addition to initial seedling size, the area under the time−temperature curve above 60 °C was an important predictor of seedling survival after the first growing season. Several publications have discussed the relevance of Area60, as a measure of heat dosage, to biotic response (Bova and Dickinson 2005, Kennard *et al.* 2005, Wally *et al.* 2006). The measure of maximum temperature, used to standardize treatment delivery in our study, may not as strongly indicate conditions experienced by plant tissues exposed to fire because both temperature and duration affect tissue damage (Bova and Dickinson 2008, Stephan *et al.* 2010). Strong *et al.* (2013) found that the area under the time−temperature curve was a better predictor of bunchgrass (*Aristida purpurea* Nutt.) mortality than maximum temperature or the duration above 60 °C. In contrast, the best model for seedling survival after the second growing season in our study included maximum temperature rather than the area under the curve. Given the highly controlled treatment delivery in this study, correlations among fire intensity variables (Max, Area60, Dur60) were likely higher than what would be expected from a natural fire environment (Bova and Dickinson 2008). In addition, the thermocouples, having been placed immediately adjacent to the terminal bud during treatment delivery, provided an estimate of the fire environment of each seedling but did not measure actual tissue temperature.

The best model for seedling survival at the end of the second growing season, which encompassed both the direct, immediate mortality as well as delayed effects, included the month of treatment application. There was greater mortality within the second growing season across all size classes for both burn treatments in the May application, whereas mortality patterns for the January application were similar after the first and second growing season. We speculate that interactions among the fire treatment and environmental conditions may have contributed to our results. Although we achieved similar maximum temperatures with each burn application month, the area under the time−temperature curve and the duration above 60 °C were both greater in the May application than in the January application, perhaps due to higher air temperature during burn application in May. Moreover, the 2014 growing season was drier than average, and it is not known how interactions among environmental stress and fire affect mortality patterns in longleaf pine seedlings. Additional research is warranted to explore the mechanistic drivers of seasonal fire effects on longleaf pine seedling responses.

Sprouting is widely accepted as a persistence mechanism for hardwood trees (Bond and Midgley 2001, Del Tredici 2001) and is commonly discussed as an important fire adaptation for several pine species (*e.g.,* shortleaf pine (*Pinus echinata* Mill.), pitch pine (*P. rigida* Mill.); Mattoon 1915, Welch *et al.* 2000). However, sprouting of longleaf pine seedlings has received relatively little attention. Farrar (1975) used mechanical clipping to test for sprouting responses and reported that up to 60% of small grass stage seedlings sprouted, with lower sprouting rates as tree size increased. We observed sprouting across all study treatments, including the control, but the rate of sprouting did not exceed 30% of the original population for any seedling size and treatment combination. However, sprouting was more common for small seedlings and seedlings in the high-temperature burn treatment, suggesting that the sprouting response was associated with severity of seedling damage. Although sprouting appears to contribute to the short-term fire resistance of longleaf pine seedlings, additional research is needed to determine if sprouting affects the vigor, development, or survival of longleaf pine seedlings through time.

Our results support the hypothesis that prescribed burning causes short-term reductions in seedling growth (Hypothesis 2), although responses depended on fire treatment and varied between the two application months. We did not quantify foliar consumption following the burns but observed that the high-temperature burn treatment completely consumed seedling foliage (Fig. 2c), while low-temperature burn treatment had more variable needle consumption. Regardless, all burned seedlings experienced either nearly complete needle consumption or scorch. These results suggest that short-term growth reductions of longleaf pine seedlings may be due to allocation of carbohydrates for needle production rather than to direct effects of heat damage. This is further supported by the lack of significant differences in needle biomass among treatments, as seedlings prioritized needle growth following consumption or removal.

Regardless of treatment, root collar area increment was low for seedlings treated with the May application, and the majority of root collar diameter growth of seedlings in the Control treatment of the January application occurred between January and May 2013 (data not shown). Low growth rates from May 2013 through the end of the study for seedlings in all treatments (including the Controls) in both treatment application months suggest that additional factors (external to study treatments) were limiting growth. For example, abnormally high rainfall in the 2013 growing season (*e.g.,* Knapp *et al.* 2008) and abnormally low rainfall in the 2014 growing season (*e.g.,* Rodríguez-Trejo *et al.* 2003) may have reduced the growth potential for all seedlings and contributed to the growth difference observed between the Control seedlings from the January and May application months. Assuming that external factors were limiting growth of all seedlings in this study, it is likely that growth reductions due to treatment effects may have been more pronounced in years with more favorable growing conditions.

Emergence from the grass stage is a critical event for longleaf pine seedling development. Previous studies reported that burning in May can stimulate height growth of longleaf pine seedlings, possibly due to control of competition or reduced infection of brown-spot needle blight (Maple 1977, Grelen 1978). We did not address effects of our experimental burning on the incidence of brown-spot needle blight by excluding infected seedlings from the sampling population. We removed understory competition adjacent to each seedling across all treatments in this study and found no evidence that burning further improved grass stage emergence. The size of the root system (often expressed by the surrogate measure of root collar diameter) tends to provide consistent indication of height growth emergence (Knapp *et al.* 2006). Although other studies have suggested that competition control may affect the relationship between seedling root collar diameter and height (Ramsey *et al.* 2003), our results support the rule of thumb that height growth begins when the root collar reaches approximately 25 mm diameter.

In contrast to our expectation, several of our results indicate that season of burn affected longleaf pine seedling response (Hypothesis 3). Although previous experimental studies have generally reported no effects of burn month or season on longleaf pine mortality across tree size classes (Glitzenstein *et al.* 1995, Jack *et al.* 2010), our study, which considers a smaller range of seedling sizes, suggests that season of burn may interact with seedling size and fire intensity to affect survival response. For example, mortality of Small seedlings was greater for the growing season application than the dormant season application for the low-temperature burn treatment, but the high-temperature burn treatment resulted in high mortality regardless of season. In contrast, Medium seedlings were large enough for high survival regardless of burn season for the low-temperature burn treatment but had lower survival with growing season burns than dormant season burns for the high-temperature burn treatment (Fig. 3).

For Large seedlings, burn season had no effect regardless of fire intensity. Given that ambient temperatures were higher during burns in May than in January, and the fire intensity measures of Area60 and Dur60 were greater in May than in January, we cannot determine if the burn season effect would be attributed to seedling physiology or to differences in fire treatment intensity. However, the mortality models suggest that the effect of burn season on seedling mortality was primarily attributed to differences in mortality that took place during the second growing season.

The manipulative, experimental approach taken in this study provides unique insight into fire's effects on naturally regenerated, grass stage longleaf pine seedlings, yet comes with important trade-offs and limitations. For example, the thermocouples used in the study were positioned adjacent to the terminal bud of the target seedling but did not reflect the true temperature of the plant tissue. Thermocouples are commonly used to describe characteristics of fire behavior, and, while having been found to provide useful information, were limited to recording the temperature of the thermocouple device itself, as influenced by its materials and construction, rather than the energy output of the fire (Kennard *et al.* 2005, Bova and Dickinson 2008, Kremens *et al.* 2010). Although the treatments we applied were developed based on comparable data collected from actual prescribed burns (Fig. 1), the use of a PBST does not recreate all aspects of prescribed burning (Kral *et al.* 2015); for example, the delivery of heat from above with the PBST differs from fire movement with an operational prescribed burn, and we purposefully removed most surrounding fuels to better control the time–temperature curves. Thus, the study design includes a trade-off between experimental control and direct representation of operational conditions.

Management implications

In naturally regenerated longleaf pine forests and woodlands, seedlings and saplings are commonly observed in aggregations within canopy openings (Platt *et al.* 1988b, Pecot *et al.* 2007), which previous studies have attributed to competitive exclusion by canopy trees (Brockway and Outcalt 1998, Gagnon *et al.* 2004) and seedling mortality beneath the canopy due to greater fire intensities caused by needle accumulation (Grace and Platt 1995a, Avery *et al.* 2004). Our results suggest that these two factors likely work in combination to affect the spatial distribution of natural regeneration. Growth suppression of longleaf pine seedlings by canopy trees has been well documented (Boyer 1963, Croker and Boyer 1975, Grace and Platt 1995b), with little seedling growth occurring when basal area exceeds 9 m^2 ha^{-1} (Mitchell *et al.* 2006). Likewise, fire intensity has been reported to increase with proximity to longleaf pine canopy trees (Williamson and Black 1981). Our results demonstrate that seedlings across the size range observed in this study had relatively good survival with low-temperature burns, but survival was stratified by seedling size with greater fire intensity. Fire behavior is variable at fine scales within longleaf pine ecosystems (Hiers *et al.* 2009), suggesting that seedling survival may also be spatially variable. As indicated by our findings, the probability of survival would decrease beneath canopy trees, where seedling size is reduced by competition and fire intensity is likely greater due to needle accumulation.

Longleaf pine plantations are established as an initial step in ecosystem restoration where canopy longleaf pines no longer exist (Brockway *et al.* 2005) or to meet objectives related to wildlife, timber, or pine needle production (South 2006). In a restoration context, reintroducing fire is considered to be critical for maintaining ecosystem function over long timescales (Freeman and Jose 2009, Martin and Kirkman 2009, Addington *et al.* 2012). Results from this study indicate that the risk of mortality in longleaf pine plantations is relatively high for seedlings with root collars less than 15 mm diameter. High-quality container-grown longleaf pine seedlings are recommended to have root collar diameters of 7 to 9 mm before planting (Barnett and McGilvray 2000), although studies have reported root collar diameters of container-grown seedlings to range from 2.2 to 11.0 mm at planting (South *et al.* 2005). Growth rates of longleaf pine seedlings are variable but have been reported to range from 2 to over 10 mm per year without canopy competition (South *et al.* 2005, Hu *et al.* 2012a). Depending on size at planting and subsequent growth rates, longleaf pine seedlings may take several years to develop root collars greater than 15 mm diameter. Recently, underplanting has been suggested as a viable option for converting existing pine stands to longleaf pine (Kirkman *et al.* 2007, Hu *et al.* 2012b, Knapp *et al.* 2013). The retention of canopy trees has been reported to reduce growth rates of planted seedlings, which potentially extends the vulnerability of longleaf pine seedlings to fire mortality.

Conclusion

Although fire simulation methods are imperfect in mimicking prescribed burn conditions and effects, the controlled and repeatable application of burn treatments, as used in this study, cannot be achieved with prescribed burning. Our results demonstrate fire resistance of longleaf pine seedlings, but at the same time reveal that greater fire intensity selects against small longleaf pine seedlings. Moreover, fire season may impact survival of grass stage longleaf pine seedlings but further interacts with seedling size and fire intensity. Other factors that may affect seedling response to fire, such as seedling age and vigor, environmental conditions, or interactions with nearby plants, were not tested in this study; thus, additional research is needed to determine mechanisms for seedling responses. Understanding the effects of fire on grass stage longleaf pine seedlings can inform burn prescriptions to ensure that natural or artificial regeneration needs are met while maintaining a frequent-fire regime for ecosystem management.

Abbreviations

ANOVA: analysis of variance; Area60: the area under the thermocouple temperature curve above a threshold of 60 °C; DBH: diameter at breast height; Dur60: the duration (number of seconds) thermocouple temperature remained above a threshold of 60 °C; HB: a high-temperature burn treatment; LB: a low-temperature burn treatment; Max: maximum thermocouple temperature; PBST: prescribed burn simulation tool; RCD: root collar diameter; TC: thermocouple

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Availability of data and materials

The datasets used or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions

B.O. Knapp had major contribution to study conception and design, data collection, data analyses, and writing the manuscript, as well as minor contribution to securing funding support. L.S. Pile had major contribution to study conception and design, data collection, and writing the manuscript, as well as minor contribution to data analyses. J.L. Walker had major contribution to study conception and design and writing the manuscript, as well as minor contribution to data analyses. G.G. Wang had major contribution to study conception and design, securing funding support, and writing the manuscript, as well as minor contribution to data analyses. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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