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Factors affecting the sprouting of shortleaf pine rootstock following prescribed fire

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ABSTRACT

Shortleaf pine (*Pinus echinata*) is a fire dependent species that is declining across the southeastern US. Its unique basal crook is an adaptation that protects dormant buds from fire and facilitates prolific sprouting of seedling rootstocks following top-kill. Understanding what influences shortleaf pine sprouting after fire could greatly increase success of natural regeneration efforts. We examined the relationship between sprouting and seedling size, basal crook depth, and maximum basal crook temperature of shortleaf pine seedlings following a mid-intensity prescribed fire in the Ozark-St. Francis National Forest of northwestern AR, US. We hypothesized that larger seedlings with deeper buried crooks would exhibit greater sprouting after top-kill from fire. A total of 195 seedlings were measured for a variety of site, size, and fire damage characteristics. 'Simulated crooks' were constructed and calibrated to estimate basal crook temperature and were buried adjacent to each seedling. Prescribed fires were implemented during the early growing season, resulting in a wide range of seedling damage from slightly charred stems to complete immolation of aboveground biomass. Fourteen of 195 seedlings were not top-killed and were larger and experienced lower crown scorch than those that were top-killed. Of the 181 seedlings that suffered top-kill, 72 did not sprout and died. Over the course of the growing season 40 of the sprouted seedlings died. Sprouted seedlings that survived the entire growing season had similar size and crook soil depths as seedlings that initially died and were smaller (ground line diameter of 1.5 vs. 3.1 cm) with shallower crook depth (0.2 vs. 0.7 cm) than seedlings that sprouted and later died. Crook temperature and crown scorch values were similar among sprouted seedlings that lived and died, but were lower than for seedlings that never sprouted. These results suggest that the ability of top-killed seedlings to sprout following fire is sensitive to heat and fire damage, while the ability of a seedling to survive once sprouted decreases with seedling size. Low intensity fires when seedlings are 1–2 cm in diameter can be used to bank seedlings until adequate stocking is achieved or until regeneration cutting can be timed with a bumper seed crop to supplement existing advanced regeneration.

1. Introduction

The natural range of shortleaf pine (*Pinus echinata* Mill.) is from New York to Texas to Florida (Little, 1971). It is among the four most important commercial pine species in the southeastern US (McWilliams et al., 1986). Historically, shortleaf pine dominated between 65,000 and 69,000 km^2 of forest land (Smith, 1986) and reached its zenith in the Ozark and Ouachita Mountains of Arkansas and Oklahoma. Between 1950 and 1990, this important ecosystem decreased by 40% due to fire suppression, land conversion, and selective harvesting (Guldin et al., 1999; South and Buckner, 2003). Recent evidence indicates that shortleaf pine is further at risk from introgression with loblolly pine (*Pinus taeda* L.) a process likely exacerbated by fire suppression (Stewart et al., in press).

Fire was a critical factor in the development of shortleaf pine dominated ecosystems. Human caused and natural fires prior to 1920 occurred at frequencies ranging from 2 to 20 years in the mountains of Arkansas and return interval decreased with Native American population density and drought and increased with topographic roughness (Guyette et al., 2006). Although early settlers of European descent continued the practice of burning to clear brush, subsequent fire suppression reduced mean fire frequencies to approximately 50 years between the 1920s and present time (Elliott and Vose, 2005; Guyette et al., 2006).

Shortleaf pine is adapted to low-intensity surface fires (Schwilk and Ackerly, 2001). Prolific sprouting from near the root collar after top-kill is the most important adaptation for young seedlings and saplings (Mattoon, 1915). The ability of shortleaf pine seedlings to survive fire provides it with a competitive advantage when intermixed with species that do not normally sprout, such as

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loblolly pine (Williams, 1998). Sprouting in shortleaf pine occurs from dormant buds that developed in the axils of primary needles (Stone and Stone, 1954). These buds are harbored in a unique basal double-crook just above the root collar. The crook's development usually occurs during the first few months of seedling establishment. Formation of compression and tension wood just above the cotyledon causes the seedling to tilt so that it is horizontal; shortly after, it resumes upward growth through a similar process leaving a horizontal section 2.5–7.5 cm long (Mattoon, 1915; Stone and Stone, 1954). The lethal temperature range of dormant plant tissues generally is between 93 and 108 °C (Kayll, 1968) and decreases to approximately 60 °C for metabolically active tissue (Hare, 1961). The basal crook has been widely speculated to increase the odds of sprouting by keeping the bud cluster closer to soil surface where the heat from a fire is lower. In addition the crook facilitates the accumulation of soil and duff above the dormant buds cluster which further insulates them from the heat of a fire. The importance of the basal crook decreases as individuals grow as the thickening bark insulates the cambium.

Understanding the use of fire to manage shortleaf pine regeneration has gained new importance. There has been a policy shift of the USDA Forest Service away from plantation forestry (Robertson, 2004) as well as recent efforts to restore shortleaf pine savannas for wildlife habitat and to foster recovery of shortleaf pine from past high-grading in mixed oak-pine stands (Guldin, 2007). Because shortleaf pine is shade intolerant (Eyre, 1980) and initially grows slower than most competing tree species (Lawson, 1990; Williston, 1972), the persistence of shortleaf pine regeneration by sprouting in ecosystems that incorporate surface fire increases likelihood of establishment after larger-scale disturbance. In regard to management of shortleaf pine using natural regeneration, fire is often required to prepare the seed bed and reduce competition. Therefore, sprouting is necessary for survival of shortleaf pine advanced regeneration (Barnett et al., 1986; Cain, 1987; Williams, 1998; Yocom and Lawson, 1977) which is an important supplement to highly variable seed crops and provides flexibility with multi-year logging windows of modern timber sale contracts (Guldin, 2007).

With the exception of a few studies, e.g., Cain and Shelton (2000), Grossman and Kuser (1988), and Williams (1998), most studies conducted on shortleaf pine seedling survival after fire fail to differentiate between survival of seedlings/saplings that are not top-killed from the sprouting of top-killed seedlings. In addition, most studies involving shortleaf pine sprouting were done with top-clipping which provides much needed information, but ecologically is not the same effect as fire (Campbell, 1985; Little and Somes, 1956; Stone and Stone, 1954). We are not aware of any studies that measured the temperatures of basal crook buds during fire to determine the relationship between sprouting and fire intensity as well as the potential importance of the basal crook.

Given the uncertainty inherent with natural regeneration, the necessity of fire for success of shortleaf pine natural regeneration, and the importance of advanced regeneration, a better understanding of top-killed seedling sprouting and the factors that affect it is needed. This information will assist forest managers to modify fire prescriptions to enhance shortleaf pine regeneration and hopefully restore or at least forestall further decline of this important tree species and associated ecosystems. The goal of this study was to determine the factors that affect sprouting of shortleaf pine after fire, specifically those related to the seedling size, fire intensity, and the basal crook. We hypothesized that the ability of a shortleaf pine seedling to sprout and survive after a fire (1) decreases with maximum temperature reached for the dormant buds on the basal crook; (2) increases with the depth of insulation (soil and/or duff) over the basal crook; and (3) increases with seedling size.

2. Materials and methods

2.1. Study area

Three stands in the Big Piney Ranger District of the Ozark-St. Francis National Forest were chosen for this study. The stands are immediately adjacent to and east of Arkansas State Highway 7 about 16 km north of Dover, AR. The USDA Forest Service manages these stands as open shortleaf pine woodlands and is studying the effects of repeated prescribed fire on sprouting and shortleaf pine seedling accumulation. The overstory of the three stands is dominated by shortleaf pine with a variable understory consisting of forbs, shrubs, and grasses. The area has a mean annual temperature of 23 °C and receives a mean annual precipitation of 127 cm (NOAA, 2011). Soils of stand 1 (35°33′29.98″N, 93°03′48.41″W) are classified as a Nella–Mountainburg series association which is a gravelly, fine sandy loam, siliceous, semiactive, thermic Typic Paleudult with average slopes of 12%. It faces mainly east and southeast and is at an elevation of approximately 365 m. Soils of stand 2 (35°31′58.95″N, 93°05′19.27″W) are classified as a Linker–Mountainburg series association which is a well drained, fine sandy loam, siliceous, semiactive, thermic Typic Hapludault with average slopes of 6%. It faces mainly west and southwest and is at an elevation of approximately 427 m. Stand 3 (35°32′15.02″N, 93°04′50.45″W) is adjacent to stand 2, and is a mix of both Linker–Mountainburg and Nella–Mountainburg soil series associations. It faces mainly east and is at an elevation of approximately 396 m with an average slope of 17% (NRCS, 2011).

Stands 2 and 3 were harvested in 2002 and stand 1 was harvested in 2003 using a seed-tree with reserves reproduction cutting method. Residual basal area after harvest ranged from 2.3 to 6.9 m^2 ha^{-1}. Non-commercial hardwoods were removed mechanically in summer 2004. In addition to the existing natural regeneration, these stands were planted in the early spring of 2005 with 2244 shortleaf pine seedlings ha^{-1} of bare-root genetically improved 1-0 stock on 1.8 × 2.4 m spacing. All stands exhibited poor planted seedling survival and developed natural shortleaf pine regeneration post-harvest. In July to August of 2005, competing hardwood species were treated using a directed foliar spray of Accord (5% glyphosate, Dow Agrosciences, Indianapolis, IN, USA) via backpack sprayers. The stands were previously burned in February 2006 by aerial ignition.

2.2. Simulated crook calibration

To estimate the temperature of the buds inside the bark of shortleaf pine crooks, we created simulated crooks. Simulated crooks were constructed from three layers of aluminum tags; the middle tag had ten 0.15 cm diameter holes drilled into them and were attached to a base tag using glue. We used ten different temperature indicating crayons (OMEGA, Stamford, CT, USA) to fill each of the ten holes. Melting points of the crayons ranged from 50 to 104 °C in 3–6 °C intervals. This range of temperature was chosen because it included the upper end of typical temperatures that are reached in the upper 2 cm of soil (100 °C) during a low to mid intensity fire (Elliott and Vose, 2005; Preisler et al., 2000; Raison et al., 1986) and it bracketed the expected killing temperature of growing plant tissues, i.e., 50–60 °C (Hare, 1961; Vines, 1968). In addition, three drops of OMEGALAQ temperature indicating liquid (OMEGA, Stamford, CT, USA) were placed on one end of the tag to both calibrate the liquid to the crayon and to capture any temperatures that rose above the 104 °C maximum crayon melting point. Melting points of the liquid paints were 79, 107, and 135 °C, which bracketed the lethal temperature range for dormant plant tissue of 93–108 °C (Kayll, 1968). A final tag was placed on top and the three tags were wrapped in a single layer of aluminum foil to keep out moisture and to hold them together.

Because the thermal properties of aluminum tags and basal crooks differ, we calibrated the simulated crooks to actual shortleaf pine dormant buds. Several basal crook sections of shortleaf pine seedlings of various sizes were obtained from the study sites. A large crook (averaging 2.1 cm in diameter) and a small crook (averaging 1.2 cm in diameter) were heated together in the oven. Each crook had a hole drilled 2 mm beneath the bark directly under the bottom side of the crook. This hole was just big enough to place a thermocouple to measure temperatures in the location of dormant crook buds. Petroleum jelly was used to seal the hole around the thermocouple wire. The two crooks started at room temperature, and were placed in the oven at temperatures ranging from 50 to 120 °C at 10 °C intervals along with a simulated crook tag. These were heated for intervals of 1–5 min. After each time interval for each oven temperature, the temperature inside the crook was recorded and the simulated crook was checked to see which crayons had melted. The result was that the temperature of the simulated crook was on average 23 °C higher than the temperature of the basal crook. The results below present raw simulated crook tag temperatures.

2.3. Plot design

On 9 April 2010 we overlaid our study on plots of a larger USDA Forest Service study examining the effects of prescribed fire on shortleaf pine regeneration. We used 13 plots in stand 1, 15 plots in stand 2, and 14 plots in stand 3 (42 plots total). At each plot we located up to four seedlings that we tagged and then measured for height and ground line diameter (GLD). In addition, we carefully unearthed the basal crook of each seedling and measured its diameter at midpoint and depth below mineral soil and duff layer. After measuring, a simulated crook was placed next to the basal crook at mid-crook depth and was carefully covered by the soil and surface layer previously removed.

To measure surface temperature during the fire, an aluminum metal tag was hung by a steel wire 25 cm above the ground surface next to each seedling (Iverson et al., 2004). These tags were dotted with 20 different temperature indicating liquid paints (Omega, Stamford, CT) with ten paints on each side ranging in melting point from 75 to 575 °C in approximately 25 °C intervals.

Slope (0–30%) and aspect at each 4 seedling plot was recorded. To ensure a large range in fire intensity, we chose one additional tree in ten plots of each stand. The soil and duff was cleared away from the crooks of these seedlings and a pre-measured quantity of dried shortleaf pine litter was placed around them in a 7.5 cm radius. Each of these seedlings was randomly assigned a litter weight of 20, 40, or 80 g, for a total of 30 (10 of each litter treatment) seedlings added to the study.

2.4. The fire

The USDA Forest Service conducted a prescribed burn on 14 April 2010 for stand 1 and on 15 April 2010 for stands 2 and 3. Branch terminal elongation had begun classifying this as an early growing season burn, a common time of year for prescribed fire in this region. Stand 1 burned from approximately 1030–1330 and stands 2 and 3 were burned together from 1000 to 1400. The average air temperature during both fires was 26 °C, with 3–8 km h^{-1} SE winds. Surface temperatures reached between 79 and 593 °C according to painted tags. The fires were started as slow backing fires at the northern ends of the units. Head fires were started at the southern ends of each unit and three strip fires were burned through the center of each unit. Backing fires were estimated to move at 20 m h^{-1}, while head fires were estimated to be 100 m h^{-1}.

Immediately following the fires on 14 and 15 April, post fire measurements were taken. For each seedling, surface fuel consumption was determined by measuring the new depth to crook. Seedlings were assessed for percent crown scorch by rounding scorch damage to the nearest 25%.

Approximately half of the crook tags (103 out of 195) experienced temperatures outside of the predicted range. Twenty-two did not reach high enough temperatures to melt any indicators, while 81 got too hot and exceeded the maximum temperature of the indicator paints. This is likely due to many crooks (81%) not being buried by soil as expected. Crook tags where no crayons melted indicate a range between the air temperature of 26 °C and the lowest crayon melting point of 49 °C; the midpoint of 38 °C was used for this category. Tags where all indicator crayons melted but the crayon did not turn into a yellow gel were later determined in the lab to range from 135 to 260 °C; a midpoint of 200 °C was used for this group. The remaining tags where the crayon material turned into yellow gel or turned completely black and charred were assumed to have reached a temperature above 260 °C. These tags exceeded our temperature measurement capabilities and were removed from analyses pertaining to crook temperature, but corresponding seedling data were included in all other analyses.

2.5. Sprouting

Sprout data were collected on 2 June 2010. Seedlings were classified into three categories: non-top-killed, top-killed and sprouted, or dead. Seedlings were considered to be non-top-killed if undamaged 2009 foliage persisted. Seedlings were considered top-killed and sprouted if all 2009 foliage was dead or consumed by the fire and new sprouts were originating from the lower stem or basal crook. Seedlings were classified as dead if all foliage was dead or consumed by the fire and there were no new sprouts. The number of sprouts per top-killed seedlings was counted and heights of the average and tallest sprouts of each seedling were measured to the nearest cm. The location of where sprouts were originating on the stem was recorded, with note made if sprouts were only originating from below the upper bend of the basal crook. Sprouts were measured again on 12 January 2011. Each seedling was re-measured for sprout count, average and maximum sprout height, and to see if seedlings that had previously sprouted were now dead.

2.6. Analysis

Data were analyzed using ProcMixed (SAS ver. 9.3, Cary, NC). Correlations between measured seedling size, fire intensity, and site variables were determined. A multiple regression was conducted with sprout count per seedling as the dependent variable.

3. Results

3.1. Initial sprouting two months following fire

Initial heights of seedlings before prescribed fire ranged from 7 to 150 cm and GLD ranged from 0.3 to 9.0 cm. Depth of the crook below mineral soil ranged from 0 to 5 cm and depth beneath duff layer ranged from 0 to 9 cm. Crook diameter and GLD were correlated [$c = 7.15 + 0.591g$] where c = crook diameter (mm) and g = GLD (mm) ($r^2 = 0.61$) ($P < 0.0001$). Tree height was negatively correlated to crown scorch ($r = -0.36$, $P < 0.0001$). Surface fire temperatures correlated to crown scorch ($r = 0.27$, $P < 0.0001$) but not crook temperatures ($r = 0.07$, $P = 0.36$).

There were three seedling fates two months following fire: non-top-killed seedlings (14 of 195), top-killed and sprouted seedlings (109 of 195), and dead seedlings (72 of 195). The seedlings that were not top-killed were initially taller than seedlings that were top-killed and sprouted and more than twice as tall as seedlings that were top-killed and did not sprout ($P < 0.0001$) (Table 1). Likewise, GLD and crook diameters were smallest for dead seedlings, intermediate for sprouted seedlings, and largest for non-top-killed seedlings ($P < 0.0001$). The basal crooks of non-top-killed seedlings were more than twice the depth beneath the soil as sprouted seedlings and crooks of dead seedlings were barely covered with soil on average ($P < 0.0001$) (Table 1). Surface temperature for non-top-killed seedlings was lower than for those that died ($P = 0.07$) and crook temperature for the non-top-killed and the sprouted seedlings was lower than those in the dead seedling category ($P = 0.008$) (Table 2). All seedlings exhibited some amount of crown scorch, with those that were not top-killed having an initial scorch of 25%. Dead seedlings had the highest initial crown scorch ($P < 0.0001$) (Table 2). No other measured variables significantly differed among seedling survival categories.

In June, sprouts ranged in height between 1 and 24 cm. The number of sprouts per seedling ranged between 1 and 51, and was predicted by the regression [$n = 5.61 - 0.026t + 0.350c + 0.173d$] where n = number of sprouts per seedling, t = crook temperature (°C), c = crook diameter (mm), and d = soil depth (mm) ($r^2 = 0.29$) ($P = 0.06$)].

3.2. Sprout survival after one growing season

When remeasured after the growing season on 12 January 2011, all seedlings that were not top-killed were still alive and had exhibited new growth. For further analyses, the 14 of 195 seedlings that were not top-killed were removed to focus on the fate of sprouted seedlings. After one full growing season, 40 of the 109 top-killed and sprouted seedlings had died. Sprouted seedlings that died were originally taller ($P = 0.001$) and had larger GLD and crook diameters ($P = 0.001$) than those that sprouted and lived. The net effect was that sprouted seedlings that survived the entire first growing season were similar in size to those that were initially killed by the fire (Table 3). Initially, 91% of all seedlings with more than 0.5 cm of soil covering their basal crook sprouted compared to 49% survival for seedlings with less than 0.5 cm of soil covering the crook. At the end of the growing season, the effects of soil depth no longer differed among the seedlings that sprouted and survived the entire season and those that initially died, but both classes were buried more shallowly than those that sprouted and later died ($P = 0.005$) (Table 3). Crown scorch and crook temperature did not differ among seedlings that sprouted and died from those that sprouted and lived (Table 4).

Seedlings that sprouted and survived the first growing season initially had fewer sprouts per seedling (8.8 ± 0.7 SE vs. 14.4 ± 1.9 SE) ($P = 0.001$) and more vigorous initial sprouts (based on average sprout height) than those that sprouted and died (7.3 cm ± 0.4 SE vs. 6.1 cm ± 0.5 SE respectively) ($P = 0.05$). For seedlings that sprouted and survived the first growing season, sprout count did not vary significantly over the growing season (8.8 ± 0.7 SE sprouts initially vs. 9.6 ± 0.8 SE sprouts at the end of the growing season). Final average sprout height was 19.7 cm ± 0.7 SE, average maximum sprout height was 31.2 cm ± 1.3 SE, and final sprout counts ranged from 1 to 28 sprouts per seedling. The ability to predict sprout count per seedling diminished after a full growing season. The final regression was [$n = 10.41 - 0.025t - 0.814s$] where n = final number of sprouts per seedlings, t = crook temperature and s = crown scorch index ($r^2 = 0.06$, $P = 0.06$).

Table 1
All significant ($P < 0.05$) seedling size and pre-fire basal crook variables (± 1 SE) among non-top-killed (alive), top-killed and sprouted (sprouted), and top-killed and non-sprouted (dead) shortleaf pine seedlings following an early spring prescribed fire in northwestern AR, US, 2010. Seedlings were measured for pre-fire characteristics on 9 April 2010, 6 days before the fire on 15 April 2010.

Seedling status	n	Height (m)	GLD[a] (cm)	CD[b] (cm)	SDC[c] (cm)
Alive	14	*a* 1.8 ± 0.2[d]	*a* 4.1 ± 1.9	*a* 3.2 ± 0.3	*a* 1.0 ± 0.3
Sprouted	109	*b* 1.0 ± 0.1	*b* 2.1 ± 0.1	*b* 2.0 ± 0.1	*b* 0.4 ± 0.1
Dead	72	*c* 0.8 ± 0.1	*c* 1.5 ± 0.1	*c* 1.5 ± 0.1	*c* 0.1 ± 0.1

[a] Ground line diameter.
[b] Crook diameter.
[c] Soil depth to basal crook.
[d] Within each variable, means with the same letters are not significantly different, $P < 0.05$, Tukey–Kramer multiple range test.

Table 2
All significant ($P < 0.05$) fire severity variables (± 1 SE) among non-top-killed (alive), top-killed and sprouted (sprouted), and top-killed and non-sprouted (dead) shortleaf pine seedlings following an early spring prescribed fire in northwestern AR, US, 2010. Seedlings were measured on 15 April 2010 immediately following the fire.

Seedling status	n	Crook temperature (°C)	SF Temp.[a] (°C)	Crown scorch (%)
Alive	14	*a* 80 ± 12[b]	*a* 256 ± 27	*a* 25 ± 0
Sprouted	109	*a* 89 ± 5	*ab* 297 ± 11	*b* 58 ± 3
Dead	72	*b* 112 ± 7	*b* 326 ± 13	*c* 77 ± 3

[a] Surface fire temperatures measured at 25 cm above ground adjacent to each seedling.
[b] Within each variable, means with the same letters are not significantly different, $P < 0.05$, Tukey–Kramer multiple range test.

Table 3
All significant ($P < 0.05$) seedling size and pre-fire crook variables (± 1 SE) for top-killed shortleaf pine seedlings that sprouted and survived (survivor), those that sprouted and did not survive (sprout died), and those that did not sprout (no sprout) one growing season following an early spring prescribed fire in northwestern AR, US, 2010. Seedlings were measured for pre-fire characteristics on 9 April 2010, 6 days prior to the fire on 15 April 2010.

Seedling Status	n	Height (m)	GLD[a] (cm)	CD[b] (cm)	SDC[c] (cm)
Survivor	69	*a* 0.8 ± 0.1[d]	*a* 1.5 ± 0.1	*a* 1.6 ± 0.1	*a* 0.3 ± 0.1
Sprout died	40	*b* 1.4 ± 0.1	*b* 3.1 ± 0.2	*b* 2.7 ± 0.2	*b* 0.7 ± 0.2
No sprout	72	*a* 0.8 ± 0.1	*a* 1.5 ± 0.1	*a* 1.5 ± 0.1	*a* 0.1 ± 0.1

[a] Ground line diameter.
[b] Crook diameter.
[c] Soil depth to basal crook.
[d] Within each variable, means with the same letters are not significantly different, $P < 0.05$, Tukey–Kramer multiple range test.

Table 4
All significant ($P < 0.05$) and previously significant (two months after fire) fire severity variables (± 1 SE) for top-killed shortleaf pine seedlings that sprouted and survived (survivor), those that sprouted and did not survive (sprout died), and those that did not sprout (no sprout) one growing season following an early spring prescribed fire in northwestern AR, US 2010. Seedlings were measured for post-fire characteristics on 15 April 2010 immediately following the fire.

Seedling Status	n	Crook temperature (°C)	SF Temp.[a] (°C)	Crown scorch (%)
Survivor	69	*a* 87 ± 6[b]	*a* 289 ± 14	*a* 58 ± 4
Sprout died	40	*a* 92 ± 8	*a* 311 ± 20	*a* 56 ± 5
No sprout	72	*b* 112 ± 7	*a* 326 ± 13	*b* 77 ± 3

[a] Surface fire temperatures measured at 25 cm above ground adjacent to each seedling.
[b] Within each variable, means with the same letters are not significantly different, $P < 0.05$, Tukey–Kramer multiple range test.

Figures 1–3 portray the number of top-killed seedlings that sprouted and survived compared to dead seedlings (never sprouted + sprouted and died). Ground line diameter was chosen to represent general size of the seedlings due to strong correlations between GLD and crook diameter ($r = 0.78$) and GLD and height ($r = 0.89$). The majority of seedlings less than 0.5 cm and greater than 3.5 cm GLD died (75% and 87% respectively). Seedlings with a GLD between 0.6 and 3.5 cm exhibited the greatest overall survival (45%) (Fig. 1). Below uncorrected basal crook temperatures of 70 °C, the majority of seedlings survived (68%). Survival was less between 70 and 107 °C (41%). Above 107 °C only 24% survived (Fig. 2) (subtract 23 °C to estimate actual crook temperature based on calibration described above). While some seedlings of all crown scorch categories died, the majority (77%) of seedlings with crown scorch greater than 25% did not survive (Fig. 3).

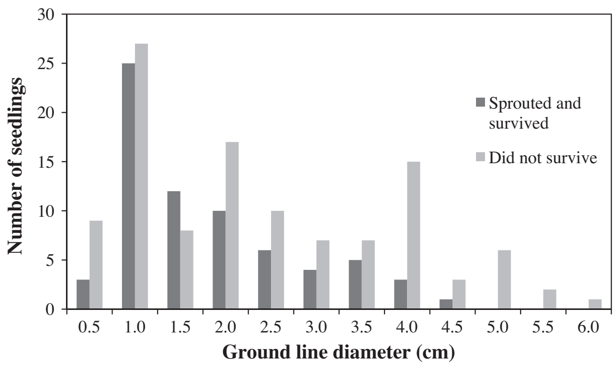

Fig. 1. Ground line diameter and number of top-killed shortleaf pine seedlings that sprouted and survived vs. the total of those that did not survive (did not sprout + those that sprouted but did not survive one growing season) after prescribed fire in northwestern AR, USA, 2010. Each unit on the *X*-axis represents the upper limit of the size class (i.e. 0.5 corresponds to a size class of 0–0.5 cm).

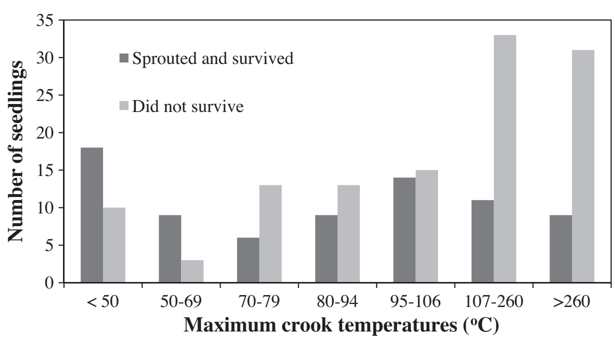

Fig. 2. Maximum basal crook temperature reached during fire and number of top-killed shortleaf pine seedlings that sprouted and survived vs. the total of those that did not survive (did not sprout + those that sprouted but did not survive one growing season) a prescribed burn in northwestern AR, USA, 2010. Temperatures shown indicate temperatures reached in the simulated crook tags. To correct for actual temperatures reached 2 mm under the bark, subtract 23 °C.

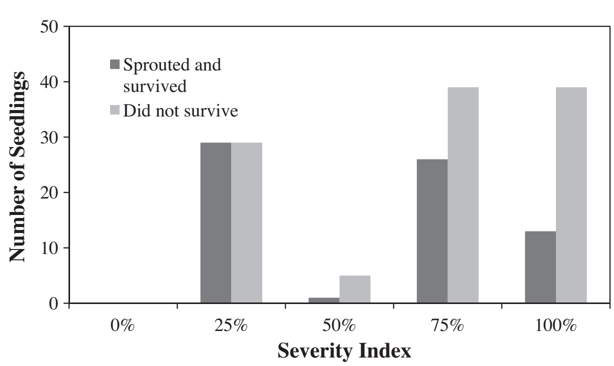

Fig. 3. Crown scorch severity in percent crown scorch classes and number of top-killed shortleaf pine seedlings that sprouted and survived vs. the total of those that did not survive (did not sprout + those that sprouted but did not survive one growing season) a prescribed burn in northwestern AR, USA, 2010.

4. Discussion

The greater survival of smaller sprouted seedlings was contrary to our hypothesis and opposite the findings from most previous studies. Reasons for this difference may be due to other studies combining counts of sprouted and non-top-killed seedlings, not accounting for long-term survival of sprouts, or by simply ignoring sprouted seedlings all together. Some studies examining survival of shortleaf pine advanced regeneration following fire focused on non-top-killed seedlings and saplings. This results in the conclusion that survival increases with size, particularly if shortleaf pine seedlings are greater than 10–15 cm in GLD, 2.5–5.0 m in height, and 8–15 years of age (Cain and Shelton, 2002; Dey and Hartman, 2005; Lawson, 1990; Mattoon, 1915). This also was true in our study where the non-top-killed seedlings were larger than top-killed seedlings. Our low percentage of non-top-killed seedlings (7%) was probably because all of our measured seedlings/saplings were smaller than 10 cm GLD. Forest managers wishing to use prescribed fire in stands with smaller shortleaf pine seedlings will observe high rates of top-kill as we and others have shown (Cain and Shelton, 2000; Dey and Hartman, 2005; Williams, 1998) and reliance on sprouting will be critical (Williams, 1998). In that a greater proportion of larger sprouted seedlings died between June and the following January, waiting a full growing season to assess survival and associated effects of seedling size on sprout success is essential.

One study that focused on sprouting was Little and Somes (1956), which reported that sprouting in response to top-clipping increased with root collar diameter when measured after 1 year. In contrast, two others studies found that sprouting decreased with seedling size. Grossman and Kuser (1988) used clipping and fire to induce sprouting in shortleaf pine seedlings. While the seedlings in their study were 8–10 years old, they found that clipping produced more sprouts than burning and that as size increased, sprouting and survival decreased. In another clipping study, Campbell (1985) found that as shortleaf pine seedlings increased in size and from 3 to 7 years old, sprouting decreased.

The previous fire on our study sites 4 years earlier may have affected sprouting capacity of the older seedlings if sprouting is limited by the number of preformed, dormant buds. However, several studies reported that shortleaf pine will maintain sprouting potential over multiple disturbance events with little reduction in capacity (Little and Somes, 1956; Mattoon, 1915), including after multiple fires (Cain and Shelton, 2002; Dey and Hartman, 2005). Although seedling size and age are confounded, distinguishing between size and age for predicting sprouting potential and survival is probably not important as size and age will usually be correlated.

Escaping top-kill was associated with lower crown scorch and lower crook temperatures. Likewise, initial sprouting was associated with lower crown scorch and crook temperature than for seedlings that never sprouted. When measured after the growing season, sprouted seedlings that lived or died did not differ in crown scorch or crook temperature suggesting the effects of fire intensity are acute and do not influence survival post-sprouting. Rather, survival post-sprouting was negatively related to tree size.

The negative relationship between tree height and crown scorch occurred because larger trees maintained more of their crowns above the flames. However, even for top-killed seedlings of similar size, sprouting seedlings had lower crown scorch than seedlings that initially died. Cain and Shelton (2002) also found that greater crown scorch on shortleaf pine seedlings lowered survival. The significance of crown scorch may change with season of fire; Cain and Shelton (2000) found that every seedling burned in a dormant season fire suffered 100% crown scorch, yet 95% sprouted and survived. Similar crown scorch resulting from a summer fire killed 100% of seedlings.

Crook temperature was a much better predictor of survival than surface temperature. From a biological standpoint, this makes sense since crook temperature reflects the temperature of the dormant buds from which sprouts arise. Unfortunately, measuring crook temperature is not feasible for forest managers.

The best sprout survival occurred when the basal crook temperatures were under 70 °C. This temperature corresponds to actual crook temperature near the dormant buds of 47 °C or below. This is consistent with mortality of metabolically active plant tissues when exposed to temperatures of 50–60 °C for more than 1 min (Hare, 1961). At least half of our seedlings survived after exposure of crook temperatures less than 107 °C. After correction, this is approximately 84 °C, which might suggest that some of these seedlings were still dormant and maintaining a higher heat tolerance (lethal range for dormant tissues is 93–108 °C; Kayll, 1968). Crooks that reached temperatures above this range and sprouted most likely survived due to uneven heating of the crook that differed from the simulated crook tags or due to higher variation in temperature survival thresholds than previously documented.

We hypothesized that greater survival would be associated with more deeply buried crooks because of better insulation of dormant buds. While greater frequency of sprouting was associated with deeper crooks when measured in June, greater mortality of sprouted seedlings was associated with deeper crooks when measured the following January. This indicates that increasing crook depth is negatively correlated to survival post sprouting. Negative effects of deeper crooks on survival could be due to greater exposure of succulent tissues of the new sprouts to mineral soil and soil fauna. Additionally, long-term sprout survival may have been confounded by size or age if more deeply buried crooks belonged to seedlings that were older because older seedling had more time for soil accumulation over basal crooks.

The idea that the basal crook protects buds by keeping them lower and insulated from fire dates back at almost 100 years (Mattoon, 1915). Every seedling we measured had a basal crook, as is common for naturally regenerated shortleaf pine (Mattoon, 1915; Stone and Stone, 1954). Little and Somes (1956) showed that longer crooks produced more sprouts and better survival after top-clipping. Sprouting location (whether it be from above or below the upward bend of the crook) did not seem to be dependent on any fire severity factors we measured. However, sprouting only appeared to occur below the area of the stem exhibiting char. Without formation of the crook, the axial buds would be several cm higher and undoubtedly have suffered greater mortality. Similar to shortleaf pine, loblolly pine seedlings also sprout when top-clipped, although at a lower frequency (Campbell, 1985). However, loblolly pine does not sprout following fire (Williams, 1998), probably because the dormant buds on a loblolly pine seedling are held higher above the soil surface in the absence of a basal crook and damaged by fire.

Season of burn is important for shortleaf pine survival, with better sprout survival associated with dormant season burns (Cain and Shelton, 2000; Grossman and Kuser, 1988; Guyette et al., 2007). While survival rates from dormant season burns typically are close to 90%, results are variable and some dormant season burns can kill a majority of seedlings (Elliott and Vose, 2005; Ferguson, 1957). Our study resulted in 43% survival after the first growing season (including non-top-killed seedlings), possibly due to our burn occurring just as seedlings were breaking bud and transitioning between dormancy and active growth. Given these findings, season of burn, i.e., dormant, early growing season, growing season, can be used to increase or decrease shortleaf pine seedling survival as desired. Likewise, fire intensity during a given season can be used to alter the likelihood of sprouting. However, these variables can be difficult to implement because of the variability of burning conditions and the need that managers have to burn many stands at an operational scale across a landscape.

5. Management implications and conclusions

Seedling size needs to be considered before employing prescribed fire. Our study shows that a successful prescribed burn can be implemented in the late dormant season/early growing season and achieve 37% survival of top-killed seedlings. We found that sprouting is more sensitive to fire damage and intensity and that sprout survival decreases with seedling size. To achieve at least 50% survival of top-killed seedlings, seedlings should be smaller (0.6–1.6 cm GLD and 0.3–0.8 m tall), sustain 50% or less crown scorch, and have actual crook temperatures below 83 °C. Of all these, size is the easiest factor to consider, since both crook temperature and crown scorch cannot be sufficiently predicted and are highly heterogeneous within burned areas. In addition, it is important to wait at least one a year before assessing seedling sprout success as we found significant mortality occurred during the growing season that was proportionately greater for larger seedlings.

Repeated dormant season fires prevent transition of shortleaf pine from seedling to sapling size categories (Cain and Shelton, 2002). However repeated burns can increase shortleaf pine seedling frequency compared to competing species (Dey and Hartman, 2005) and can shift understory dominance to shortleaf pine (Williams, 1998). Natural regeneration of shortleaf pine is often successful by relying on seed fall following a hot summer burn to kill hardwood competition and expose mineral soil (Cain, 1987). However, seed fall is often unpredictable, especially in the mountains of Arkansas and Oklahoma (Shelton and Wittwer, 1996). In these cases, banking advanced regeneration may be an important opportunity to increase regeneration success. For instance, Dey and Hartman (2005) and Williams (1998) recommend burning on 1–3 year intervals to reduce competing species until advanced shortleaf pine regeneration can be augmented by new seed fall. After satisfactory establishment, burning should be discouraged for 8–15 years to allow seedlings to grow into larger size classes that can withstand fire damage without suffering top-kill (Stambaugh et al., 2007).

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