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Fire Survival of Longleaf Pine (*Pinus palustris*) Grass Stage Seedlings: The Role of Seedling Size, Root Collar Position, and Resprouting

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Abstract: Longleaf pine (*Pinus palustris* Mill.) forest is a well-known fire-dependent ecosystem. The historical dominance of longleaf pine in the southeast United States has been attributed to its adaptation known as the grass stage, which allows longleaf pine seedlings to survive under a frequent surface fire regime. However, factors affecting post-fire survival of grass stage seedlings are not well understood. In this study, we measured live and dead longleaf pine grass stage seedlings to quantify the role of seedling size, root collar position, and sprouting in seedling survival following a wildfire in the sandhills of South Carolina. We found that fire resulted in almost 50% mortality for longleaf pine grass stage seedlings. Fire survival rate increased with seedling size, but a size threshold for fire tolerance was not supported. Fire survival depended on the position of root collar relative to the mineral soil. Seedlings with protected root collars (i.e., buried in or at the level of mineral soil) experienced <21%, while seedlings with exposed root collars (i.e., elevated above mineral soil) suffered >90% post-fire mortality. Ability to resprout contributed to 45.6% of the total fire survival, with the small seedlings (root collar diameter (RCD) < 7.6 mm) almost exclusively depending on resprouting. Our findings had significant implications for fire management in longleaf pine ecosystems, and the current frequency of prescribed fire in sandhills might need to be lengthened to facilitate longleaf pine natural regeneration.

Keywords: fire ecology; tree regeneration; fire adaptation; seedling mortality; ecosystem restoration

1. Introduction

Longleaf pine (*Pinus palustris*) forest, including woodland and savanna, is a well-known fire-dependent ecosystem [1]. Before European settlement, there were an estimated 37 million hectares of longleaf pine forest in the southeastern United States [2,3]. The range of the longleaf pine ecosystems stretched from Virginia to Texas, mainly in Coastal Plain, but also found in the Piedmont and mountains of Alabama and Georgia [4]. Most of these longleaf pine forests were consisted of pure stands, with a distinctive structure characterized by an open canopy, sparse mid-story woody vegetation, and a well-developed herbaceous layer often dominated by grasses [5].

The historical dominance of longleaf pine in the southeast United States has been attributed to its superior ability to regenerate under a frequent (1–3 years) surface fire regime that prevailed throughout its native range [1,4,5]. To survive frequent surface burning, longleaf pine seedlings have evolved an adaptation known as the grass stage, defined as a juvenile life-history stage characterized by a height growth inhibition in which the seedling develops secondary foliage, but the shoot does not elongate [6]. Depending on site conditions and the degree of vegetation competition, the grass stage may last as few as two or more than ten years [4]. While in the grass stage, seedlings develop a large taproot [1,4], and their growth is often indicated by root-collar diameter, measured just below where needles grow [7].

How does the grass stage adaptation help longleaf pine seedlings survive fires? A synthesis from literature (e.g., [1,4,8–11]) suggests the following. Seedlings in the grass stage survive fires because the apical bud stays near the soil surface and is protected by a tuft of surrounding needles as well as by protective bud scales. During the grass stage, burning reduces vegetation competition and controls diseases, such as brown-spot needle blight (*Mycosphaeralla dearnessii* Barr), both of which could result in seedling mortality [4,8]. Seedlings in the grass stage build a carbon (C) reserve in the taproot that may be mobilized for initiating height growth. When root collar diameter approaches 25 mm (1 inch), most seedlings start to initiate height growth [4,7]. Once emerging out of the grass stage, rapid height growth quickly elevates apical meristems above the reach of surface fire, typically about 60–90 cm [9]. However, most of the above descriptions found in the literature remain speculative because they are largely based on field observations and lack of necessary data support. Recent studies provided some evidence to support the existence of a C reserve in the taproot [12] but also suggested that rapid height growth might not be a viable strategy for fire survival [13]. Therefore, there is a need for further investigation of longleaf pine fire adaptation.

Despite their well-known fire tolerance, longleaf pine seedlings in the grass stage are far from invulnerable, and high fire-induced mortality has been reported in many studies (e.g., [14–16]). During the grass stage, burning often scorches and even consumes the needles around the apical bud. As a result, some longleaf pine seedlings are killed by fire even during the grass stage. Previous studies suggested that seedling size [14,16–21] and fire behavior [16,22–25] could significantly affect fire-induced mortality of longleaf pine seedlings.

A range of root collar diameter thresholds for fire resistance has been reported, including 5.1 mm [17], 7.6 mm [8], and 13 mm [11]. Burning during the early grass stage, when root collar diameter is <7.6 mm (0.3 inches), often results in substantial mortality [15,26]. In arid and nutrient-poor soils (e.g., sites in sandhills), new seedlings may take more than four years to reach 7.6 mm in root collar diameter. Consequently, the mortality of 72% was reported in the year following a fire for seedlings of 3–4 years old in Florida sandhills [14]. For seedlings >7.6 mm in root collar diameter, fire-induced mortality was reported at less than 25% (e.g., [14,17,27]). In a recent experimental study, however, Knapp et al. [16] reported that mortality could approach 50% for seedlings with root collar diameters >15 mm under high-intensity burns. Seedling size is an important factor affecting the fire survival of grass stage seedlings, but it remains uncertain if fire survival changes continuously with the size or abruptly with size thresholds.

Previous studies have also shown that longleaf pine grass stage seedlings resprout after being cut at the ground line [1,28–30]. Stone and Stone [28] determined that sprouts arose from primary needle axillary buds above the cotyledonary level, which is located approximately at the root collar and generally occurs at or below ground level. No sprouts were observed when seedlings were cut below this point [28,29]. Farrar [30] reported that the resprouting ability of artificially severed seedlings depended on size, with the grass stage seedlings (≤18 cm tall) three times more likely to resprout than the height-growth seedlings (>18 cm but ≤137 cm tall) and no saplings >137 cm tall resprouted. Although all previous studies were conducted on cut seedlings and saplings, the strong, size-dependent resprouting ability has been speculated to give the grass stage seedlings an advantage to survive fire over those seedlings and saplings that have resumed height growth [30]. However, the contribution of resprouting to the fire survival of the grass stage seedlings has never been quantified.

Resprouting may only become important when a fire kills the apical bud but spares the dormant axillary buds in the root collar. However, any fire severe enough to kill the apical bud may also be capable of killing the dormant axillary buds in the root collar, given their physical proximity to each other. Therefore, it is likely that the survival of the dormant axillary buds in the root collar would depend on the protection from soil insulation. Although a previous study observed that seedlings with exposed root collars were about twice as susceptible to the fire-induced mortality as seedlings whose root collars were at or near the soil surface [20], no study has related fire survival from resprouting to the position of root collar relative to the surface of mineral soil.

The objective of our study was to investigate the fire-induced mortality of longleaf pine grass stage seedlings in relation to seedling size, root collar position, and resprouting. We hypothesized that (1) seedling survival during the grass stage is positively affected by the seedling size, (2) resprouting contributes significantly to post-fire seedling survival, and (3) the position of root collar in relation to mineral soil is key to seedling surviving via resprouting. To test these hypotheses, we sampled a naturally regenerated seedling population of longleaf pine after a wildfire in the sandhills of South Carolina, USA.

2. Materials and Methods

2.1. Study Site

The study site is located within the Aiken Gopher Tortoise Heritage Preserve (AGTHP, 656 ha; Latitude 33.505 and Longitude 81.413) in Aiken County, South Carolina, USA, which is part of the xeric sandhills [31]. Based on our previous study [15], most of the AGTHP, including our study site, was covered by longleaf pine stands that were planted 40 years ago. The stand basal area ranged from 10 to 16 m^2/ha. The midstory was made up of scrub shrubs dominated by oaks (*Quercus* spp.). The understory contained a diverse native herbaceous ground layer dominated by wiregrass (*Aristida stricta* Michx.) and bluestems (*Andropogon* spp.). The soils that dominate AGTHP are a mix of Lakeland, Troup, and Fuquay Series [32], characterized as deep, marine-deposited, relatively sterile, and well-drained. We identified the soil at the study site as Lakeland Series. The mean monthly temperature ranges from 8.3 °C in January and 27.1 °C in July; the mean monthly precipitation ranges from 6.5 cm in November to 12.8 cm in July, based on climate normals [33]. The studied wildfire occurred on 27 October 2013, and weather conditions reported from the nearest weather station are given in Table 1. Before this wildfire, the site was historically burned by prescribed fires with variable frequency, seasonality, and intensity, with the last burn dated back to March 2005.

Table 1. Weather conditions for the day (27 October 2013) when the studied wildfire occurred. The nearest weather station is Aiken Municipal Station, South Carolina, and the data was obtained from search historical weather station online: c.

Variable	Mean	Minimum	Maximum
Temperature (°F)	57	41	73
Humidity (%)	58	35	82
Wind speed (MPH)	5	0	10
Dew point (°F)	40	34	48
Precipitation (mm)	0	-	-

2.2. The Studied Seedling Population

Based on the time of last prescribed burn (May 2005) and the good seed year observed in fall 2006, our measured seedlings were mostly from the same cohort germinated during winter 2006 [15]. Longleaf pine is a masting species, and good seed crops would occur irregularly averaged once every 4–5 years [4]. To provide additional verification, we attempted to date grass stage seedlings based on growth rings. However, this effort was not successful, confirming that longleaf pine seedling does not form identifiable annual rings while in the grass-stage [34]. In the same plantation adjacent to our study site, seedling density was measured as about 119,000/ha in fall 2007 [15]. Due to the arid and nutrient-poor soil conditions in sandhills, longleaf pine seedlings on our study site grew slowly. After seven growing seasons, at the time of the wildfire, no seedlings had yet initiated height growth.

2.3. Data Collection

The studied wildfire only burned about two hectares of a longleaf pine forest in the AGTHP before it was controlled to protect the adjacent research plots. The fire was likely a typical low-intensity surface fire as it did not cause mortality of any canopy trees, although there was no information on the fire behavior. Sampling was conducted in May 2014, the start of the next growing season when survival, resprouting, or mortality of each seedling could be determined. Within the burn, we set up five transect areas, each of 30 m long and 0.2 m wide. We placed the first transect area at one end of the burn (20 m from the burn boundary), with the other four transects set up to best cover the entire burn evenly. All live and dead seedlings found within each transect were sampled, and their status (alive or dead) was recorded. For each live seedling, we further identified its survival mode (terminal bud survived or from resprouting); measured its root collar diameter (RCD) to the nearest 0.1 mm using a digital caliper; determined its RCD position by measuring the distance (to the nearest mm using a ruler) from the mineral soil surface to the RCD (recorded 0 if RCD at or below mineral soil). A total of 298 longleaf pine seedlings were measured.

2.4. Data Analyses

Based on field measurements, each measured seedling was assigned to a status class (live or dead), a size class (RCD < 7.6 mm, between 7.6 and 15 mm, or > 15 mm), and a root collar exposure class (exposed—root collar elevated above mineral soil or protected—root collar at or in mineral soil). For each seedling that survived the fire, it was also assigned into a mode of survival class (sprout—apical meristem killed or no sprout—apical meristem survived). The three size classes were constructed by using the minimum threshold of fire tolerance at 7.6 cm [8,26] and the median of the seedling size range (4.7 to 25.2 mm) at 15 mm. For all seedlings, the Chi-square test was used to test seedling status in relation to size and root collar exposure class. For live seedlings, the Chi-square test was also used to test survival mode in relation to size class and root collar exposure class. Analysis of variance (ANOVA) was used to test differences in RCD and root collar position between live and dead seedlings, and for live seedlings, between the two survival modes. Pearson's correlation analysis was used to examine if the RCD position was correlated to seedling size. Logistic regression was used to better visualize seedling mortality in relation to seedling size and root collar exposure. All statistical analyses were conducted using SYSTAT version 13 [35].

3. Results

A total of 298 seedlings were measured, and their root collar diameters ranged from 4.7 to 25.2 mm. Most seedlings (225 or 75.5%) were in the intermediate (7.6 mm > RCD < 15 mm) size class, and small (RCD < 7.6 mm) and large (RCD > 15 mm) size class only had 30 (10%) or 43 (14.5%) seedlings, respectively (Table 2). Of the seedlings sampled, 42.3% (126 seedlings) had their root collars exposed by elevating above the mineral soil up to 3 mm, while the remaining seedlings, 57.7% (172 seedlings), had their root collars protected by being either buried in mineral soil or stayed at the mineral soil level (Table 2). For those seedlings with root collar elevated above mineral soil, their root collar position neither differed among the three seedling size classes ($p = 0.287$) nor correlated with root collar diameter ($r = 0.138$, $p = 0.230$; Figure 1).

The wildfire resulted in significant mortality, with a little less than one-half of the sampled seedlings, 49.5% (147 seedlings), survived the fire. Among those seedlings survived the fire, 54.4% (80 seedlings) survived as non-sprouts (i.e., having their terminal buds survived the fire), while 45.6% (67 seedlings) survived as sprouts (i.e., have their terminal buds killed but resprouted from root collar).

Table 2. The number of longleaf pine seedlings and percent fire-induced mortality by root collar size classes and exposure classes. RCD = root collar diameter.

	of Seedlings	Mortality (%)
Size Class		
RCD < 7.6 mm	30	76.7%
7.6 mm > RCD < 15 mm	225	51.1%
RCD ≥ 15 mm	43	30.2%
Root Collar Exposure Class		
Exposed	126	91.3%
Protected	172	20.9%

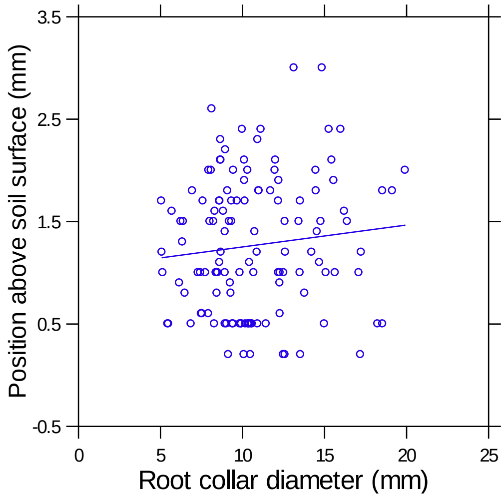

Figure 1. The root collar position above the soil surface (mm) in relation to seedling root collar diameter (mm). The locally weighted linear smoothing line is not statistically significant ($p = 0.230$). Seedlings with root collar at the soil surface or buried in soil were excluded from the analysis.

Seedling size class was significantly associated with the ability of fire survival (Chi-square = 15.3, $p < 0.001$). Mortality was observed to be 76.7%, 51.1%, and 30.2% for seedlings with RCD < 7.6 mm, between 7.6 and 15 mm, and > 15 mm, respectively (Table 1). Results of the ANOVA showed a significant difference in root collar diameter between dead and live seedlings ($p < 0.001$). Dead seedlings had root collar diameter averaged 10.54 mm, while live seedlings averaged 12.86 mm (Figure 2).

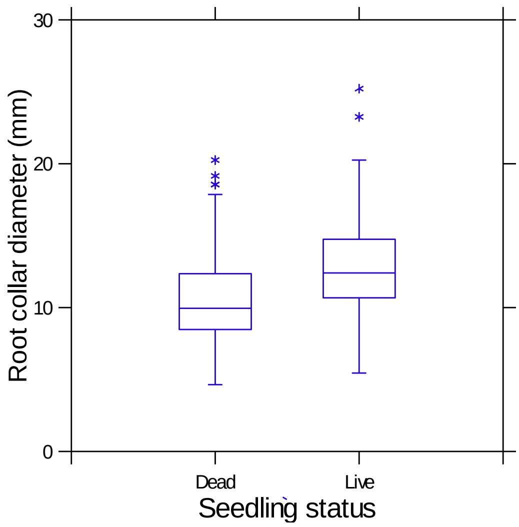

Figure 2. Root collar diameter stratified by post-fire seedling status, showing live seedlings having significantly larger pre-fire root collar diameter ($p < 0.001$).

Root collar exposure was also significantly associated with the ability of fire survival (Chi-square = 143.9, $p < 0.001$). The wildfire resulted in over 90% mortality for seedlings with an exposed root collar, but only <21% mortality for seedlings with a protected root collar (Table 2). Regardless of size class, most dead seedlings (>75%) had an exposed root collar, and a small proportion (<17%) of seedlings with an exposed root collar survived the fire (Figure 3). However, seedlings with an exposed root collar had an improved chance of survival with increased seedling size, with 0%, 6.5%, and 33.4% survival observed for seedlings with RCD < 7.6 mm, between 7.6 and 15 mm, and > 15 mm, respectively.

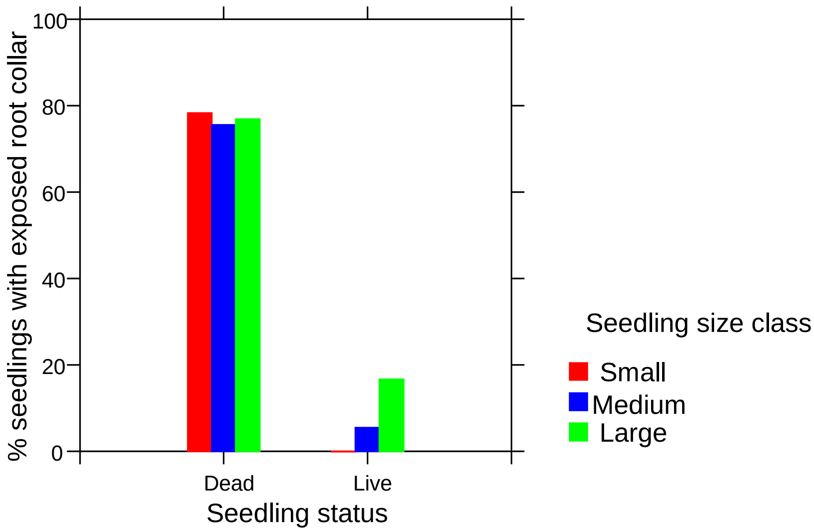

Figure 3. Percentage of seedlings with exposed root collar by size class for post-fire dead and live seedlings. Regardless of seedling size, dead seedlings were mostly with exposed root collar. Live seedlings were mostly without exposed root collar, especially for smaller seedlings.

For those seedlings that survived the fire, the mode of survival was not affected by the position of root collar (Chi-square = 0.385, $p = 0.535$), but it was significantly affected by seedling size class (Chi-square = 8.77, $p = 0.012$), with more small seedlings survived as sprouts. Of surviving seedlings, 85.7%, 58.2%, and 33.3% survived as sprouts for seedlings with RCD < 7.6 mm, between 7.6 mm and 15 mm, and > 15 mm, respectively. However, no difference in root collar diameter was detected between the two survival modes ($p = 0.116$).

A logistic regression equation was developed to predict the probability of seedling mortality using seedling size and root collar exposure ($R^2 = 0.615$, $p < 0.001$). As expected, mortality probability declined with increasing seedling size regardless of the status of root collar exposure (Figure 4). For any given seedling size, mortality probability remained much higher if their root collar was exposed compared to protected (Figure 4). Using a threshold probability of 0.9, our model achieved 74% and 91% correct prediction for dead and live seedlings, respectively.

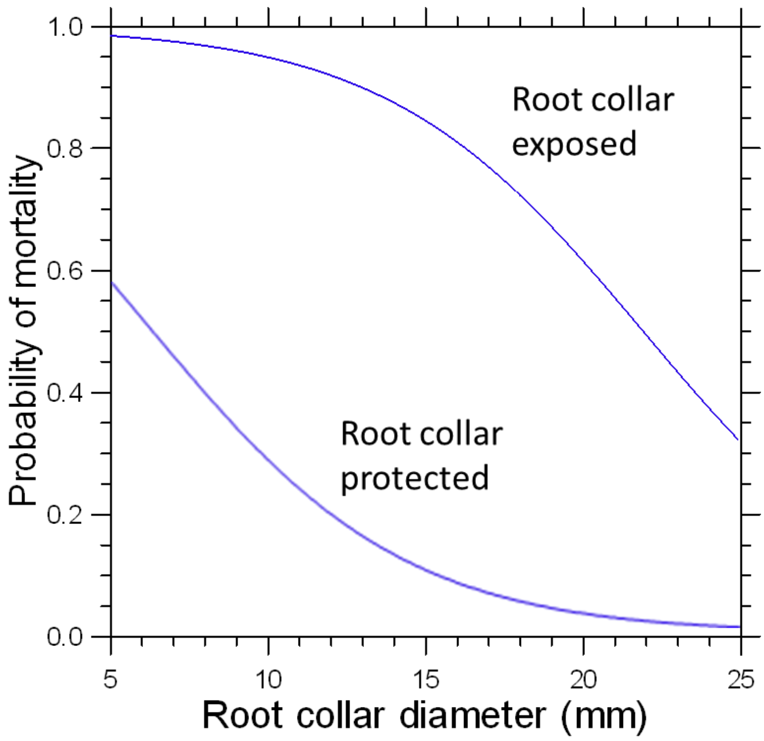

Figure 4. The logistic regression equation that predicts seedling mortality using seedling root collar diameter (RCD) and root collar exposure (RCDe; 1 = exposed; 0 = not exposed or protected): $P = 1/(1 + \exp(-(1.571 - 0.246RCD + 3.781RCDe))$. The interaction between two independent variables was not significant and thus was not included as an additional predictor.

4. Discussion

The success of longleaf pine regeneration under a frequent surface fire regime has been attributed to its adaptation of the seedling grass stage. Our results indicated that longleaf pine seedlings in the grass stage were vulnerable to fire, given that significant fire-related mortality (50.5%) was observed among those grass stage seedlings measured in our study. Indeed, previous studies have also documented the mortality of grass stage seedlings (e.g., [7,14,15]).

Previous studies have demonstrated that fire behavior (e.g., season, intensity, patchiness) significantly affected the mortality of longleaf pine grass stage seedlings (e.g., [7,25]). Consequently, we acknowledged that the absolute fire-induced mortality rate of longleaf pine seedlings was necessarily varying with fire behavior that is largely determined by the weather conditions and fuel properties during the burn. For this reason, our study, like most studies on wild or prescribed fires, might be best regarded as a case study, and the estimated fire-induced mortality rate is likely unique to the site or the fire event. However, the focus of our study was to investigate how seedling size, root collar position, and resprouting contribute to the fire survival, and the importance of each factor revealed in our study should remain valid for the species. Furthermore, given all studies on fire-induced mortality of longleaf pine seedlings were previously conducted using prescribed or experimental fires, we argued results from wildfire studies would further expand our understanding of fire effects. We noted that the wildfire in our study was probably more severe than the prescribed fires in previous studies, both because of higher fuel accumulation over eight years and the occurrence of the fire under non-prescription conditions.

4.1. Seedling Size and Fire Survival

Several studies proposed a size threshold of 0.3 in (7.6 mm) for fire tolerance, below which high fire-induced mortality would be expected [8,26]. Results from our study supported this previously proposed threshold, given that seedlings <7.6 mm in our study suffered 76.7% mortality, much higher than the overall mortality rate of 50.5%. In an early study on sites adjacent to this study, prescribed burning resulted in 98% fire-induced mortality for the same cohort of seedlings at 18-month old [15]. Although not measured, the size of those seedlings was likely much smaller than 7.6 mm in RCD. The same seedling cohort, as studied by [15], only averaged 4.9 mm with a range from 3.6 to 6.8 mm when measured at about 48 months old.

In contrast, our study showed that significant mortality could also occur to the grass stage seedlings in all size classes. It has been suggested that seedlings with RCD > 7.6 mm (0.3 in) are considered fire-tolerant [17,18], while seedlings with RCD > 25.4 mm (1 in) are ready for initiating height growth (e.g., [4,7]). Among all seedlings measured in our study, most (89.9%) fell into the RCD range between 7.6 and 25.4 mm. Previous studies indicated that seedlings within this size range suffered a mortality of less than 25% [18]. Our study, however, reported much higher mortality that averaged 47.8%, with 51.1% and 30.2% for seedlings with RCD between 7.6 mm and 15 mm and RCD > 15 mm, respectively. The higher fire-induced mortality in our study could be a result of a more intense, homogeneous burn. Although we did not measure fuel loading, our study site had fuel accumulated for eight years before the burn. Furthermore, the studied forest was planted and had a relatively uniform distribution of longleaf pine trees. With needle litter, the main fuel component, cast evenly on the ground, fire may have burned uniformly and impacted all seedlings [36], making survival due to fire escape (i.e., on the unburned spots) less likely [25]. Therefore, the mortality estimation from this study might represent the upper threshold of fire-induced mortality for seedlings of the same size. Indeed, our previous study found that, when a high-intensity experimental burn was implemented to individual seedling, fire-induced mortality for longleaf pine seedlings of the same size range as this study averaged 52.5% [16], comparable to the 50.5% mortality of this study.

Regardless the absolute mortality rate associated with each size class, which is necessarily depended on the fire behavior of each study, the trend of decreasing mortality with increasing size was clear in our data (Figure 4), which supported previous findings [7,16–18,26]. Based on the results from this study and previous studies, we concluded that size was a critical factor affecting the fire survival of longleaf pine grass stage seedlings, with fire-induced mortality rate decreasing with increasing seedling root collar size. However, grass stage seedlings of any size could be killed by fire, and the decline of mortality with size appeared to be continuous (Figure 4).

4.2. Root Collar Position and Fire Survival

Our study indicated that the position of root collar relative to the surface of mineral soil was a critical factor affecting the fire-induced mortality of longleaf pine seedlings during the grass stage. Seedlings with protected root collars (i.e., buried in or at the level of mineral soil) had a distinctive advantage over seedlings with exposed root collars (i.e., elevated above mineral soil), even though most exposed root collars were only elevated slightly (up to 3 mm) above the mineral soil. Indeed, we found that those seedlings with their root collars exposed above the mineral soil only averaged 7.5% survival. For small seedlings (RCD < 7.6 mm), none survived when the root collar was exposed (Figure 3). These results suggested that the root collar of longleaf pine seedlings during the grass stage was sensitive to fire damage due to inadequate bark protection, and insulation from mineral soil was, therefore, required. Although more frequent fires characteristic of this community type are not expected to be as severe as the fire we studied, the high vulnerability of seedlings with exposed root collars suggested that they would be eliminated by repeated burning. Therefore, it is critically important for seeds to germinate on completely exposed mineral soil because such a condition likely results in root collar either being buried or close to the level of mineral soil. Previous studies also indicated that the large winged seeds of longleaf pine might prevent good contact between seeds and soil covered by litter or vegetation [8,10]. In addition to exposing mineral soil, burning may also reduce vegetation competition so that seedlings may grow faster to gain the size advantage discussed above, although the facilitation effect of midstory oaks on the survival of young (<2 years) longleaf pine seedlings was also reported in the xeric sandhills of Florida [37].

4.3. Sprouting Ability and Fire Survival

Previous studies found that longleaf pine seedlings in the grass stage could readily resprout after top-kill by cutting [28–30]. However, the importance of resprouting to fire survival for longleaf pine grass stage seedlings has seldom been studied. Our result indicated that resprouting accounted for almost one half (45.6%) of the seedlings that survived the wildfire, and the importance of resprouting increased with decreasing seedling size. Knapp et al. [16] also reported that resprouting was more common for small seedlings, but a low resprouting rate <30% was observed in their study. Unlike wildfire or prescribed fires, the experimental fire used by Knapp et al. [16] was delivered to each seedling via a burn tool placed directly above the seedling, which likely generated more downward heating affecting the dormant primary needle axillary buds at the root collar.

Seedling survival in the smallest size class (RCD < 7.6 mm) highly depended on resprouting, with ~86% of the survived seedlings being sprouts. This result suggested that the apical meristem of small seedlings was not effectively protected against fire, and their fire survival depended on resprouting from the root collar. Therefore, unless present in the unburned patches, smaller seedlings could be effectively eliminated by repeated burning if not for their ability to resprout from the protected root collar. However, given the limited sample size of seedlings in the small size class (30 total and seven survived) in our study, additional studies with a large sample size might be needed to further validate this result. The contribution of resprouting to the survival of larger seedlings was also significant, with 58% and 30% survival being attributed to sprouting for seedlings with RCD between 7.6 and 15 mm and between 15 and 25.4 mm, respectively. Together, our results suggested an important role of resprouting in the short-term fire survival of grass stage seedlings. We speculated that the strong ability to resprout during the grass stage might be a fire-adaptive trait as saplings >1.37 m lose the ability to resprout altogether [30].

5. Conclusions and Management Implication

Our study confirmed that longleaf pine grass stage seedlings could be killed by fire, but their survival rate increased with seedling size. Longleaf pine seedlings grow extremely slow on our study site in the xeric sandhills of South Carolina, and no seedlings have yet emerged out of grass stage after seven years at the time of our study. Given the high mortality observed for small seedlings (RCD < 7.6 mm) in a previous study (98% for 18 months old seedlings; [15]) and this study (77% for 7 years old seedlings), any prescribed burning regime that is more frequent than once every 3–4 years may not be conducive to longleaf pine natural regeneration in plantations established on our study sites or other similar sites in xeric sandhills. Currently, a relatively fixed burning schedule with a short return interval has been widely used in the management of longleaf pine forests. Fire-induced mortality of longleaf pine seedlings under such burning regime would be high, and unburned patches would become important to seedling survival [25]. Given the uniformed topography in sandhills, the presence of any unburned patches is likely dependent on within-stand variation in the fuel complex [22,23]. In longleaf pine plantations, unburned patches become less likely because planted trees are regularly spaced and provide continuous coverage of dead needles [25,36]. Therefore, we recommended a more flexible burning schedule with a variable return interval in longleaf pine plantations in sandhills to ensure the success of natural longleaf pine regeneration. For example, a very frequent burn (e.g., every 2 years) should be implemented to expose mineral soil for seed germination. Once new seedlings establish after a good seed year, avoiding burn for at least 4–5 years would allow seedlings to develop into a large size for better fire survival.

Our results indicated that having the root collar below or at the level of mineral soil was critically important to the fire survival of longleaf pine seedlings. Therefore, exposed mineral soil seedbeds are necessary for the success of longleaf pine natural regeneration. Considering the irregular seed production and the large seed wings of longleaf pine, conducting a prescribed fire before the seed fall during a good seed year becomes a necessary management practice to ensure the regeneration success, both in terms of initial germination success and subsequent fire survival. Our results also supported the current recommendation by the Longleaf Alliance, which stated"plant bare-root seedlings so that the terminal bud is at or slightly below the soil surface" [38].

The ability to resprout contributes significantly to the fire survival of longleaf pine grass stage seedlings, especially for small seedlings with RCD < 7.6 mm. However, the future growth of these resprouted seedlings is likely being set back significantly because of the cost of repairing lost needles [16,39], which could prolong the grass stage even more. With the time for seedlings to stay in the grass stage increasing, seedling vigor is likely to decline because of vegetation competition and brown-spot needle blight [8]. Therefore, the viability of those resprouted seedlings as an important regeneration source remains uncertain. Additional research is needed to monitor the vigor and development through time for those seedlings survived fire by resprouting.

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