Fire Ecology

ORIGINAL RESEARCH

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Direct and indirect effects of fire on germination of shortleaf pine seeds

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Abstract

Background Shortleaf pine is a fire-adapted tree species, and prescribed fire is commonly used to increase its regeneration success, improve wildlife habitat, and reach conservation objectives associated with open forest ecosystems. We studied direct effects of heat and smoke on shortleaf pine germination in a greenhouse study and effects of season of burning on the number of new germinants in a field study. Improved understanding of fire effects on shortleaf pine seed and regeneration success can help refine burn prescriptions to better meet specific management objectives.

Results Temperatures ≥ 120 °C eliminated germination of shortleaf pine seeds in a greenhouse trial, and exposure of seeds to 60 °C resulted in no reduction in germination compared to the unheated control regardless of duration of exposure. At 80 °C, duration of heat exposure mattered, with exposure for 10 min reducing germination compared to unheated controls. Smoke exposure had no effect on germination. A field experiment showed that fall burns (prior to seedfall) resulted in greater initial germinant counts than early spring burns (after seedfall but before germination) or unburned controls, which both resulted in greater initial germinant counts than late spring burns (after germination).

Conclusions Season of prescribed burning can affect the success of shortleaf pine germination. Late spring burning resulted in high mortality of young germinants. Burning in early spring likely resulted in direct damage to some seeds due to heating but may have also had indirect benefit by exposing mineral soil. Fall burning, before the dispersal of shortleaf pine seed, yielded the highest germinant count and is recommended if improving natural regeneration from seed is the primary objective.

Keywords Fire ecology, Germination, Heat, Natural regeneration, Shortleaf pine, Smoke

Resumen

Antecedentes El pino amarillo o pino de hoja corta, es un árbol adaptado al fuego, y las quemas prescritas son comúnmente usadas para incrementar el éxito en su regeneración, mejorar el hábitat para la fauna silvestre, y conseguir objetivos de conservación asociados con ecosistemas forestales abiertos. Estudiamos los efectos directos del calor y del humo en la germinación del pino de hoja corta en condiciones de invernadero y los efectos de la estación de quema en nuevas semillas germinantes en condiciones de campo. Una mejora en el conocimiento de los efectos del fuego en la germinación de semillas de pino de hoja corta y del éxito en la regeneración pude refinar las prescripciones de quema para lograr mejorar los objetivos específicos de manejo.

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Resultados Temperaturas ≥ 120 °C eliminaron la germinación de semillas de pino de hoja corta en el ensayo en vivero, y la exposición de semillas a 60 °C no resultó en una reducción en la germinación comparada con semillas no tratadas (control), independientemente de la duración del tempo de exposición. A 80 °C, la duración de la exposición al calor tuvo efectos, como que la exposición al calor por 10 minutos redujo la germinación comparada con el control no expuesto al calor. La exposición al humo no tuvo efectos sobre la germinación. El experimento de campo mostró que las quemas de otoño (previas a la lluvia de semillas) resultaron en un conteo de mayor germinación inicial que las quemas de primavera temprana (luego de la lluvia de semillas, pero antes de la germinación) o en parcelas no quemadas, las que resultaron en mayores conteos de geminación iniciales que luego de las quemas en la primavera tardía (después de la germinación.

Conclusiones La estación de quemas prescritas puede afectar el éxito en la germinación del pino de hoja corta. Las quemas en la primavera tardía resultaron en una alta mortalidad de plántulas recién emergidas. Las quemas en la primavera temprana resultaron en daños directos sobre algunas semillas debido al calentamiento, pero también se podrían haber beneficiado indirectamente al exponer el suelo mineral. Las quemas de otoño, antes de la dispersión de las semillas del pino de hoja corta, alcanzaron los números de germinación más altos, y son las recomendadas si la mejora en la regeneración natural por semilla es el principal objetivo.

Background

Fire is an important ecosystem process that affects forest structure, composition, and function. In the eastern United States, changes in forest ecosystems over the past century, including increased tree densities and shifts to more fire-sensitive, mesic species, have been attributed, in part, to changes in fire regimes (Nowacki and Abrams 2008; Hanberry et al. 2020). The effects of fire on forest composition may be related to several factors, such as differential rates of removal through mortality (Huddle and Pallardy 1996) or impacts on the success of tree establishment during regeneration (Brose 2014). Tree regeneration is a complicated process that includes several stages (seed production; germination; seedling survival; sustained growth) (Dey et al. 2019; Grubb 2021). Failure at any of these stages can prevent regeneration. Following seed production, fire may affect regeneration outcomes through (1) direct effects on seeds, such as stimulating or inhibiting germination through heat or smoke; (2) effects on seedbed conditions; and (3) reduced competition for developing seedlings. As a result, successfully incorporating fire into regeneration prescriptions requires an understanding of the prevailing fire regime's effects on each stage of the regeneration process (Arthur et al. 2012).

In the eastern United States, shortleaf pine (*Pinus echinata*) occurs in forests and woodlands adapted to frequent surface fires, but such forests have greatly decreased in abundance and extent over the past few centuries. Before European colonization, shortleaf pine covered approximately 300,000 km^2 (30,000,000 ha) (Anderson et al. 2016) but has been reduced to approximately 25,000 km^2 (2,500,000 ha) (Oswalt al., 2012) or only 8% of historic abundance. This precipitous decline was primarily caused by overharvesting followed by widespread and effective fire exclusion efforts that facilitated conversion to hardwood species in many harvested areas. At present, most areas with mature shortleaf pine remaining in the overstory lack sufficient shortleaf pine seedlings and saplings to naturally regenerate (Moser et al. 2007; Vickers et al. 2019), even following timber harvests that increase understory light levels (Olson et al. 2017). Given the historic importance of fire in shortleaf pine ecosystems, prescribed burning is commonly recommended for improving regeneration success. Shortleaf pine is capable of resprouting following topkill, a trait that is important to its success in ecosystems with relatively frequent fire regimes, and several studies examine the sprouting response of shortleaf pine to prescribed burning (Dey and Hartman 2005; Lilly et al. 2012; Clabo and Clatterbuck 2019). In areas currently lacking shortleaf pine advance reproduction, initial establishment of regeneration from seed appears to be an important bottleneck in the regeneration process, yet few studies examine the effects of prescribed burning on germination of shortleaf pine seeds.

Germination of shortleaf pine seed requires contact with mineral soil, and the accumulation of leaf litter on the forest floor reduces seedling establishment (Grano 1949; Baker 1992). In the Missouri Ozarks, Stambaugh and Muzika (2007) found that the number of regenerating shortleaf pine seedlings decreased as litter depth increased from 2.5 to 6 cm, and no shortleaf pine seedlings were found when litter depth exceeded 6 cm. Prescribed burning can improve seedbed conditions by removing accumulated litter, thereby increasing the abundance of shortleaf pine seedlings. However, no information is available about possible direct effects of heat or smoke on shortleaf pine germination. Shortleaf pine primarily disperses seeds in November and

December (Bramlett 1965; Cain 1991), and seeds are then cold stratified during the winter and germinate in early spring (Lawson 1990). Therefore, prescribed burns applied before seedfall would reduce leaf litter without direct effects on the seed, whereas prescribed burns during the winter and spring dormant seasons may have additional, direct effects on seeds.

In fire-adapted ecosystems, the direct effects of fire on plant seeds vary, with germination of some species triggered by fire-related cues. This may be caused by exposure to heat, as for bay cedar (*Guazuma ulmifolia*) (Dayamba et al. 2008), red acacia (*Acacia seyal*), and multiple *Desmodium* species in Ethiopian savannas (Gashaw and Michelsen, 2002), or by exposure to smoke, as seen in species of *Cistaceae*, *Poaceae*, *Fabaceae*, and *Asteraceae* in Spanish woodlands (Pérez-Fernández and Rodríguez-Echeverría, 2003). Though pine seeds are not commonly stimulated to germinate by smoke exposure, the seeds of Douglas pine (*Pinus douglasiana*) found in Mexican montane forests have been shown to be (Zuloaga-Aguilar et al. 2011). However, the opposite type of effect also occurs, as heat can damage seeds and reduce germination. This has been observed for common oak species found within the range of shortleaf pine across the eastern United States, including white oak (*Quercus alba*), Shumard oak (*Q. shumardii*), and northern red oak (*Q. rubra*) acorns (Greenberg et al. 2012, Nation et al. 2021), as well as for several Mediterranean pines (Escudero et al. 1999). Direct effects of fire on shortleaf pine seeds remain unknown.

This study was designed to improve the understanding of the fire ecology of shortleaf pine regeneration and had two objectives. The first objective was to determine the direct effects of heat and smoke exposure on shortleaf pine seeds through a greenhouse experiment. We hypothesized that smoke and heat exposure could stimulate greater germination of shortleaf pine seeds as is seen in some other fire-adapted species, but there would be a heat exposure threshold at which seeds are damaged and germination decreased, as seen in Mediterranean pines. The second objective was to determine the effect the time of year of prescribed burning had on the germination of shortleaf pine seeds in the field. We hypothesized that burning in the fall, before seed dispersal, would increase germination compared to unburned controls by improving the seedbed, while burning in the late spring would kill young germinants. Burning in the early spring, after seeds had fallen, was of particular interest. We expected burning to improve the seedbed, but it was unknown if either heat/smoke stimulation effects or heat damage would result in a net increase or decrease in germinants. This combination of field and greenhouse techniques will help explain both practical and mechanistic aspects of shortleaf pine germination in relation to burning regimes.

Methods

Greenhouse heat and smoke exposure study

Experimental design

The greenhouse study was designed to test effects of heat exposure and smoke exposure on germination of shortleaf pine seeds. The study included heat exposure treatments that combined five temperatures (60, 80, 120, 200, and 270 °C) with each of three durations (1, 5, and 10 min). It also included an untreated control, for 16 total temperature and time combinations. We chose 60 °C as the lowest temperature because it is commonly associated with the initial point of tissue necrosis (Stephan et al. 2010). The range of temperature and duration combinations is similar to that used in other published studies (e.g., Escudero et al. 1999; Wiggers et al. 2017) and expected to be representative of the conditions created by prescribed burns in the region (e.g., Lilly et al. 2012; Dey and Hartman 2005). These heat exposure treatments were applied by placing shortleaf pine seeds in a Yamato DKN-602C (Yamato Scientific American Inc., Santa Clara CA, USA) oven for each specific combination of temperature and time. Smoke exposure treatments were applied separately and included four treatments: an untreated control and smoke exposure (without heat) for 5, 10, and 90 min. The smoke was generated using an electric portable smoke infuser (manufactured by TMK-EFFC), designed for flavoring food without cooking it. Shortleaf pine needles gathered from local stands were used as the fuel for the smoker, and the smoke infused into sealed containers of seeds via rubber tubing. The heat exposure or smoke treatments were each applied to sets of 30 shortleaf pine seeds, replicated three times per treatment (90 total seeds within each treatment) on 17–19 March 2021. The seeds used were produced from Missouri trees grown in a seed orchard on the Ouachita National Forest in Arkansas. They were collected in 1986 and stored in a −15.5 °C freezer since then at the George O. White Nursery, managed by Missouri Department of Conservation in Licking, MO.

After treatment, the seeds were sown in 98 cell propagation trays in a mixture of 40% peat, 40% vermiculite, and 20% perlite (Pile et al. 2017). One seed was sown within each cell on 19 March 2021. The timing of this experiment is consistent with typical timing of shortleaf pine germination. Treatments were randomly assigned to trays, and each tray contained three treatments with the exception that no tray could have two of the same treatment. The propagation trays were kept in greenhouses on the University of Missouri campus, and the trays were watered daily.

Data collection and analysis

For 40 days following planting, trays were monitored for germination daily, and cells with live germinants were recorded. The number of total germinants peaked on day 30, and only one seed germinated after day 35, so the experiment was ended on day 40. A small number of germinants died during the 40 days, and these were still counted as having germinated. The probability of a seed germinating by the end of the 40-day sampling period was modeled using logistic regression, with a generalized linear mixed model that used a binomial distribution and logit link function. The binary response of germination status (yes or no) was the response variable, and the heat exposure and smoke exposure treatments, respectively, were the independent variables in separate models. Each model included random terms to specify the replicate experimental unit (set of 30 seeds to which treatments were applied) and the planting tray used in the greenhouse. For significant effects of heat exposure or smoke exposure, pair-wise comparisons among treatment levels were made using Tukey's HSD adjustment for multiple comparisons. For all models, differences were assumed statistically significant when $p < 0.05$.

Field burn timing study

Experimental design

We used a randomized complete block design, with four treatments applied in each of four shortleaf pine plantations (i.e., blocks). Treatments included a control (no fire), a fall burn (applied before seed dispersal), an early spring burn (applied following seed dispersal but before germination), and a late spring burn (applied after germination). The study plots were 0.01-ha rectangles with dimensions of 8.35 m × 17.25 m. Within a block, the study treatments were randomly assigned to the plots.

Study site

The field study was conducted at the Baskett Wildlife Research and Education Center (BWREC), a University of Missouri property located approximately 25 km south of campus (Table 1). The land where BWREC currently exists was privately farmed, with much of the area cleared of trees before consolidation under federal ownership in the 1930s. Since that time, the area has been managed by the University of Missouri. Agricultural reclamation practices included widespread tree planting in the late 1930s and early 1940s, including several plantations of shortleaf pine. There are no records of management activities (thinning, prescribed burning, etc.) in the plantations after the time of planting. The average temperature in Boone County, MO, from 1991 to 2021 was 18 °C, and the average annual precipitation was 1075 mm (NOAA, 2021). The soils of the study were mapped as Weller silt loam, with 5–9% slopes. The Weller soils are deep, moderately well-drained, and formed of loess (Soil Survey Staff, 2021).

Treatment application and seeding

Study treatments were applied to each plot by establishing fire breaks around plot boundaries, so that each plot was a burn unit. The fall burns took place on 5 November 2020, the early spring burns on 6 March 2021, and the late spring burns on 1 May 2021. All burns were conducted in the afternoon hours. Given the small size of the plots, ring ignitions were used for all plots, with spot fires ignited at the center of plots during the fall burns. Flame lengths were visually estimated during the burns to be 30 cm, with flame lengths rarely exceeding 50 cm. Weather conditions during the burns are summarized in Table 2.

Shortleaf pine seeds (of the same origin as in the greenhouse experiment) were sown by hand across all plots on 11 November 2020, at a rate of ~74,000 seeds/ha. Though shortleaf pine was present in the overstories of these stands, all study plots were seeded because of the variation in seed production annually and to ensure adequate sample sizes. The seeding rate was determined to be sufficient based on a 10-year study in Oklahoma, Arkansas,

Table 1 Characteristics of the four shortleaf pine stands used in the field study. All litter collections occurred following fall burns and prior to spring burns; "burned litter" was taken from the fall burn treatment plot in each block, and other litter samples were averaged across the three other treatment plots

Variable	Block 1	Block 2	Block 3	Block 4	Average
Basal area (m^2/ha)	49.1	49.3	43.9	59.6	50.5
Density (trees/ha)	1001	420	803	988	803
Quadratic mean diameter (cm)	24.8	38.3	26.2	27.5	29.2
Litter (dry g/m^2)	978.3	1018.7	1185.2	1136.7	1079.7
Burned litter (dry g/m^2)	962.0	610.0	667.8	827.9	766.9
Establishment year	1942	1939	1942	1940	

Table 2 Summary of prescribed burn conditions, with weather conditions (air temperature, relative humidity, wind speed, and wind direction) from data collected at the Columbia-Bradford Research and Extension Center weather station, located 16 km from the study site. Flame lengths were estimated in the field during the burns

Treatment	Date	Burn time (start/end)	Air temp (°C)	Relative humidity (%)	Wind speed (m/s)	Wind direction (degrees)	Flame length (cm)
Fall	5 November 2020	13:00	21.2	44	2	197	30
		17:00	20.2	48	1	178	
Early spring	6 March 2021	12:00	10.8	29	3	222	30
		16:00	14.0	36	2	199	
Late spring	1 May 2021	12:00	24.1	42	6	226	30
		16:00	25.4	34	6	214	

and Missouri, in which shortleaf pine produced a range of 5000–1,846,000 seeds/ha during the study years, with most years resulting in at least 66,700 seeds/ha, and no two consecutive years with less than 79,000 seeds/ha (Shelton and Wittwer 1996).

Data collection and analysis

In late May 2021, plots were surveyed for germination. In each plot, three parallel transects were established across the length of the plot (17.25 m), and all germinants within 0.38 m on each side of the transect were counted. The total sampling area was 40.5 m^2 in each plot. Natural regeneration was assessed outside the seeded plots, using three non-parallel transects of equal length within each of the stands. All transects were re-surveyed in October 2021.

The abundance of shortleaf pine germinants (number per hectare) at the start of the growing season (May sampling) and at the end of the growing season (October sampling) was modeled using a generalized linear mixed model with a repeated measures design. Burn treatment, sampling period, and the interaction of burn treatment and sampling period were fixed effects. Stand (i.e., block) was included as a random effect, and the repeated measures structure was specified with a random term with a first-order autoregressive covariance structure for the experimental unit measured in each sampling period. For significant fixed effects, pair-wise comparisons were tested using Tukey's HSD adjustment. For all models, differences were assumed statistically significant when $p < 0.05$. All analyses were conducted using SAS 9.4 software (SAS Institute, Cary, NC, USA).

Results

Greenhouse heat and smoke exposure study

Germination began 12 days after planting and leveled off approximately 20 days after planting (Fig. 1). The patterns of germination through time were generally similar

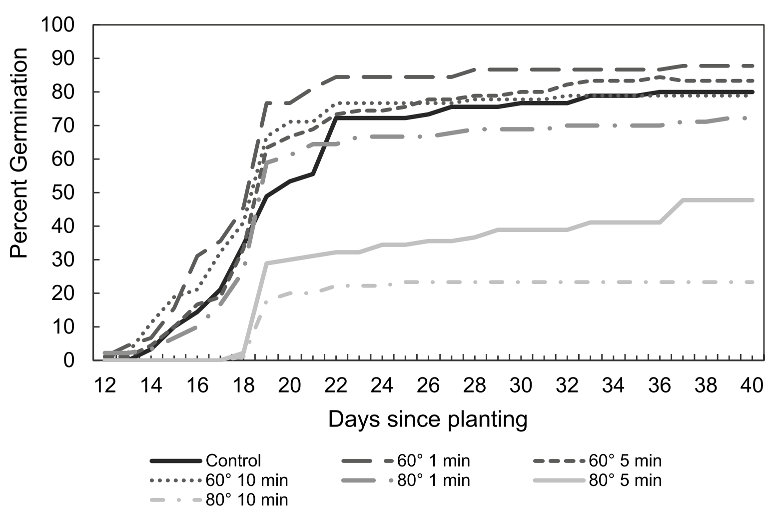

Fig. 1 Cumulative percent germination through time for shortleaf pine seeds following exposure to various temperatures for 1, 5, or 10 min. No germination occurred for any treatment with temperature ≥ 120 °C

among treatments, with the exception that the 80 °C treatments with 5- and 10-min durations had later initiation of germination (day 18). After the 40-day monitoring period, the germination rate for the untreated shortleaf pine seeds was 81.1% (Fig. 2), and the heat exposure treatments had significant effects on germination ($P<0.001$). No seeds germinated when exposed to 120 °C or higher, regardless of the duration, and therefore treatments greater than 80 °C were excluded from the model. Seeds exposed to 60 °C did not differ significantly from controls, regardless of the duration of exposure. For seeds exposed to 80 °C, the duration of exposure was important. Seeds with exposure to 80 °C for 1 min and 5 min did not significantly differ from controls, but seeds exposed to 80 °C for 10 min had significantly lower germination than all other treatments except for 80 °C for 5 min, which were also low (Fig. 2).

There were no significant effects of smoke exposure ($P=0.814$). The model estimated 79.9% germination for the controls and 79.5%, 82.7%, and 75.5% germination for 5 min, 10 min, and 90 min of smoke exposure, respectively.

Field burn timing study

There was a significant interaction between burn treatment and sampling period ($P<0.001$), with a significant effect of the burn treatments on the number of new germinants in the May sampling ($P<0.001$) but no effect of the burn treatments on the number of new germinants in the October sampling ($P=0.126$). For the May sampling, the fall burn resulted in significantly more germinants than all other treatments (Fig. 3). The abundance of germinants in the early spring burn treatment did not differ from the control ($P=0.983$), and the late spring burn had significantly fewer germinants than all other treatments ($P=0.011$ for the control comparison, $P<0.001$ for the fall comparison, $P=0.002$ for the early spring comparison). From the May sampling to the October sampling, the number of germinants significantly decreased for all burn treatments ($P<0.001$) other than the late spring burn treatment, for which there was no significant difference ($P=0.339$).

The unseeded, unburned areas had approximately 1606 shortleaf pine germinants per hectare when surveyed in May and 371 germinants per hectare when surveyed in October. Comparison to the seeded, unburned areas (the control treatment), which had 10,000 germinants per hectare in the May survey and the 988 germinants per hectare in the October survey (Fig. 3), suggests that contribution from natural seedfall was relatively low during the study year.

Discussion

This study demonstrates the potential for prescribed burning to have both direct and indirect effects on the germination success of shortleaf pine seeds. Exposure of seeds to temperatures of 80 °C or greater can partially or completely inhibit shortleaf pine germination. We found that burning before seed dispersal increased germination in the field, an indirect effect of fire that was likely due to combustion of forest floor material and exposure of mineral soil. Burning following dispersal but before

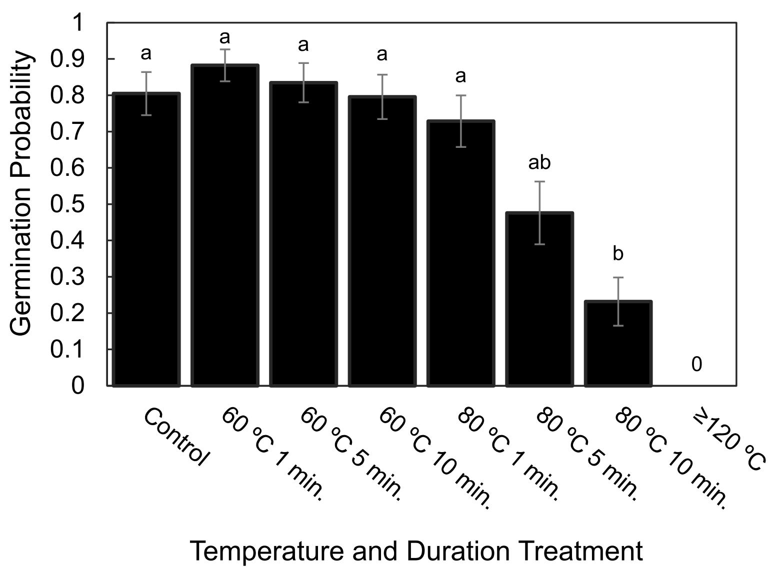

Fig. 2 Germination probability (modeled mean ± standard error) of shortleaf pine seeds by heat exposure treatment. Different letters represent Tukey -adjusted significant differences between pairwise comparisons. No germination occurred for any treatment with temperature ≥ 120 °C

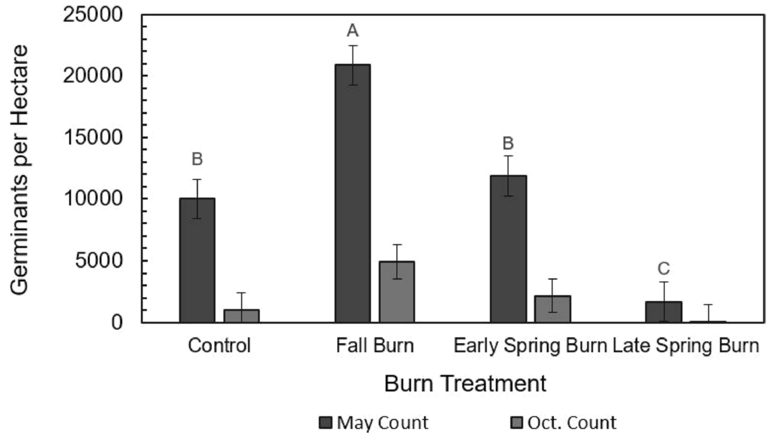

Fig. 3 Least squared means (± standard error) of germinant counts across four shortleaf pine stands by burn treatment for May (dark gray) and October (light gray) sampling periods. Different letters represent significant differences between treatments within the May sampling period

germination, which would represent the period during much of the contemporary dormant season prescribed burn window in the region, resulted in germinant abundance similar to the unburned control. It is possible this treatment was a balance of direct effects of heat exposure that reduced germination for affected seeds with the indirect effects of improved germination sites due to forest floor removal. We found poor success when burning occurred following germination, likely due to direct effects of fire on first-year seedling mortality.

Although other plant species are stimulated by exposure to heat (Wiggers et al. 2017; Herranz et al. 1998) and heat in combination with smoke (Singh and Raizada 2010), pine seed germination has generally been shown to be suppressed by heating. Seeds of seven Spanish pine species, Aleppo pine (*Pinus halepensis*), stone pine (*P. pinea*), maritime pine (*P. pinaster*), mountain pine (*P. uncinata*), black pine (*P. nigra*), Scots pine (*P. sylvestris*), and Canary Island pine (*P. canariensis*) were exposed to temperatures between 50 and 150 °C for 1–15 min (Escudero et al. 1999). Germination was decreased rather than stimulated by heat exposure for all species, although the thresholds varied among species. For the least heat-tolerant species, Aleppo pine, germination suppression began at 70 °C, and for the most tolerant species, maritime pine, germination was significantly lower only at 130 °C (Escudero et al. 1999). In a different study, Turkish red pine (*P. brutia*) showed no effect of exposure to temperatures up to 130 °C, at which point the duration of exposure became more important than increased temperature up to 170 °C (Boydak and Caliskan 2016).

While the results of our greenhouse study show that heat exposure can reduce germination of shortleaf pine seed, we were not able to quantify the level of heat exposure experienced by seeds in our field study. The position of the seeds within the leaf litter profile may affect their vulnerability to heat exposure and germination success. This has been experimentally tested for acorns; Greenberg et al. (2012) placed northern red oak and white oak acorns on the leaf litter surface, in the duff layer, or in the mineral soil during winter prescribed burns and then germinated the acorns in a greenhouse. They found that for all acorns on the litter surface germination rates decreased with increasing fire temperature, but acorns in the duff layer and mineral soil were not generally affected. For shortleaf pine seedlings, it is possible that the timing of prescribed burning may interact with the position of seeds in the litter to affect heat exposure experienced by seeds. Boggs and Wittwer (1993) suggested that shortleaf pine seeds move from the surface of the litter layer to the mineral soil in the months following dispersal. Therefore, a burn in December or January might damage more seeds than an early spring burn (e.g., the March burn in our study), because the seeds might be closer to the litter surface in the earlier burn.

For some species, including a few tree species, smoke stimulates germination (see Brown and van Staden 1997 for review). Scientists have isolated the compound butenolide 3-methyl-2H-furo[2,3-c]pyran-2-one, now referred to as karrikinolide (Dixon et al. 2009), as the main component within smoke that stimulates germination (Flematti et al. 2004). In previous studies, seeds have been experimentally germinated in aqueous smoke solution (Todorović et al. 2005), on smoked filter papers (Singh and Raizada 2010), with direct application of the butanolide compound (Kulkarni et al. 2007), and with direct smoke application as done in this study. Other examples of direct smoke application include pumping smoke from burning material in a 130 L drum through a tube into a sealed plastic tent using bellows (De Lange and Boucher 1990) or using a beekeeper's smoker (Baxter et al. 1995). We found no effects of direct smoke exposure on shortleaf pine seeds in our study. Similarly, applying smoke to seeds of Scots pine, black pine, mountain pine, and maritime pine for 5 to 20 min had no effect on germination (Reyes and Casal 2006). However, Douglas pine (*Pinus douglasiana*) germination was increased with application of an aqueous smoke solution (Zuloaga-Aguilar et al. 2011).

Collectively, our results and those of past studies indicate that rather than stimulation from heat or smoke, pines use other adaptive strategies suited for specific fire regimes (Schwilk and Ackerly 2001; Keeley 2012). Historically, shortleaf pine ecosystems were associated with frequent, low- to mixed-severity fire regimes. Prior to European settlement, mean fire return intervals in shortleaf pine stands have been reported to be around 5 years in the Cumberland Plateau (Stambaugh et al. 2020), around 5 to 7 years in the Ouachita Mountains (Flatley et al. 2023), and ranging from range from 4 to 18 years in the Missouri Ozarks (Guyette and Cutter 1997; Batek et al. 1999). While low severity fires were most common, periods of drought were often associated with extensive fire activity, suggesting fires of greater severity occurred every few decades (Guyette et al. 2006). Shortleaf pine has traits associated with frequent surface fire regimes, such as thick bark, highly flammable litter, and sprouting from the basal crook of seedlings (Mattoon 1915; Bradley et al. 2016; Shearman and Varner 2021; Varner et al. 2022). Sprouting allows seedlings to persist following low-intensity surface fire (Clabo and Clatterbuck 2019), providing opportunity for recruitment when conditions are favorable. However, shortleaf pine has also been recognized as being adapted to stand-replacement fires (Keeley and Zedler 1998), suggesting regeneration from seed following disturbance of the forest floor as another stand establishment pathway for shortleaf pine.

In fire history studies, the majority of recorded fire scars occurred during dormancy, a period that encompasses late fall through early spring (Guyette et al. 2006; Stambaugh et al. 2020; Flatley et al. 2023) and thus includes both our fall and early spring treatment. Consequently, it is difficult to infer the historical importance of burning prior to seed dispersal for success of naturally regenerated shortleaf pine. However, historical accounts indicate that fall burning was practiced by Native Americans (Flatley et al. 2023) and was likely more common than with contemporary prescribed burning, which typically occurs in February to March in the study region.

Our results support prescribed burning in the fall as an effective site preparation treatment that increases the number of seedlings established per sound seeds produced (or seeded), also referred to as seedling percent (Yocom and Lawson 1977; Cain 1991; Shelton 1995). Seedling percents estimated for our field study, from the May and October sampling, respectively, were as follows: control—13.5%, 1.3%; fall burn—28.2%, 6.7%; early spring burn—16.0%, 2.9%; late spring burn—2.3%, 0.1%. Boggs and Wittwer (1993) observed seedling percents (measured in December for seeds sown in January) of 4.0%, 1.9%, and 1.0% in areas that had been treated the previous July with a hot burn, a medium burn, or no burn respectively. Yocom and Lawson (1977) reported 3-year seedling percents for naturally regenerated shortleaf pine of 0.42% for unburned, unlogged areas, 0.98% in both burned only and logged only areas, and 1.29% in areas both logged and burned. By improving seedbed conditions, prescribed burning can be a tool for increasing the number of shortleaf pine germinants despite the interannual variability in shortleaf pine seed production (Bramlett 1965; Stephenson 1963; Wittwer and Shelton 2004).

While our results support the use of prescribed burning in the fall for improving establishment of shortleaf pine, germination is just one part of the regeneration process. The low seedling percents reported in previous studies (Yocom and Lawson 1977; Boggs and Wittwer 1993), along with the observed attrition of seedlings between the May and October sampling in our field study, suggest that low survival of new shortleaf pine germinants in the first year may be an additional bottleneck for regeneration success. Our study sites had high stand densities, likely reducing first-year survival due to shade and competition. More open conditions characteristic of shortleaf pine woodlands may improve survival for new germinants, possibly reducing the importance of fall burning as site preparation for seedling establishment. In addition, local variability in fuels and fire behavior can have important implications for fire effects on litter consumption and heat exposure to seeds. Our field study used low-intensity burns that may have generally dampened the effects of the burns, on both the reduction of the forest floor in the fall burn (the indirect positive effect) and the heat exposure to shortleaf pine seeds in the early spring burn (the direct negative effect).

Conclusions

Our study provides evidence that prescribed burning can be used to increase the number of shortleaf pine germinants, but the seasonality of the burns can affect the outcomes. Fall burning, before seed dispersal, maximized the number of new germinants during the next growing season by preparing the seedbed but avoiding direct damage to seeds through heat exposure. Burning during the winter or early spring, after seed dispersal, is likely to reduce viable seed through heat exposure but also consume the litter layer to improve the seedbed. The burns in our study were done in a small area and were low-intensity, so higher intensity burns in early spring could result in more damage to seeds. Late spring burns, following germination, drastically reduced regeneration success. Forest managers specifically interested in shortleaf pine natural regeneration can use this information to better time prescribed burning to increase shortleaf pine germination from seed.

Acknowledgements
We thank Drew Anderson, Abby Huffman, Ian Vaughan, Trystan Harpold, Lance Vickers, Lauren Pile Knapp, and George Jensen for assistance with the prescribed burns. Sloane Scott, Aaron Fujiki, and Taylor Hurley assisted with field germinant counts, and Michelle Brooks was helpful with setting up the greenhouse.

Authors' contributions
HF and BK designed the experiment, analyzed the data, and wrote the manuscript, MS contributed to smoke element of study design. DD, JK, GE, and MS provided technical advice throughout the study, and all authors provided editorial review on manuscript drafts.

Funding
This research was funded by the USDA Forest Service, Northern Research Station, under Task Agreement 17-JV-11242311–032 within the Great Rivers Cooperative Ecosystem Studies Unit JVA 13-JV-11242311–071.

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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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Received: 23 May 2023 Accepted: 21 August 2023
Published online: 19 September 2023

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