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Acorn viability following prescribed fire in upland hardwood forests

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ABSTRACT

Restoration of structure and function of mixed-oak (*Quercus* spp.) forests is a focal issue of forest land managers in the eastern United States due to widespread regeneration failure and poor overstory recruitment of oaks, particularly on productive sites. Prescribed fire is increasingly used as a tool in oak ecosystem restoration, with the goal of reducing competition, and creating light and seedbed conditions conducive to germination and growth of oak seedlings. Yet, oak seedling establishment is dependent on the presence of viable acorns, which may be vulnerable to prescribed fire. We assessed the effect of prescribed burning and fire temperature on the viability of white oak and northern red oak acorns placed on the leaf litter surface, in the duff, or in the mineral soil during five winter prescribed burns in southern Appalachian upland hardwood forests. Fire temperatures varied among acorn plots, ranging from <79 to <371 °C. After the burns, acorns were planted in trays with water-saturated vermiculite, exposed to 14 continuous hours of light daily, and maintained at 27 °C on germination beds in a greenhouse. After three weeks we recorded the proportion of acorns germinating and the proportion of germinants with shoots. Our study indicated that patchy, low-intensity dormant season prescribed fire in upland hardwood forests reduced viability of white oak and northern red oak acorns located on the leaf litter surface, but did not generally affect acorns in the duff or mineral soil. Germination rates of both northern red oak and white oak acorns on the leaf litter surface decreased with increasing fire temperature. Shoot production by northern red oak germinants from acorns on the leaf litter surface (and less so in the duff), also decreased with increasing fire temperature. Acorns of both species on the leaf litter surface burned at temperatures $\geqslant 204$ °C showed high mortality levels, with mortality virtually 100% at temperatures $\geqslant 260$ °C. Fall burns, especially after a heavy acorn crop, could result in high acorn mortality, potentially impacting oak regeneration from seedlings for many years given erratic acorn production patterns among years and species. Frequent burning that reduces litter and duff depth could compromise availability of 'safe sites' where acorns are insulated from high fire temperatures. When oak ecosystem restoration is a goal, land managers should consider the timing and size of acorn crops, as well as the forest floor condition when determining the timing and frequency of prescribed burning.

1. Introduction

Restoration of structure and function of mixed-oak (*Quercus* spp.) forests is a focal issue of forest land managers in the eastern United States. Widespread regeneration failure and poor overstory recruitment of oaks is problematic, particularly on intermediate and highly productive sites (Aldrich et al., 2005). It is likely that anthropogenic forest disturbances such as timber harvesting, livestock grazing, loss of American chestnut (*Catanea dentata*), and low-intensity surface fires promote conditions conducive to oak establishment, development, and recruitment (Abrams, 1992; Lorimer, 1993; Sharitz et al., 1992). Historically, burning was practiced widely by American Indians and later by European settlers (Delcourt et al., 1993). Beginning in the 1920–1930s, the federal government developed fire suppression policies that curtailed the use of fire in forest management (Spetich et al., 2011). Absence of fire and other disturbances in upland hardwood forests results in reduced light conditions at the forest floor, potentially altering the composition of hardwood regeneration

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and associated competitive pressure on oaks (Abrams, 1992; Aldrich et al., 2005).

Prescribed fire is increasingly used as a tool in oak ecosystem restoration, with the goal of reducing competition between fire-tolerant oak species and shade-tolerant competitors, and creating light and seedbed conditions conducive to germination and growth of oak seedlings (Van Lear and Watt, 1993; Wang et al., 2005). Wang et al. (2005) reported higher establishment of white oak (*Quercus alba*) seedlings following an abundant acorn crop in 2002, on stands that had been burned 2.5 and 3.5 years prior, compared to unburned stands. They attributed this to reduced leaf litter and more light reaching the forest floor, even 2.5 years after the burn. Garcia et al. (2002) also found that reduced leaf litter thickness enhanced northern red oak (*Quercus rubra*) seedling emergence in the field, but that low soil moisture reduced germination. Royse et al. (2010) found higher survival and growth of white oak and chestnut oak (*Quercus prinus*) seedlings in burned stands with reduced leaf litter depth and more light compared to unburned sites. Thus, forest floor conditions created by prescribed fire may promote establishment and early growth of oak seedlings from acorns that drop post-burn. Yet, oak seedling establishment is dependent on the presence of viable acorns, which may be vulnerable to prescribed fire.

In upland hardwood forests of the Central Hardwood Region, prescribed burns are most commonly conducted during the dormant season (November–March), not long after acorns drop in the fall. Yet, very few studies have addressed effects of prescribed fire or fire temperature on acorn viability, how acorn species may differ in their responses, or whether vulnerability to high temperatures varies with acorn location in the forest floor. Auchmoody and Smith (1993) reported that fall burning killed northern red oak acorns on the leaf litter surface by "cooking" embryos. Acorn desiccation is a potentially lethal effect of otherwise non-lethal temperatures, as well (Garcia et al., 2002; Connor and Sowa, 2003). Desiccation below critical moisture levels is shown to compromise acorn viability by damaging embryonic and cotyledon tissues (Connor and Sowa, 2003). Korstian (1927) reported that acorn moisture content must be at least 30–50% for white oak and 20–30% for red oak for germination to occur.

Acorn survival during prescribed fire is mediated by several factors. First, prescribed burns are often patchy and burn at low temperatures in upland hardwood forests (Hutchinson et al., 2005; Waldrop et al., 2010), increasing the likelihood that acorns will escape damage. Fuel moisture and loading, recent and current weather, and method of ignition influence both the temperature and duration of prescribed fire. In addition, acorns may not remain on the leaf litter surface for long after dropping in the fall. Acorns that are not consumed by wildlife (McShea, 2000) may settle under the leaf litter or into crevices in the soil surface by the action of gravity, weather, and falling leaves (personal observation). Many acorns are cached by squirrels, chipmunks, mice, and blue jays for later consumption (Haas and Heske, 2005; Thorn and Tzilkowski, 1991). More acorns may remain on the leaf litter surface in years of high mast production, when acorn production is greater than consumption by wildlife (McShea, 2000). The potential effects of fire temperature on acorn viability may be mediated by the insular properties of soil or duff compared to the leaf litter surface.

Effects of winter prescribed burns and fire temperature on acorn viability are also likely to differ between species in the white and red oak subgenera (*Leucobalanus* and *Erythrobalanus*, respectively) because of differences in germination phenology. White oak acorns germinate immediately after dropping in the fall, whereas northern red oak acorns overwinter on the ground and germinate the following spring (Olson, 1971). Higher heat-associated mortality or damage to white oak acorns might be expected due to increased vulnerability of the already-germinating embryo and associated cracks in the acorn seed coat.

We assessed the effect of fire temperature on white oak and northern red oak acorn viability (germination and shoot growth) for unprotected acorns exposed on the leaf litter surface, and for two levels of protected acorns in the duff layer and in mineral soil, during winter prescribed burns in upland hardwood forests of the southern Appalachians. We hypothesized that (1) acorns on the litter surface are more vulnerable (as measured by viability) to effects of prescribed fire than acorns protected by duff or mineral soil; (2) white oak acorns are more vulnerable than red oak acorns; and (3) acorn viability is reduced with higher fire temperature. Understanding the effects of prescribed fire on acorn viability is an important component of oak ecosystem restoration, and has important implications for timing and intensity of prescribed burns.

1.1. Study area

This study was conducted on the North Carolina Wildlife Resource Commission's Cold Mountain Game Lands (CMGL) in western North Carolina (35 40′N; 82 93′W). The CMGL encompass 1333 ha and is located on the Blue Ridge physiographic province of the southern Appalachian Mountains. Terrain is mountainous with steep slopes. Slopes of areas used in this study varied from ~35 to 55 percent. Elevations within the study area range from 975 to 1280 m. Bedrock is predominantly felsic to mafic high-grade metamorphic biotite and granitic gneisses (Hadley and Neslon, 1971). Soils are inceptisols and ultisols that are shallow to very deep, well drained, moderately to extremely acid, and range in texture from coarse-loamy to clayey, stones are scattered on the surface of some sites (Allison and Hale, 1997). The climate is characterized by warm summers and cool winters. Average annual temperature ranges from 10 to 16 °C and ranges from 3 °C in January to 24 °C in July (McNab and Avers, 1994). Precipitation averages 1200 mm annually and is evenly distributed throughout the year (McNab and Avers, 1994). Vegetation on CMGL consists of mature, second-growth upland mixed-oak forests. Oak species (*Q. rubra*, *Quercus velutina*, *Quercus coccinea*, *Q. alba*, *Q. prinus*), hickory species (*Carya ovalis*, *Carya cordiformis*, *Carya glabra*, *Carya tomentosa*), and yellow-poplar (*Liriodendron tulipifera*) are the predominant overstory trees while the midstory consists primarily of shade-tolerant species including sourwood (*Oxydendrum arboreum*), flowering dogwood (*Cornus florida*), blackgum (*Nyssa sylvatica*), silverbell (*Halesia tetraptera*), and red maple (*Acer rubrum*) (Schafale and Weakley, 1990). Site productivity generally varies with topographic position with mesic lower slopes more productive than xeric ridge top locations.

2. Methods and materials

2.1. Acorn sources

We collected northern red oak acorns from several sources in western North Carolina and east Tennessee during fall 2008 (for the February 2009 burns) and 2009 (for the April 2010 burns). Acorns from all sources were mixed prior to study establishment. White oak acorns were ordered from a seed company because we were unable to collect enough from local trees. We conducted a float test for acorn soundness by submerging them in water, and discarded those that floated as presumed unsound. Acorns that sank in water were air dried, placed in plastic baggies, and then stored (white oak) or stratified (northern red oak) by refrigerating at 0.6–3.3 °C for >12 weeks (e.g., Adams et al., 2006; Hopper et al., 1985), until the day of prescribed burns.

2.2. Field methods

Burns were conducted in five randomly selected 5-ha square (225 m × 225 m) units which were part of a larger study on oak ecosystem restoration. Within each unit we systematically established 2–3 experimental acorn plots spaced approximately 62 m apart along each of two parallel transects, separated by >30 m. Transects were parallel to and >30 m from a unit boundary, and positioned across a slope gradient. The first transect was located by picking a random distance along the boundary line from the farthest downslope corner of each burn unit.

The study consisted of three experimental treatments (acorn location within the forest floor) applied to two species of acorn (white oak and northern red oak). Acorn location treatments were: (1) on the leaf litter surface (litter); (2) in the duff layer within about 0.6 cm of duff surface or, if no duff was present, in the mineral soil within about 0.3 cm of surface (duff); and (3) in the mineral soil about 5 cm deep with duff and leaf litter replaced on top of the soil after acorn placement (soil). Each plot contained all six species-treatment combinations. Three white oak acorn subplots were established along the north side, and the three northern red oak acorn subplots were established on the south side (in mirror sequence) of a 30–40 cm centerline within each plot. Subplots were not randomized to reduce the likelihood of confusing them during post-burn collection, however, due to the small size of acorn plots and close proximity of subplots non-randomization this was unlikely to affect results. Subplots were about 225 cm^2 each and adjacent to one another, with about 15 cm between them (Fig. 1). We placed 15 white oak acorns in each of the three adjacent white oak acorn subplots and 20 northern red oak acorns in each of the three northern red oak acorn subplots, different number of acorns used was due to a greater supply of northern red oak than white oak acorns. In each subplot, acorns were placed in a loose cluster (not touching or on top of one another) within about a 12 cm diameter area.

For reference purposes, we established one plot (one reference plot for every 4–6 burn plots) at least 50 m outside of each burn unit, and beyond the potential influence of fire temperature. Reference plots were identical to plots within the burn units, as described above, but were not part of the same experimental design as they were not randomly assigned within the 5-ha units.

Within the burn units, we used Tempilaq temperature sensitive paints (Tempil Inc., South Plainfield, NJ) to assess fire temperature at each plot. Different paints melted at increasingly higher temperatures starting at 79.4 °C and at successive 28 °C increments up to 315.6 °C, or at 55 °C increments if temperature ranged 315.6 to 815.6 °C. Four metal tags, each with a different, successively higher melt-point series of temperature sensitive paints (79.4–148.9 °C, 176.7–287.8 °C, 315.6–537.8 °C, and 593.3–815.6 °C), were wrapped separately in aluminum foil to reduce char or soot that could obscure melted paints, and attached as a set to a pin wire (Iverson et al., 2004). One set of tags was placed at the center of each plot, positioned so that the bottom of the tags was barely (about 0.6 cm) above the leaf litter surface (Fig. 1).

Two units (15 and 16) were burned by the North Carolina Wildlife Resources Commission on February 25, 2009 and three units (7, 8, and 11) were burned on April 1, 2010. Due to their proximity to one another, units 15 and 16 (in 2009), and units 7 and 8 (in 2010) were burned as single prescribed fires, respectively. Because of 50-m buffers between the units, we considered all units to be independent replicates. Prescribed burns on both dates were cool, backing fires ignited with short, strip lighting and/or flanking strip lighting. Ten hour fuel moisture on the burn days ranged from 9% to 11% and relative humidity was between 20% and 40%.

Acorns and temperature sensitive paints were retrieved from the burned units and reference plots the day after prescribed fires.

Acorns were placed in plastic baggies and labeled by date, unit, plot number (or reference), species, and experimental treatment (litter, duff, or soil) and refrigerated for 1–3 days before planting them in the greenhouse. In many cases we were unable to find all acorns within a subplot, thus the number of acorns planted in the greenhouse was sometimes less than the original number placed in field.

2.3. Greenhouse methods

We planted acorns approximately 1 cm apart in water-saturated vermiculite in 10 × 38 cm, 10 cm deep trays, with 2 or 3 sub-

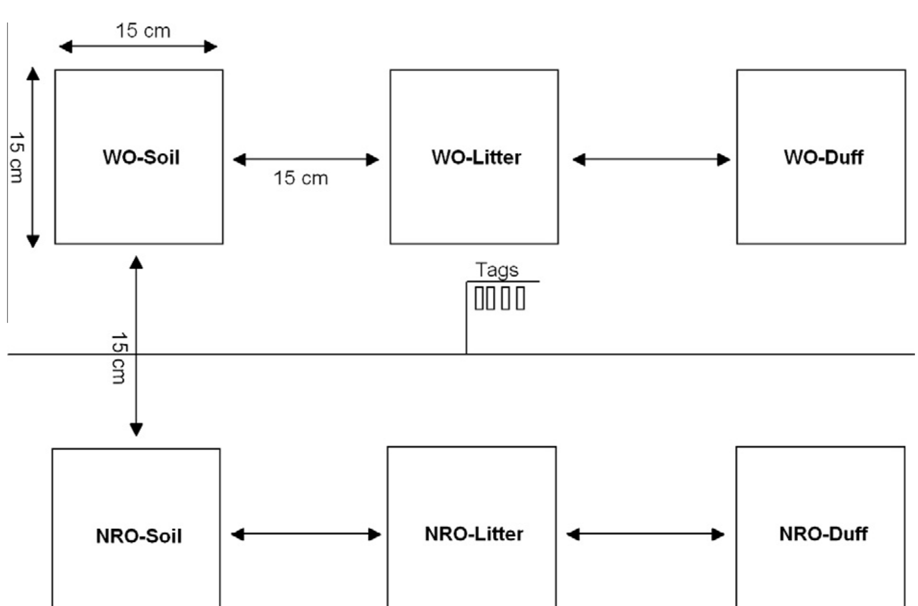

Fig. 1. Diagram of experimental plot layout for testing effects of prescribed burning on viability of white oak and northern red oak acorns located on the leaf litter surface, duff, or in the mineral soil at time of burn.

plots planted (<50 acorns) per tray and labeled. Trays were placed on germination beds in a greenhouse, with heating pads beneath that maintained vermiculite temperature at a constant 27 °C. Acorns were watered at 15-min intervals using misters and exposed to 14 h of continuous light daily. Acorns were harvested 19 (for 2009 burns) or 22 (for 2010 burns) days after planting. We recorded presence or absence of germination (presence of a seminal root) for all planted acorns, and presence or absence of shoots for each germinant.

2.4. Statistical analyses

We used a generalized linear mixed model (PROC GLIMMIX) to test for differences in the proportion of acorns germinating and the proportion of germinants with shoots in response to treatment (litter, duff, or soil), species (northern red oak or white oak), and the treatment x species interaction. The data was dichotomous (0, 1) and not normally distributed and, thus, the model was based upon the binomial distribution with the logit link function. The experimental design for the prescribed burn acorn study consisted of five units selected within the forest each having 4–6 plots. The six combinations of treatment and species were applied to six separate subplots within each plot with each subplot consisting of 15 white oak or 20 northern red oak acorns. The fixed factors in the analysis were treatment, species, and their interaction while the random factors consisted of unit, plot (unit), and the interactions of unit with each fixed factor.

Reference plots were analyzed separately, as they were not part of the experimental design testing effect of fire on acorn viability. Further, the experimental design for reference plots differed slightly. Only four of the original five units were used and only one plot per unit was established, with each plot containing six subplots, each with one of the combinations of treatment and species. The fixed and random factors were the same as in the analysis for the burn experiment except there was no plot (unit) random factor because there was only one plot associated with each unit. Results from the unburned reference plots were used to evaluate the effect of treatment, species, and their interaction under reference conditions of no fire.

Results from the burn experiment allowed testing for treatment, species and interaction effects under a random set of fire temperatures because the temperature in each plot was not controlled. Thus, the effect of fire temperature was not evaluated directly. Significances discovered were further analyzed using linear regression analysis (PROC REG) to determine the possible effects of fire temperature on acorn viability. Predictive equations of the relationship between fire temperature and the proportion of acorns germinating, and proportion of germinants with shoots were developed for each treatment-species combination. The dichotomous data for each subplot were converted to proportions yielding 26 or 27 observations for each treatment-species regression. A general linear model (PROC GLM) was used to contrast regression lines for each species-treatment pair and differences between the slopes were compared assuming that intercepts were not necessarily equal using a test of conditional error (Milliken et al., 1984). In all analyses we considered $P < 0.05$ to be significant. However, when performing the comparisons between all possible pairs of regression lines, an experimentwise alpha level of 0.05 was used which requires a Bonferroni adjustment alpha level of 0.05/15 = 0.0033 for significance for each comparison.

3. Results

Fire temperatures varied among acorn plots, ranging from <79.4 °C (no temperature sensitive paints melted) to between 315.6 and 371.0 °C (temperature sensitive paints melted at 315.6 °C but no higher). Across all five units, litter depth was reduced from (mean ± SE) 5.9 ± 0.3 to 2.7 ± 0.2 cm, percent litter cover was reduced from 88.3 ± 1.8% to 55.0 ± 2.5%, and duff depth increased from 4.0 ± 0.2 to 8.2 ± 0.5 cm (unpublished data).

Generalized linear mixed model ANOVA for the prescribed burn treatments indicated a lower proportion of leaf litter surface acorns germinated compared to duff or mineral soil treatments, which did not differ from one another, and a higher proportion of northern red oak than white oak acorns germinated, no treatment × species interaction was detected (Table 1, Fig. 2). A lower proportion of leaf litter surface germinants had shoots than duff or mineral soil germinants which did not differ from one another, and a greater proportion of northern red oak than white oak germinants had shoots, no treatment × species interaction was detected (Table 1, Fig. 2).

Results of generalized linear mixed model ANOVA for the unburned reference plots indicated no difference among treatments

Table 1
Results of generalized linear mixed model ANOVA (PROC GLIMMIX) testing the proportion of white oak and northern red oak acorns germinating, and the proportion of germinants with shoots, in response to prescribed fire under three acorn placement treatments. Treatments were placement on the leaf litter surface, in the duff, or in the mineral soil.

Source[a]	df	% Germinating		% Shoots	
		F	*p*-value	*F*	*p*-value
Treatment	2	8.68	0.0099	8.65	0.0100
Species	1	55.45	0.0017	52.79	0.0019
Treatment × species	2	1.42	0.2966	0.15	0.8623

[a] Treatment, species, and treatment × species were fixed effects in the ANOVA, unit (df = 4), unit × treatment (df = 8), unit × species (df = 4), and unit × treatment × species (df = 8) were considered random effects.

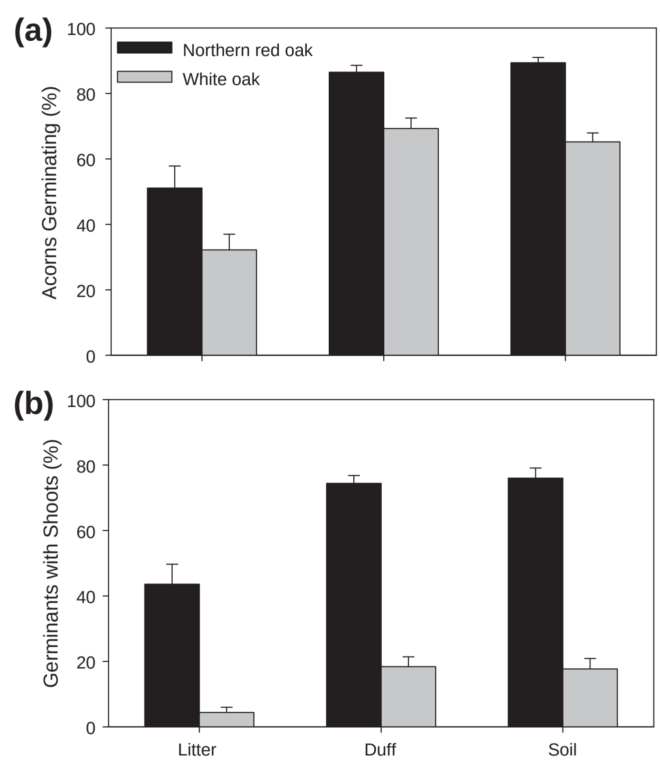

Fig. 2. Mean (+SE) (a) proportion of northern red oak and white oak acorns germinating, and (b) the proportion of germinants with shoots, after a prescribed fire under three acorn placement treatments. Treatments were placement on the leaf litter surface, in duff, or in mineral soil at time of burn.

Table 2
Results of generalized linear mixed model ANOVA (PROC GLIMMIX) testing the proportion of white oak and northern red oak acorns germinating and the proportion of germinants with shoots, in unburned reference plots under three acorn placement treatments. Treatments were placement on the leaf litter surface, in duff, or in mineral soil.

Source[a]	*df*	% Germinating		% Shoots	
		F	*p*-value	*F*	*p*-value
Treatment	2	0.76	0.5060	2.20	0.1923
Species	1	15.27	0.0298	32.97	0.0105
Treatment × species	2	1.91	0.2276	0.75	0.5128

[a] Treatment, species, and treatment × species were fixed effects in the ANOVA, unit (*df* = 3, unit × treatment (*df* = 6), unit × species (*df* = 3), and unit × treatment × species (*df* = 6) were considered random effects.

Table 3
Regression[a] of the proportion of northern red oak (NRO) and white oak (WO) acorns germinating, and the proportion of germinants having shoots on prescribed fire temperature under three acorn placement treatments. Treatments were acorn placement on the leaf litter surface (LITT), in duff layer (DUFF), or in mineral soil (SOIL).

Species	Treatment	b_0	b_1	R^2	*P*-value
Proportion of acorns germinating					
NRO	LITT	1.017	−0.003	0.49	<0.0001
NRO	DUFF	0.910	−0.000	0.04	0.3189
NRO	SOIL	0.850	0.000	0.07	0.1907
WO	LITT	0.682	−0.002	0.49	<0.0001
WO	DUFF	0.764	−0.000	0.04	0.3032
WO	SOIL	0.653	−0.000	0.00	0.9926
Proportion of germinants with shoots					
NRO	LITT	0.877	−0.003	0.45	0.0002
NRO	DUFF	0.849	−0.001	0.16	0.0400
NRO	SOIL	0.885	−0.001	0.12	0.0799
WO	LITT	0.096	−0.000	0.09	0.1276
WO	DUFF	0.079	0.001	0.11	0.0930
WO	SOIL	0.128	0.000	0.02	0.4574

[a] b_0 = model intercept, b_1 = slope coefficient.

in the proportion of acorns germinating or the number of germinants with shoots (Table 2). However, the proportion of acorns germinating (mean ± SE 65 ± 5% vs. 86 ± 2%) and the proportion of germinants with shoots (24 ± 6% vs. 77 ± 3%) were lower for white oak than for northern red oak.

Germination rates of both northern red oak and white oak litter surface acorns were negatively correlated with fire temperature ($P < 0.0001$, $R^2 = 0.49$ for both species) (Table 3, Fig. 3), but duff and mineral soil acorn germination rates of both species were unaffected by fire temperature ($P \geqslant 0.1907$) (Table 3). The proportion of northern red oak litter surface germinants with shoots was negatively correlated with fire temperature ($P = 0.0002$, $R^2 = 0.45$), the proportion of northern red oak duff germinants with shoots was also significant, but less closely negatively correlated with fire temperature ($P = 0.0400$, $R^2 = 0.16$). There was no relationship between shoot production and fire temperature for mineral soil germinants ($P = 0.0799$, $R^2 = 0.12$) (Table 3). We did not detect a relationship between the number of germinants with shoots and fire temperature for white oak in any treatment ($P \geqslant 0.0930$; Table 3).

Regression line slope comparisons of acorn germination rates between species-treatment pairs indicated that slopes for acorns on the litter surface differed from acorns in the duff or soil in response to fire temperature for both species, but the slopes of northern red oak and white oak in the same treatments (litter, duff, or mineral soil) did not differ from one another ($P \geqslant 0.1503$) (Table 4, Fig. 3). Slope comparisons of shoot production rates indicated that slopes for northern red oak germinants from acorns on the leaf litter surface were more affected by increasing fire temperature than those in the duff or soil ($P \leqslant 0.0029$), but slopes for white oak shoot production by germinants were similar for acorns in all three treatments in response to fire temperature ($P \geqslant 0.0829$) (Table 4). Slope comparisons also indicated that increasing fire temperature had a greater effect on shoot production by northern red oak than white

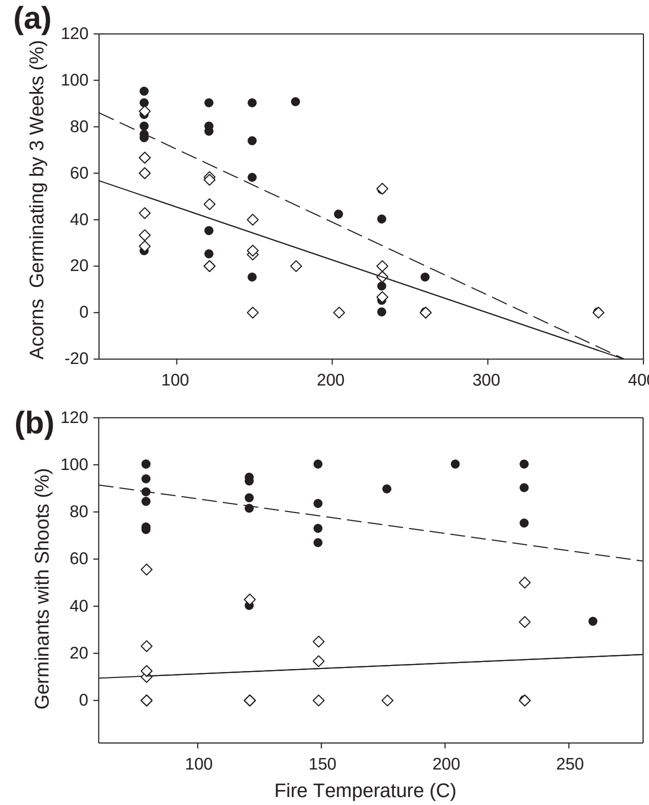

Fig. 3. Regression of (a) proportion of acorns germinating, and (b) proportion of germinants with shoots on prescribed fire temperature on northern red oak (solid circle, dotted line) and white oak (hollow diamond, solid line) for acorns placed on the leaf litter surface at time of burn.

Table 4
Results from testing for differences between each species-treatment pair of regression lines of the proportion of northern red oak (NRO) and white oak (WO) acorns germinating and the proportion of germinants with shoots on prescribed fire temperature under three acorn placement treatments. Treatments were placement on the leaf litter surface (LITT), in duff (DUFF), or in mineral soil (SOIL). An experimentwise alpha level of 0.05 is used which requires a Bonferroni adjustment alpha level of 0.05/15 = 0.0033 for significance.

Contrast	% Germinating			% Shoots		
	MS	*F*-test	*P*-value	MS	*F*-test	*P*-value
NRODUFF vs. NROLITT	0.60	22.39	<0.0001	0.32	13.12	0.0004
NRODUFF vs. NROSOIL	0.02	0.88	0.3487	0.00	0.08	0.7785
NROLITT vs. NROSOIL	0.87	32.74	<0.0001	0.22	9.21	0.0029
WODUFF vs. WOLITT	0.25	9.54	0.0024	0.07	3.05	0.0829
WODUFF vs. WOSOIL	0.02	0.57	0.4497	0.01	0.38	0.5393
WOLITT vs. WOSOIL	0.39	14.79	0.0002	0.03	1.28	0.2600
NRODUFF vs. WODUFF	0.00	0.08	0.7790	0.13	5.35	0.0221
NRODUFF vs. WOLITT	0.30	11.13	0.0011	0.01	0.32	0.5704
NRODUFF vs. WOSOIL	0.01	0.22	0.6401	0.07	2.88	0.09
NROLITT vs. WODUFF	0.54	20.26	<0.0001	0.86	35.27	<0.0001
NROLITT vs. WOLITT	0.06	2.09	0.1503	0.43	17.60	<0.0001
NROLITT vs. WOSOIL	0.74	27.57	<0.0001	0.69	28.35	<0.0001
NROSOIL vs. WODUFF	0.04	1.52	0.2189	0.14	5.76	0.0177
NROSOIL vs. WOLITT	0.50	18.69	<0.0001	0.02	0.64	0.4234
NROSOIL vs. WOSOIL	0.01	0.23	0.6343	0.08	3.37	0.0683

oak germinants from acorns on the leaf litter surface and in the duff during prescribed burns ($P < 0.0001$) (Table 4).

4. Discussion

Our study indicated that patchy, low-intensity dormant season prescribed fire in upland hardwood forests reduced viability of white oak and northern red oak acorns located on top of the leaf litter, but did not generally affect acorns in the duff or soil. Germination rates of both northern red oak and white oak acorns on the litter surface decreased with increasing fire temperature. Shoot production by northern red oak germinants from acorns on the leaf litter surface (and less so in the duff), also decreased with increasing fire temperature. Increasing fire temperature apparently affected shoot production by northern red oak germinants more than white oak germinants. However, shoot production by the white oak germinants from acorns used in our study was much lower than for northern red oak in reference plots (24 ± 6% vs. 77 ± 3%), suggesting that it may not be an appropriate measure for comparing the two species.

Our study was not designed to determine a critical minimum temperature or associated desiccation that causes acorn mortality. However, leaf litter-treatment acorns of both species that burned at temperatures between 204.4 and 232.1 °C showed high mortality levels, with mortality virtually 100% at temperatures ⩾260.0 °C. White oak acorns have been shown to lose viability when dried to <12% water content due to irreversible changes in their physiology and biochemistry (Connor and Sowa, 2003), suggesting that both desiccation and heat were contributing factors to mortality.

We were unable to find other studies that directly measured fire temperature in relation to acorn viability, but several suggest that acorn mortality increases with higher fire temperatures. Cain and Shelton (1998) reported 100% germination failure of southern red oak (*Quercus falcata*) acorns placed within the leaf litter during prescribed fire. Auchmoody and Smith (1993) reported that 40–49% of northern red oak acorns within the leaf litter were killed by fall burns with flame heights of 0.3–0.9 m that consumed the surface litter, fine branches and herbaceous vegetation. Korstian (1927) reported that spring fires ranging 260 to 538 °C "cooked the embryos" killing most acorns in the litter layer.

Other studies also indicate that acorns insulated by duff or soil are better protected from prescribed fire than acorns lying exposed on the litter surface. Cain and Shelton (1998) reported that germination of southern red oak acorns placed within the upper duff layer ranged from 9% to 55%, depending on fire intensity and heat shield provided by unburned litter and no effect of fire on acorns placed at the duff-mineral interface. Below ground temperature increases during low-intensity winter or early spring prescribed burns in upland hardwood forests are negligible and short-lived (Iverson and Hutchinson, 2002; Iverson et al., 2003; Riccardi, 2005).

High-intensity or repeated prescribed fire in upland hardwood forests can reduce litter and duff cover and depth, potentially reducing 'safe sites' to insulate acorns from high temperatures. In our study, litter depth and percent cover decreased postburn, apparent increases in duff depth were likely due to problems with relocating exact pre-burn sampling locations coupled with disturbance during the burn operations and data collection. Greenberg and Waldrop (2008) found that a single, comparable prescribed burn in the southern Appalachians reduced litter depth by an average of 81%, and duff depth by 22% in "burn only" treatments with moderate temperatures (mean 312 °C), in sites that had been mechanically thinned, then burned the following year with hotter temperatures (mean 517 °C), litter depth decreased by an average of 90%, and duff depth by 33% postburn (Greenberg and Waldrop, 2008; Waldrop et al., 2010). After a second prescribed burn in the same stands, leaf litter depth reduction was similar to those following a single burn, but duff depth in the "burn only" stands (mean fire temperature 158 °C) was reduced by 52% compared to the preburn depth, and by 71% in the mechanically thinned and burned stands (mean fire temperature 223 °C), compared to preburn levels (Matthews et al., 2010). Most studies indicate that reductions in litter depth and cover are typically transient, as the litter layer recovers when leaves drop from hardwood trees the following fall (e.g., Greenberg and Waldrop, 2008). Thus, land managers using prescribed fire to enhance forest floor and light conditions to promote seedling establishment and growth of oak seedlings should also consider prescribed fire effects on forest floor litter and duff that may insulate acorns from high temperatures associated with fire.

Our results indicated that prescribed fire affects germination rates of white oak and northern red oak acorns similarly. The white oak acorns we used in our study had lower germination rates, and germinants had lower rates of shoot production compared to northern red oak, overall. Generally, germination rates of sound, undamaged acorns range from 75% to 95% (Olson, 1971), suggesting that the white oak acorns we used in our study had lower than average germination rates (65%, 86% for northern red oak acorns) prior to exposure to prescribed fire. White oak acorns germinate immediately after they are fully developed in fall, whereas northern red oak acorns do not germinate until the following spring. Thus, exposed young radicles and cracked hulls associated with germination would seem likely to render white oak acorns more vulnerable to damage and desiccation from high temperatures compared to northern red oak acorns. Although early germination by white oak acorns may have reduced their viability (germination and shoot production rates) overall during storage and prior to this experiment, it did not appear to increase their vulnerability to damage from prescribed burning relative to northern red oak acorns.

Surface fire temperatures in our prescribed burns were spatially heterogeneous and relatively low, which is typical of other winter and early spring prescribed burns in upland hardwood forests. Reported mean surface temperatures of winter or early spring prescribed fire in relatively undisturbed upland hardwood forests range from 169 to 332 °C, with temperatures rarely exceeding 550 °C (e.g., Clinton and Vose, 2007; Brudnak et al., 2010; Iverson and Hutchinson, 2002; Loucks et al., 2008; Waldrop et al., 2010). Higher temperatures are likely for prescribed burns on xeric sites, or during the growing season, as they are mediated by fuel moisture levels, topography, and air temperature (Elliott et al., 1999).

Our study indicates that even low intensity surface fires are likely to kill most acorns on the litter surface, potentially eliminating an entire years' seed crop within the boundaries of a prescribed burn. Acorn production is highly variable among oak species, years, and locations (e.g., Greenberg and Warburton, 2007). Thus, prescribed fire could have a multi-year impact on establishment of oak seedlings for a given oak species, depending on the acorn crop size of a given oak species prior to the burn and the timing of prescribed burning relative to acorns dropping the prior fall.

Acorn caching by squirrels, mice, and blue jays (e.g., Haas and Heske, 2005; Thorn and Tzilkowski, 1991) is likely an important factor in promoting acorn survival during prescribed fire. Caching involves relocating acorns from the leaf litter surface to "safe sites" buried about 3 cm deep in the mineral soil. Thorn and Tzilkowski (1991) reported that gray squirrels cached 98% of acorns produced in 70,000 caches/ha in a Pennsylvania mixed oak stand. Most acorns were cached within several days of dropping, suggesting that a majority of acorns may be buried by late fall or early winter when many land managers conduct prescribed burns in upland hardwood forest.

Interestingly, an abundance of seedlings is not a predictor of successful oak recruitment into the forest canopy, sapling-size oaks are more likely than seedlings to succeed after release, when competing with faster-growing species for a canopy position. A single prescribed fire is unlikely to enhance the competitive ability of oak seedlings on productive sites in the Appalachians (Johnson, 1974; Wendel and Smith, 1986) and is unlikely to create the light conditions necessary for the development of large, advance reproduction (Alexander et al., 2008) unless the fire intensity is sufficient to cause mortality in the forest canopy (Hutchinson et al., 2005; Signell et al., 2005). Further, substantial mortality to canopy trees in productive sites in the southern Appalachians is unlikely to promote development of oak if the fast-growing competitor, yellow-poplar, is present (e.g., Shure et al., 2006). Stump sprouting from stem-killed trees is also unlikely to be a major source of oak regeneration after low-intensity winter prescribed burns in mature upland hardwood forests, because such fires typically do not kill trees, and sprouting probability diminishes with tree diameter (Dey et al., 2007; Sands and Abrams, 2009). Acorn survival and germination of oak seedlings is the first step in the oak regeneration process, and should be considered by land managers when deciding the timing of prescribed burning.

5. Conclusions

Patchy, low-intensity prescribed burns in upland hardwood forests reduce viability of white oak and northern red oak acorns on the leaf litter surface, but has little effect on acorns protected by duff or mineral soil. Acorns on the litter surface exposed to fire temperatures between 204.4 and 232.1 °C showed high mortality levels, and mortality was virtually 100% at temperatures $\geqslant$260 °C. Fall burns, especially after a heavy acorn crop, could result in high acorn mortality that could potentially impact oak regeneration from seedlings for many years, given the erratic patterns of mast production among years and species. In most years, acorns do not remain on the leaf litter surface for long, but are quickly cached by squirrels and other wildlife, or settle under the leaf litter or into crevices in the soil via gravity, weather, and falling leaves. Thus, winter burns would likely have minimal impact on acorn viability in most years. Frequent burning can reduce duff and leaf litter depth, potentially reducing ‘safe sites’ where acorns are insulated from high fire temperatures. When oak ecosystem restoration is a goal, land managers should consider the timing and size of acorn crops, as well as the forest floor condition when determining the timing and frequency of prescribed burning.

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