Forest Ecology and Management 433 (2019) 441–452

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Season of burn effects on vegetation structure and composition in oak-dominated Appalachian hardwood forests

Tara L. Keyser*, Cathryn H. Greenberg, W. Henry McNab

USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest, 1577 Brevard Rd., Asheville, NC 28806, USA

ARTICLE INFO

Keywords:
Growing-season burn
Dormant-season burn
Quercus regeneration
Restoration
Mesophication

ABSTRACT

Previous research indicates that low-intensity single or multiple prescribed burns in oak-dominated upland hardwood forest do not substantially change stand structure or species composition of the arborescent regeneration layer, leading managers and ecologists to suggest that burns during the growing-season may better achieve restoration goals. We examined season of burn effects on dry-mesic oak-hickory forests in the southern Appalachian Mountains, North Carolina. Treatments included: (1) control (CON); (2) dormant-season burn (DSB), and (3) growing-season burn (GSB). Prior to burning and again after three growing seasons post-burn, we inventoried the forest overstory (stems ≥ 25 cm dbh), subcanopy (stems ≥ 5 and < 25 cm dbh), sapling (stems ≥ 1.2 m and < 5 cm dbh), and seedling (stems < 1.2 m) strata. We found no effect of prescribed fire, regardless of burn season, on stem density or basal area of the overstory and subcanopy strata, leaving the light environment in the forest understory relatively unchanged. In general, treatment effects on the sapling and seedling layers were limited to the mesophytic species group, where seedling density post-burn was greater in GSB than both CON and DSB and sapling density post-burn was lower than pre-burn in DSB and GSB. Mortality of individually-tagged seedlings three growing seasons post-burn did not differ among treatments for the red oak, white oak, red maple, mesophytic, and pyrophilic species groups, and averaged 29.0, 28.5, 31.8, 29.3, and 25%, respectively. This study provides support for the notion that a single fire in a closed-canopy oak-hickory forest has little effect on forest structure or regeneration composition, regardless of the burn season. Prescribed fires should be repeated in subsequent years to assess whether the effects of burn season are amplified under a periodic burning regime.

1. Introduction

Oaks (*Quercus*), which are mid-tolerant of shade, are a dominant component of mature forest canopies in many forests of the eastern United States. Over the past century, changing disturbance regimes in eastern upland hardwood forests have facilitated development of dense understories dominated by shade-tolerant, fire-sensitive species (e.g., red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), and blackgum (*Nyssa sylvatica*)). Coincident with the densification of oak-hickory (*Quercus-Carya*) forests (Hanberry et al., 2014) has been a decrease in the successful regeneration and recruitment of oak and hickory across its range (Dey, 2014). Unfavorable light conditions directly related to high stem density in the subcanopy stratum have led to a dearth of competitive (i.e., large) oak and hickory advanced reproduction. Consequently, small oak seedlings, when released via a canopy-reducing disturbance, are unable to compete with faster growing species, such as yellow-poplar (*Liriodendron tulipifera*) and sweet birch (*Betula lenta*) (Loftis, 1983; Miller et al., 2006). Because oaks are a “foundation” species (Hanberry and Nowacki, 2016), the direct and indirect ecological and economic consequences associated with the replacement of oak forests to those dominated by non-oak species will have detrimental effects on ecosystem structure and function across the eastern U.S. (McShea et al., 2007; Caldwell et al., 2016).

Paleoecological, dendroechological, and stand reconstruction data suggest a large proportion of the pre-Euro-American southern Appalachian Mountains was influenced by periodic fires of low to moderate severity (Lafon et al., 2017). These fires interacted with natural and anthropogenic forces (McEwan et al., 2011) to maintain the structure and function of oak and hickory forests in the southern Appalachian Mountains over millennia (Delcourt and Delcourt, 1997; Delcourt et al., 1998). Elimination of frequent burning by Native Americans and Euro-American settlers, and suppression of primarily human-caused wildfires for several decades (Greenberg et al., 2015a; 2015b) is likely a principle factor responsible for densification and

---

* Corresponding author.
E-mail address: tkeyser@fs.fed.us (T.L. Keyser).

https://doi.org/10.1016/j.foreco.2018.11.027
Received 11 October 2018; Received in revised form 14 November 2018; Accepted 16 November 2018
0378-1127/ Published by Elsevier B.V.

associated oak regeneration and recruitment problems (Lorimer, 1993; Nowacki and Abrams, 2008).

On public lands in the eastern U.S., management efforts are often focused on the restoration of resilient forest structures and compositions. Prescribed burning, which is the predominant tool used to achieve restoration goals, is most commonly conducted during the dormant-season (September – April) due to drier fuels and more predictable fire-weather conditions (Knapp et al., 2009). Objectives associated with the reintroduction of fire to upland hardwood forests of the Appalachian Mountains often include reducing the abundance of mesophytic and shade-tolerant species in the forest understory (Brose et al., 2014), restoring open forest conditions (Dey et al., 2017), and establishing and developing competitive oak reproduction in the forest understory (Arthur et al., 2012). In the mesic systems of the Appalachian Mountains and Cumberland Plateau, research indicates that dormant-season burns, even when conducted under the semblance of a frequent fire regime (e.g., four burns over eight years (Arthur et al., 2015) and four burns over four years (Hutchinson et al., 2005), do little to alter stand structure (Arthur et al., 2015; Waldrop et al., 2016) and understory light availability (Chiang et al., 2005) in a manner that promotes the growth and recruitment of oak and hickory seedlings into more competitive size classes (Alexander et al., 2008; Keyser et al., 2017).

Limited efficacy of repeated dormant-season burns to achieve desired stand structures and compositions (Hutchinson et al., 2012b; Arthur et al. 2015) has led forest managers and scientists to suggest that growing season burns may more rapidly and effectively attain these goals (Knapp et al., 2009; Waldrop et al., 2016). Differences in the condition of the fuel complex and air and fire temperature between the dormant- and growing-seasons can greatly influence fire intensity and resultant effects on vegetation (Knapp et al., 2009). The physiological state of vegetation at the time of burning can also influence post-fire dynamics. As aboveground growth of deciduous hardwood trees begins during the spring, root carbohydrate reserves, which are positively related to re-sprouting ability following top-kill (Cruz et al., 2003), decrease (Burke et al., 1992). Damage to plant tissues incurred during different stages of physiological activity may, therefore, result in interspecific differences in post-burn mortality, re-sprouting, and subsequent regeneration dynamics of upland hardwood species (Kays and Canham, 1991; Hmielowski et al., 2014). Although several studies address season of burn effects in southern pine-dominated ecosystems (e.g. Robertson and Hmielowski, 2014; Glitzenstein et al., 1995), quantitative information regarding burn season effects on upland hardwood forest structure and composition is lacking.

In this study, we experimentally tested the effects of burn season on forest structure and the arborescent regeneration layer in a dry-mesic, oak-dominated hardwood forest in the southern Appalachian Mountains. Based on research conducted in the oak-hickory and other eastern ecosystems, we hypothesized that: (H1) Structural attributes, including density of the overstory and subcanopy strata, and canopy openness, will be altered more by a growing- than dormant-season burn; (H2) Abundance of fire-sensitive species in the arborescent regeneration layer will be reduced more by a growing- than dormant-season burn; and (H3) Population dynamics of seedlings in the arborescent regeneration layer, including mortality and height, will vary among species groups and season of burn treatment, with growing-season burns having a greater effect on seedling mortality and height of fire-sensitive, mesophytic species than dormant-season burns.

2. Methods

2.1. Study area

This study was conducted at the Bent Creek Experimental Forest, a part of the Pisgah National Forest in Buncombe County, North Carolina. Located within the Blue Ridge physiographic province in western North Carolina, the area encompasses 2500 ha with annual precipitation averaging 1400 mm (Owenby and Ezell, 1992) and elevations ranging from 700 m to 1070 m (McNab et al., 2004). Winters are cool and relatively short while summers are generally long and warm. The study site is located in the Asheville Basin portion of Bent Creek Experimental Forest, which is characterized by low hills with gentle to moderately steep slopes. Ecologically, the study area is mapped as a dry-mesic ecozone (Simone et al., 2005). Common tree species in this upland hardwood forest include black oak (*Quercus velutina*), chestnut oak (*Q. montana*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), sourwood (*Oxydendrum arboreum*), red maple, flowering dogwood (*Cornus florida*), and interspersed shortleaf pine (*Pinus echinata*) and eastern white pine (*P. strobus*) (McNab et al., 2004). Mountain laurel (*Kalmia latifolia*), an ericaceous, evergreen shrub, is common throughout.

2.2. Study design

In 2011, we established nine experimental units, which ranged in size from 3.5 to 7.4 ha, within the Bent Creek Experimental Forest. The rectangular, adjacent units were separated by fire lines and typically extended from lower slope to ridge crest. Average elevation of the experimental units was 730 m, (range 660–790 m) and the predominant aspect was southwesterly. All units were comprised of mature (~100 years old), closed-canopy oak-dominated forest types. Stands used in this study had not experienced fire during the past ~100 years, which coincides with the time that George Vanderbilt acquired the tracts. At this time, common agricultural activities (e.g., grazing, woodlot management, etc.) ceased, and lands reverted back to forested conditions. Other than background natural disturbance events (e.g., single-stem death, occasional single-stem wind-throw), the study site has not experienced anthropogenic disturbances (e.g., timber harvesting, firewood collecting, etc.) over the past 60–70 years.

Burn season treatments were randomly assigned to each of the nine units. Treatments were: (1) Growing-season prescribed burn (GSB), (2) Dormant-season prescribed burn (DSB), and (3) Control (CON). Growing-season was defined by the vegetation phenology, including the presence of new, small leaves on several deciduous tree species (e.g., red maple, sourwood (*Oxydendrum arborea*)), and full flowering by several oak species and flowering dogwood. Dormant-season was defined as the absence of live leaves on all deciduous tree species, regardless of whether the species was found in the forest understory or overstory.

The growing-season burns were conducted on 26 April 2013, and the dormant-season prescribed burns were conducted on 5 March 2014. For DSB, three separate ignitions were used to burn the three experimental units. For GSB, two separate ignitions were used to burn the three experimental units, as two of the GSB units were adjacent. In DSB and GSB units, Pisgah National Forest fire personnel ignited experimental units off the established fire lines using backing and flanking fires. Interior ignition was completed using strip-head firing techniques. According to the closest, most representative remote automated weather station (RAWS) data, air temperature at the time of ignition, relative humidity, 10 hr fuel moisture, and forecasted Keetch-Byram Drought Index (KBDI) was 18.3 °C, 26%, 7%, and 40, respectively, in GSB and 8.3 °C, 61%, 8%, and 32, respectively, in DSB.

Maximum fire temperature (°C) in GSB and DSB was measured at ground level and 30 cm above ground level using temperature-sensitive paints on tags placed at the center of the two regeneration subplots located in each of three vegetation plots per unit (see Sections 2.3 and 2.4). Maximum temperatures varied, with a greater proportion of subplots in GSB experiencing higher temperatures than DSB at both ground level and 30 cm above ground level (Fig. 1). Litter and duff depth were measured prior to and immediately after burning at three locations along three randomly oriented 12 m long transects located within each vegetation plot (see Section 2.3) in GSB and DSB. In DSB pre- and post-burn litter depth averaged (SE) 3.7 (0.9) and 1.0 (0.2) cm,

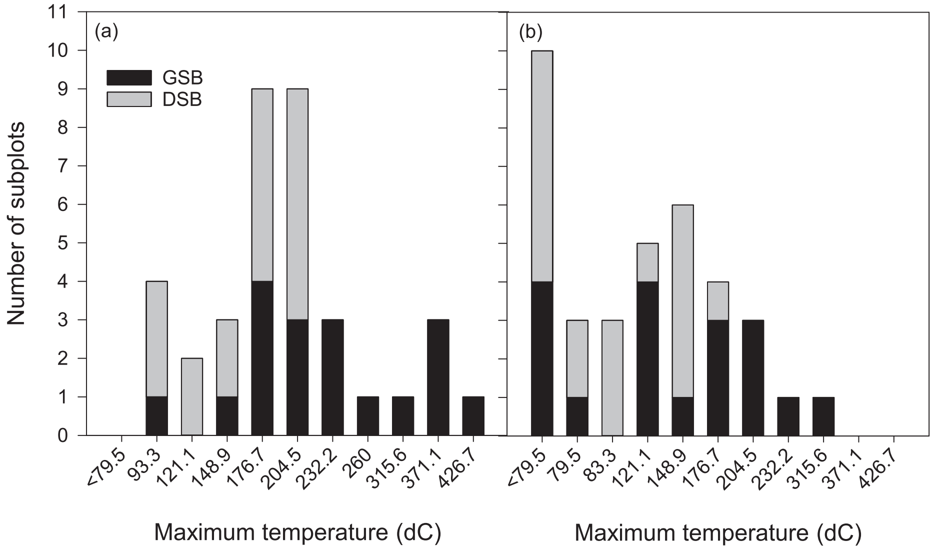

Fig. 1. Range in maximum fire temperatures (°C) as recorded at each regeneration subplot (n = 18 per treatment and location). Maximum fire temperature was recorded at ground level (panel a) and 30 cm above ground level (panel b). GSB = growing-season burn, DSB = dormant-season burn.

respectively; in GSB, pre- and post-burn litter depth averaged 6.0 (0.7) and 1.1 (0.2) cm, respectively. In DSB pre- and post-burn duff depth averaged 3.7 (0.8) and 3.4 (1.1) cm, respectively; in GSB, pre- and post-burn duff depth averaged 4.1 (0.6) and 2.3 (0.3) cm, respectively.

2.3. *Forest structure*

Prior to treatment, three permanent vegetation circular sampling plots were randomly located within each unit. Plots within each unit were separated by at least 30 m. The center of each plot was marked with rebar, and GPS coordinates were obtained. At each plot center, a 0.05 ha circular plot was established and all trees ≥25 cm diameter at breast height (dbh) were tagged and species and dbh recorded. A concentrically nested 0.01-ha circular plot was established and all subcanopy trees (stems ≥ 5 cm and < 25 cm dbh) were tagged and inventoried as described above. In GSB and DSB, the status (live or dead) of all tagged overstory and subcanopy trees were recorded at the time of plot installation (i.e., pre-burn) and again three years post-burn; in CON, status was recorded at the time of installation and again three years following the collection of pre-treatment data.

Canopy openness (%) was measured with a spherical densiometer (held at approximately 1.2 m) at the center of the two regeneration subplots (see Section 2.4). Canopy openness was measured in each cardinal direction and averaged to produce a single value per sampling location. In GSB and DSB, spherical densiometer measurements were conducted pre-burn and again three years following fire; in CON, status was recorded pre-burn and again three years following the collection of pre-treatment data.

2.4. *Regeneration*

In each of the three main vegetation plots per unit, we installed two 0.004 ha circular regeneration subplots originating 8 m from each plot center at bearings of 45° and 225°. Within each of these subplots, seedlings (stems < 1.2 m) and saplings (≥1.2 m and < 5 cm dbh) were enumerated by species. Individuals with multiple stems were recorded as a single stem. In GSB and DSB, regeneration inventories were conducted pre-burn and again three years post-burn; in CON, inventories were conducted pre-burn and again three years following the collection of pre-treatment data. To examine the effects of treatments on species in the regeneration layer, we grouped all species observed in the seedling and sapling layers into one of five species groups (Table 1). Species groups included (1) red oak (Section: *Erythrobalanus*); (2) white oak (Section: *Leucobalanus*); (3) red maple; (4) pyrophilic; and (5) mesophytic. Species in the pyrophilic and mesophytic categories were grouped as per Thomas-Van Gundy and Nowacki (2013). Red maple was excluded from the mesophytic group because the species is a strong, ubiquitous competitor on all sites and its response to fire was of particular interest. Similarly, red and white oaks were separated from the pyrophillic group, as increasing oak abundance and competitiveness is the focus of many prescribed burn programs in the region.

2.5. *Individual seedling dynamics*

Prior to treatment, we located and tagged up to six live tree seedlings per species observed in each regeneration subplot. Obvious or verifiable sprout-origin individuals were not selected and tagged. For each seedling, we recorded tag number, distance and azimuth from subplot center, species, groundline diameter (GLD; cm), and height (cm). During the re-measurement period, tagged seedlings were relocated and status and height were recorded. Seedlings that had been top-killed, but re-sprouted were classified as live. In GSB and DSB, data (status and height) on individual tagged seedlings were collected pre-burn and again three years post-burn; in CON, data were recorded pre-burn and again four years following the collection of pre-treatment data.

2.6. *Statistical analyses*

Density (overstory, subcanopy, sapling, and seedling strata), canopy openness, and height of tagged seedlings that survived through the third growing season post-burn were analyzed using a split-plot analysis of variance (ANOVA), where treatment (CON, DSB, GSB) was the main-plot factor and year (pre- and post-burn) was the split-plot factor. Treatment, year, and the interaction were fixed effects, and unit within treatment was a random effect. Pre- and post-burn measurements were equally correlated (i.e., only one repeated measurement). Therefore, the split-plot rather than a repeated-measures design was employed, as this yields an optimum method of analysis (Littell et al., 1998). When a significant treatment × year interaction was detected, we used partitioned *F*-tests with the SLICE option in PROC MIXED (SAS 9.4) to examine the significance of treatments within years, and years within treatments. The effects of treatment on third-year mortality of tagged seedlings was analyzed as a one-way ANOVA. To meet assumptions of

Table 1

Species observed within the seedling (stems < 1.2 m) and sapling (stems ≥ 1.2 m and < 5.0 cm dbh) strata, categorized by species group. Species groups are defined by information presented in Thomas-Van Gundy and Nowacki (2013) and the Fire Effects Information Database (FEIS).

Red oak	White oak	Red maple	Pyrophilic	Mesophytic
Quercus coccinea *Quercus falcata* *Quercus rubra* *Quercus velutina*	*Quercus alba* *Quercus montana* *Quercus stellata*	*Acer rubrum*	*Carya spp.* *Castanea dentata* *Castanea pumila* *Cornus florida* *Diospyros virginiana* *Nyssa sylvatica* *Oxydendrum arboreum* *Robinia pseudoacacia* *Sassafras albidum* *Pinus virginiana* *Pinus rigida* *Pinus echinata* *Pinus strobus*	*Amelanchier arborea* *Betula lenta* *Fagus grandifolia* *Fraxinus americana* *Ilex* spp. *Liriodendron tulipifera* *Magnolia fraseri* *Malus* spp. *Ostrya virginiana* *Prunus serotina*

normality and homogeneous variances, some variables were square-root transformed, $\log_e$-transformed, or arcsine square-root-transformed. In all ANOVAs, post-hoc multiple comparisons were conducted using Fisher's protected least significance difference (LSD) test. An alpha = 0.05 was used for significance tests of all ANOVAs and post-hoc tests.

We conducted Wilcoxon Rank Sum Tests to determine whether pre-burn GLD and pre-burn height differed between tagged seedlings recorded as live and dead three years post-burn (α = 0.05). Mortality data are categorical with a binary outcome (live or dead). Consequently, we used generalized linear mixed effects modelling to predict the probability of stem mortality three years post-fire:

$$P(m) = \frac{1}{1 + e^{(-(\beta_0+\beta_1 X_1+\beta_{2X_2}+\beta_3 X_3))}}$$

where $P(m)$ is the probability of mortality three years following prescribed burning, β_0, β_1, β_2, and β_3 are regression coefficients and X_1, X_2, and X_3 are the explanatory variables. Models were fitted using maximum likelihood methods and the quadrature method in PROC GLIMMIX (SAS Institute 2015). Regeneration subplot (unit * plot) was included as a random effect to account for the hierarchy in the dataset.

We developed a series of *a-priori* models that predicted the probability of individual seedling mortality three years post-burn as a function of treatment (CON, GSB, DSB), either pre-burn GLD or pre-burn height, and the interaction between treatment and GLD or height. Akaike's information criterion (AIC) was utilized to determine which models most parsimoniously fit the data. Among candidate models, we identified the best as having the lowest AIC and considered competing models as similar in quality when ΔAIC between any two models was < 2.0 (Burnham and Anderson, 2002). Akaike weights were calculated to provide information regarding the strength of evidence for each model (Burnham and Anderson, 2002). Because pre-burn GLD and height were significantly correlated ($P < 0.0001$), separate models were developed.

3. Results

3.1. Forest structure

The density (both stems ha^{-1} and basal area ($m^2 ha^{-1}$)) of the subcanopy (stems ≥ 5 cm and < 25 cm dbh) and overstory (stems ≥ 25 cm dbh) strata did not statistically differ among years or treatments, and no interaction effects were observed (Fig. 2). Across treatments and years, basal area and stems ha^{-1} averaged (SE) 10.5 (1.1) and 813 (88) in the subcanopy and 19.2 (1.4) and 168 (12) in the overstory, respectively.

Canopy openness (%) was significantly affected by year ($F = 48.09$, $P \leq 0.0001$), and treatment × year effects ($F = 4.38$, $P = 0.0374$) were detected. Canopy openness was dynamic over time in GSB and DSB, with canopy openness greater post-burn than prior to burning (Fig. 3). Despite the slight increase in canopy openness in DSB and GSB, no differences among treatments were observed pre- or post-burn.

3.2. Arborescent regeneration layer

The density of seedlings in the red maple, red oak, and white oak species groups was not significantly different among years or treatments, with density, across years and treatments, averaging (SE) 5234 (491), 3,803 (448), and 3701 (524) stems ha^{-1}, respectively (Table 2). The density of seedlings in the mesophytic species group was significantly affected by year ($F = 54.28$, $P = 0.0003$) and the treatment × year interaction ($F = 13.86$, $P = 0.0056$). Partitioned F-tests revealed that in GSB and DSB, the density of seedlings in the mesophytic group was greater post-burn than pre-burn. No differences in seedling density of mesophytic species among treatments existed prior to burning; however, post-burn, average seedling density was 184% greater in GSB than in CON and DSB. The density of seedlings classified as pyrophilic differed between years ($F = 29.25$, $P = 0.0017$), but no treatment or treatment × year effects were observed.

Sapling densities in the white oak and pyrophilic species groups did not differ among years or treatments, and no interaction effects were detected (Table 2). Across treatments and years, saplings in the white oak and pyrophilic groups averaged 90 (29) and 350 (57), stems ha^{-1}, respectively. Sapling density of the mesophytic group differed between years ($F = 26.33$, $P = 0.0022$), and a significant treatment × year interaction was detected ($F = 8.21$, $P = 0.0192$), with post-burn sapling density in GSB and DSB significantly lower than pre-burn. Saplings density in the red oak ($F = 22.43$, $P = 0.0015$) and red maple ($F = 20.98$, $P = 0.0038$) groups differed between years, but no treatment or treatment × year effects were detected.

3.3. Individual seedling dynamics

We tracked the status and height of 1096 total individual seedlings from the red oak (280), white oak (195), red maple (186), mesophytic, (115) and pyrophilic (320) species groups. Regardless of species group, we found no significant effect of treatment on three-year mortality. Averaged across treatments, three-year mortality was 29.0, 28.5, 31.8, 29.3, and 25.0% for the red oak, white oak, red maple, mesophytic, and pyrophilic species groups, respectively (Fig. 4).

We observed a significant effect of year, irrespective of treatment, on seedling height of surviving tagged seedlings for the red oak group ($F = 6.54$, $P = 0.0431$). Averaged (SE) across treatments, pre-burn height was greater than post-burn height (pre-burn: 23.0 (1.8) cm vs. post-burn: 18.8 (2.0) cm). For the white oak and red maple groups, we observed a significant year (white oak: $F = 44.39$, $P = 0.0006$; red

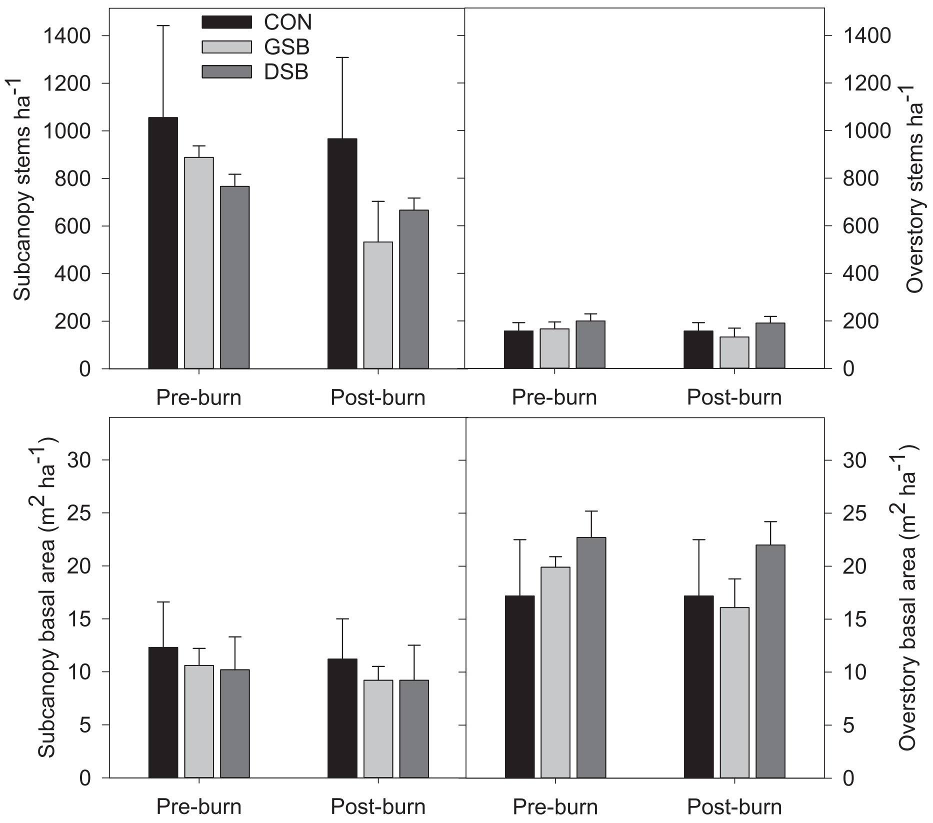

Fig. 2. Stems ha^{-1} and basal area (m^2 ha^{-1}) of the subcanopy (stems ≥ 5.0 and < 25.0 cm dbh) and overstory (stems ≥ 25.0 cm dbh) strata pre- and post-burn. CON = control, GSB = growing-season burn, DSB = dormant-season burn. Post-burn is three growing seasons following fire for GSB and DSB; three years following the collection of pre-treatment data in CON. Values and error bars represent the mean and standard error, respectively.

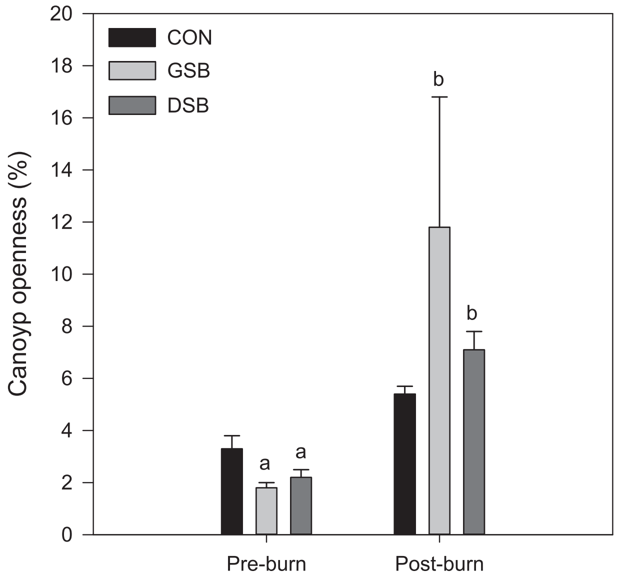

Fig. 3. Canopy openness (%) pre- and post-burn. CON = control, GSB = growing-season burn, DSB = dormant-season burn. Post-burn is three growing seasons following fire for GSB and DSB; three years following the collection of pre-treatment data in CON. Values and error bars represent the mean and standard error, respectively. Lowercase letters indicate significant differences between years within a given treatment.

maple: $F = 34.81$, $P = 0.0011$) and treatment × year (white oak: $F = 5.26$, $P = 0.0480$; red maple: $F = 14.74$, $P = 0.0048$) effect. Regardless of year, there were no significant differences in seedling height among treatments for the white oak group (Fig. 5). However, height of white oak seedlings was dynamic in GSB and DSB, with seedling height post-burn significantly lower than pre-burn. For red maple, seedling height of tagged seedling varied among treatments

Table 2

Density (stems ha^{-1}) of seedlings (stems < 1.2 m) and saplings (stems ≥ 1.2 m and < 5.0 cm dbh) by species group pre- and post-burn. CON = control, GSB = growing-season burn, DSB = dormant-season burn. Post-burn is three growing seasons following fire for GSB and DSB; three years following the collection of pre-treatment data in CON. Values represent the mean (one standard error). Lowercase letters indicate significant differences between years within a given size class and treatment. Uppercase letters indicate significant differences among treatments within a given size class and time period (pre- and post-burn). See Table 1 for composition of species groups.

	Seedlings		Saplings	
	Pre-burn	Post-burn	Pre-burn	Post-burn
Red oak				
CON	3431 (1401)	3625 (1555)	97 (77)	14 (14)
GSB	3167 (661)	2542 (851)	14 (14)	0 (0)
DSB	4778 (847)	5278 (1148)	97 (28)	0 (0)
Average	3792 (568)	3815 (728)	69 (28)^{a}	5 (5)^{b}
White oak				
CON	4083 (1764)	3750 (1735)	139 (74)	111 (61)
GSB	1778 (731)	2028 (583)	125 (125)	0 (0)
DSB	4681 (611)	5889 (653)	139 (97)	28 (14)
Average	3514 (728)	3889 (792)	134 (51)	46 (25)
Red maple				
CON	3750 (671)	4542 (679)	514 (133)	403 (109)
GSB	3778 (1457)	5681 (489)	778 (50)	347 (114)
DSB	6944 (1504)	6708 (1310)	958 (253)	250 (42)
Average	4824 (827)	5644 (547)	750 (106)^{a}	333 (52)^{b}
Mesophytic				
CON	1319 (720)	1917 (741)^{A}	125 (125)	111 (111)
GSB	778 (406)^{a}	5667 (856)^{Bb}	194 (114)^{a}	56 (56)^{b}
DSB	736 (205)^{a}	2069 (1054)^{Ab}	56 (37)^{a}	14 (14) ^{b}
Average	944 (264)	3218 (758)	125 (54)	60 (39)
Pyrophilic				
CON	7250 (1029)	7847 (1122)	500 (158)	486 (200)
GSB	4778 (984)	7500 (709)	264 (121)	347 (69)
DSB	4444 (1040)	6833 (1104)	403 (153)	97 (37)
Average	5491 (674)^{a}	7394 (520)^{b}	389 (80)	310 (84)

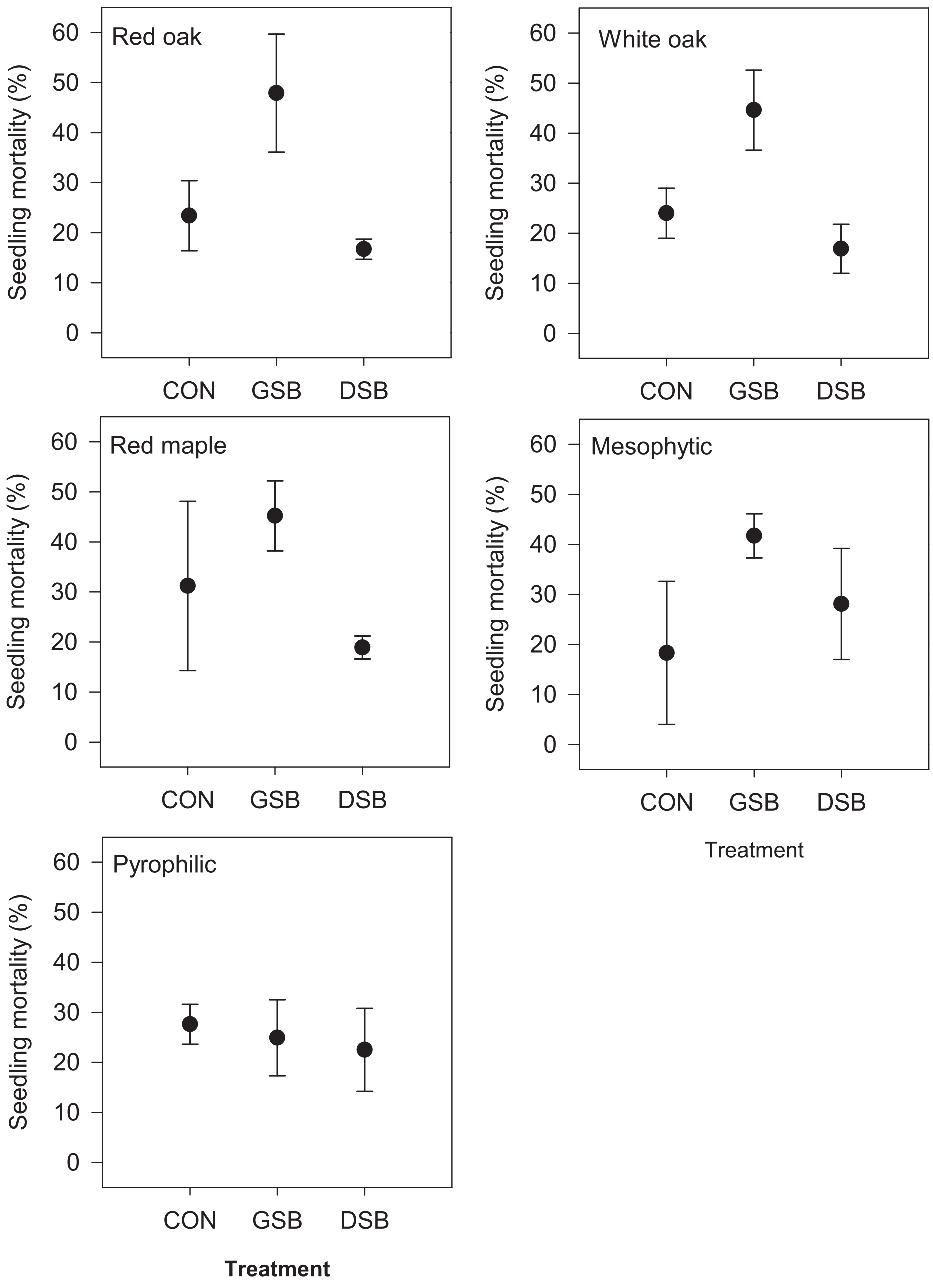

Fig. 4. Mortality (%) of individual tagged seedlings (stems < 1.2 m) in a given species group. Values and error bars represent the mean and standard error, respectively. CON = control, GSB = growing-season burn, DSB = dormant-season burn. Post-burn is three growing seasons following fire for GSB and DSB and four years following the collection of pre-treatment data in CON. Species groups are defined in Table 1.

prior to burning. Post-burn, however, differences among treatments were not detected. Red maple seedling height was dynamic in DSB and GSB, with height post-burn significantly lower than prior to burning. For the mesophytic and pyrophilic groups, no significant treatment, year, or treatment × year effects were observed. Across treatment and years, seedling height for mesophytic and pyrophilic groups averaged (SE) 21.4 (1.7) cm and 32.2 (1.5) cm, respectively.

Across species groups, pre-burn GLD and height were significantly smaller for seedlings recorded dead versus live three years post-burn (Table 3). For the red and white oak species groups, the most parsimonious (lowest AIC) and best supported (highest Akaike weight) model describing the probability of individual seedling mortality included treatment, pre-burn height, and treatment × pre-burn height (Table 4). For red oak, GSB resulted in a greater probability of mortality than DSB when pre-burn height was < 40 cm (Fig. 6). When red oak seedlings exceeded approximately 20 cm and 30 cm tall, predicted probability of mortality was greater in CON than DSB and GSB, respectively. The probability of mortality of seedlings in the white oak group was greater in GSB than CON and DSB when seedlings were < 40 cm and 70 cm tall, respectively, whereas the probability of mortality was lower in DSB than CON when seedlings were between 20 and 100 cm tall. For red maple, the best supported probability of mortality model included treatment and pre-burn height, with GSB causing greater mortality across the range of pre-burn seedling height than either DSB or CON. For both the mesophytic and pyrophilic groups, the best model predicting probability of mortality included only pre-burn seedling height. For these two species groups, the probability of mortality was inversely related to seedling size, and never exceeded 50%. (see Table 5).

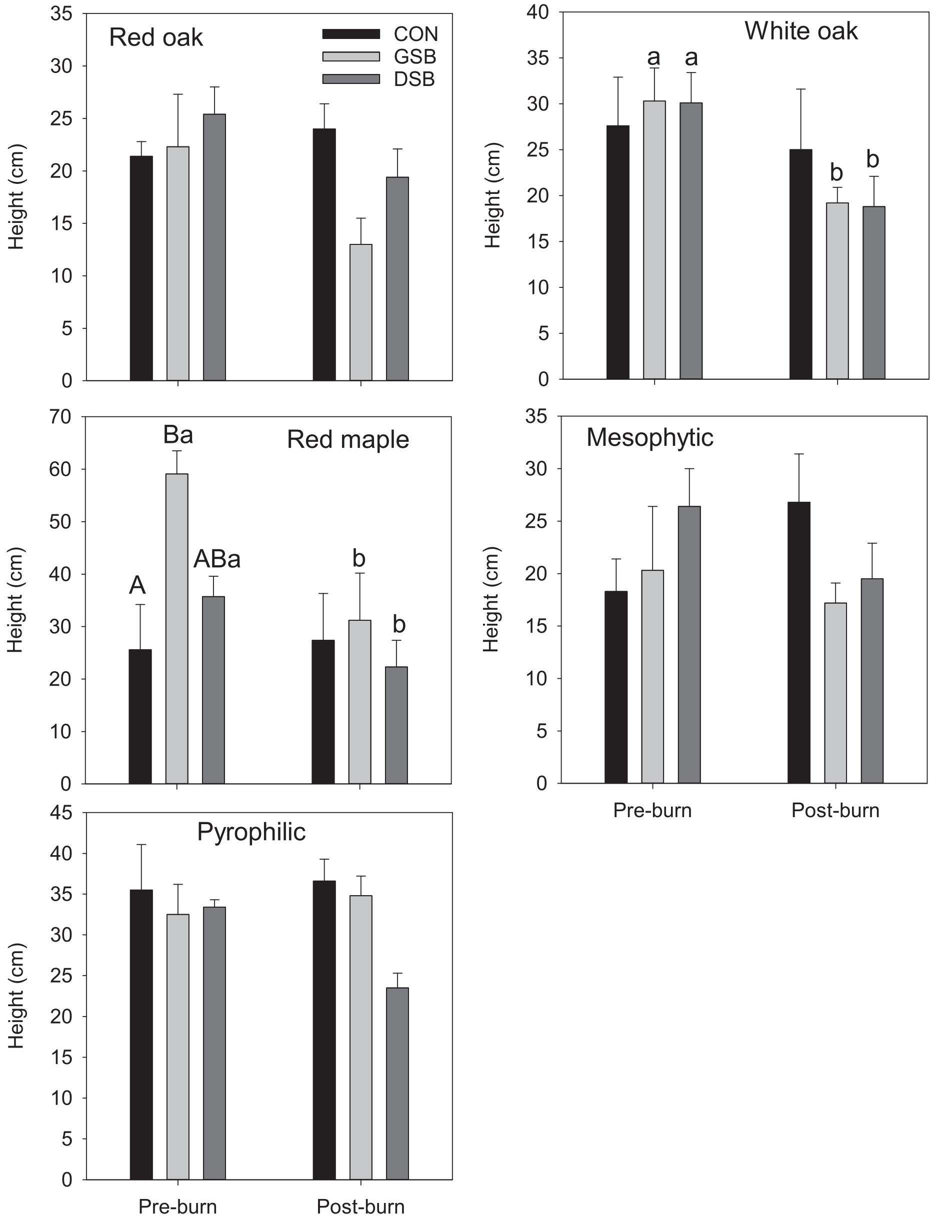

Fig. 5. Height (cm) of individual tagged seedlings pre- and post-burn. CON = control, GSB = growing-season burn, DSB = dormant-season burn. Post-burn is three growing seasons following fire for GSB and DSB; four years following the collection of pre-treatment data in CON. Values and error bars represent the mean and standard error, respectively. Uppercase letters indicate significant differences among treatments within a given year. Lowercase letters indicate significant differences between years within a given treatment.

4. Discussion

4.1. Forest structure

We found prescribed fire, regardless of season applied, was ineffective at reducing stems ha^{-1} and basal area in the overstory (stems ≥ 25 cm dbh) forest stratum after three growing seasons, providing no support for our hypothesis (H1) that a single growing-season burn would result in reduced stem density relative to a dormant-season burn and unburned sites. For species common to the overstory and subcanopy strata of oak-hickory forests, the probability of mortality following prescribed fire is inversely related to dbh (Keyser et al., 2018). This is supported by other research showing that overstory structure and composition of hardwood forests changes little following single or multiple burns low-intensity conducted during the dormant-season (Arthur et al., 2015; Waldrop et al., 2016).

Results from other studies indicate that burn season in longleaf pine (*P. palustris*) stands has little effect on overstory (stems ≥ 12.6 cm dbh) structure and composition, with annual and periodic growing-season burning doing little to kill either pine or hardwood trees (Waldrop et al., 1992). Although overstory structure and composition tend to be unaffected by low-intensity fire, crown vigor of surviving overstory trees, regardless of species, can be significantly reduced (Arthur et al., 2015). This may be the reason underlying the small, but significant, increase in canopy openness observed in DSB and GSB in this study. Given crown vigor is related to understory light availability (Eschtruth et al., 2006), the focus of this study and others on simple density metrics may over-simplify the effects of fire on post-burn forest dynamics.

We found no significant effects of a single burn, regardless of season conducted, on the stems ha^{-1} and basal area of the subcanopy (stems ≥ 5 and < 25 cm dbh) stratum, again, providing no support for our hypothesis (H1) that changes in structure would be more pronounced following a single growing- versus dormant-season burn. In contrast to our results, numerous other studies conducted in oak-

Table 3
Pre-burn groundline diameter (GLD; cm) and pre-burn height (cm) of seedlings recorded as live and dead three years following prescribed fire by species group. Values represent the median ± standard deviation (minimum, maximum). *indicates a significant difference (α = 0.05) in GLD and height between trees recorded as live and dead three years post-burn according to Wilcoxon Rank Sum Test. Species groups defined in Table 1.

	N	GLD	Height
Red oak			
Live	210	0.40 ± 0.28 (0.08, 1.72)*	21.0 ± 16.9 (10.0, 81.0)*
Dead	70	0.27 ± 0.22 (0.10, 1.13)	15.0 ± 10.9 (6.0, 72.0)
White oak			
Live	140	0.42 ± 0.45 (0.12, 3.00)*	25.0 ± 24.3 (10.0, 118.0)*
Dead	55	0.23 ± 0.18 (0.11, 1.14)	15.0 ± 7.6 (10.0, 50.0)*
Red maple			
Live	132	0.46 ± 0.46 (0.06, 2.27)*	29.0 ± 31.2 (6.0, 115.0)*
Dead	54	0.20 ± 0.34 (0.05, 1.90)	13.5 ± 18.8 (4.0, 90.0)*
Mesophytic			
Live	79	0.34 ± 0.32 (0.05, 1.75)*	18.0 ± 20.6 (5.0, 101.0)*
Dead	36	0.22 ± 0.31 (0.05, 1.82)	13.0 ± 9.6 (6.0, 59.0)
Pyrophilic			
Live	239	0.39 ± 0.39 (0.08, 3.00)*	27.0 ± 25.3 (4.0, 117.0)*
Dead	81	0.27 ± 0.36 (0.04, 2.10)	15.0 ± 22.9 (6.0, 119.0)

hickory forest types suggest even a single burn can reduce subcanopy density and modify species composition (Hutchinson et al., 2005; Blakenship and Arthur, 2006; Arthur et al., 2015), or reduce percent canopy cover (Waldrop et al., 2016). Discrepancies between the results presented in this study and those reported by others may be explained, in part, by factors unrelated to the treatments. For example, the relatively small burn units may have limited the variation in fire behavior and resultant fire effects on vegetation observed in other, large-scale studies (e.g., Alexander et al., 2008). It is also possible our sampling design (three inventory plots per burn unit) was insufficient at capturing the variability in fire effects on vegetation within the experimental units. Regardless of the initial and short-term results, numerous studies indicate that repeated burning, regardless of season burned, may be necessary to sustain initial reductions and further reduce the density and abundance of shade-tolerant and fire-sensitive species in the subcanopy (Arthur et al., 2015; Waldrop et al., 2016).

Periodic growing-season burns can be more effective than dormant-season burns at reducing the density of small diameter hardwood species and hastening the creation of more open understory conditions in a variety of southeastern U.S. pine forests. For example, in a longleaf pine forest, Glitzenstein et al. (1995) found that fire intensity, which was greater in growing-season than dormant-season burns, could not fully explain decreased density of understory oak species, providing evidence that the level of physiological activity and related root carbohydrate content at the time of burning influences the susceptibility of hardwood species to top-kill and mortality. Although we found no significant effect of burning on structure and composition of the forest subcanopy, we suggest that delayed post-fire tree mortality (e.g., Thies et al., 2006), coupled with repeated dormant- or growing-season burns, will gradually create substantial changes in the subcanopy forest structure (Hutchinson et al., 2012a; Waldrop et al., 2016)

4.2. Regeneration layer

Lack of disturbance, including fire, has resulted in a build-up of mesophytic and fire-sensitive species in the forest understory (Nowacki et al., 1990), including seedlings and saplings that are, in many instances, capable of outcompeting oak and hickory species following disturbance (Loftis, 1990). We found no support for our hypothesis (H2) that one burn would reduce the abundance of fire-sensitive species in the arborescent regeneration layer, regardless of burn season. Significant treatment effects on the seedling and sapling layers were limited to the mesophytic species group, where, unexpectedly, three years post-burn seedling density was significantly greater in GSB than in both DSB and CON. As documented by McNab (2016), the increase in mesophytic seedling density following GSB may be attributable to the germination and establishment of yellow-poplar. Our results are consistent with Vander Yacht et al. (2017), who reported no differential

Table 4
Model comparisons associated with probability of individual seedling mortality three years post-burn. TRT = treatment, HGT = pre-burn height (cm), GLD = pre-burn groundline diameter (cm).

	AIC	ΔAIC	Akaike weight		AIC	ΔAIC	Akaike weight
Red oak				*White oak*			
Null	314.55	19.21	0.0000	Null	232.09	47.5	0.0000
TRT	307.38	12.04	0.0014	TRT	225.48	40.89	0.0000
HGT	303.06	7.72	0.0120	HGT	196.72	12.13	0.0021
GLD	307.33	11.99	0.0014	GLD	210.14	25.55	0.0000
TRT + HGT	296.81	1.47	0.2729	TRT + HGT	188.91	4.32	0.1031
TRT + GLD	300.08	4.74	0.0532	TRT + GLD	200.93	16.34	0.0003
TRT + HGT + TRT * HGT	295.03	0.00	0.5691	TRT + HGT + TRT * HGT	184.59	0.00	0.8943
TRT + GLD + TRT * GLD	299.03	3.69	0.0899	TRT + GLD + TRT * GLD	201.28	16.69	0.0002
Red maple				*Mesophytic*			
Null	216.1	22.82	0.0000	Null	146.8	9.02	0.0068
TRT	214.09	20.81	0.0000	TRT	150.02	12.24	0.0014
HGT	198.46	5.18	0.0510	HGT	137.78	0.00	0.6221
GLD	204.23	10.95	0.0028	GLD	140.29	2.51	0.1773
TRT + HGT	193.28	0.00	0.6795	TRT + HGT	140.91	3.13	0.1301
TRT + GLD	200.27	6.99	0.0206	TRT + GLD	143.55	5.77	0.0347
TRT + HGT + TRT * HGT	195.34	2.06	0.2426	TRT + HGT + TRT * HGT	144.82	7.04	0.0184
TRT + GLD + TRT * GLD	203.88	10.6	0.0034	TRT + GLD + TRT * GLD	146.22	8.44	0.0091
Pyrophilic							
Null	364.38	12.41	0.0014				
TRT	367.99	16.02	0.0002				
HGT	351.97	0.00	0.6771				
GLD	358.04	6.07	0.0326				
TRT + HGT	355.61	3.64	0.1097				
TRT + GLD	361.58	9.61	0.0055				
TRT + HGT + TRT * HGT	354.8	2.83	0.1645				
TRT + GLD + TRT * GLD	360.61	8.64	0.0090				

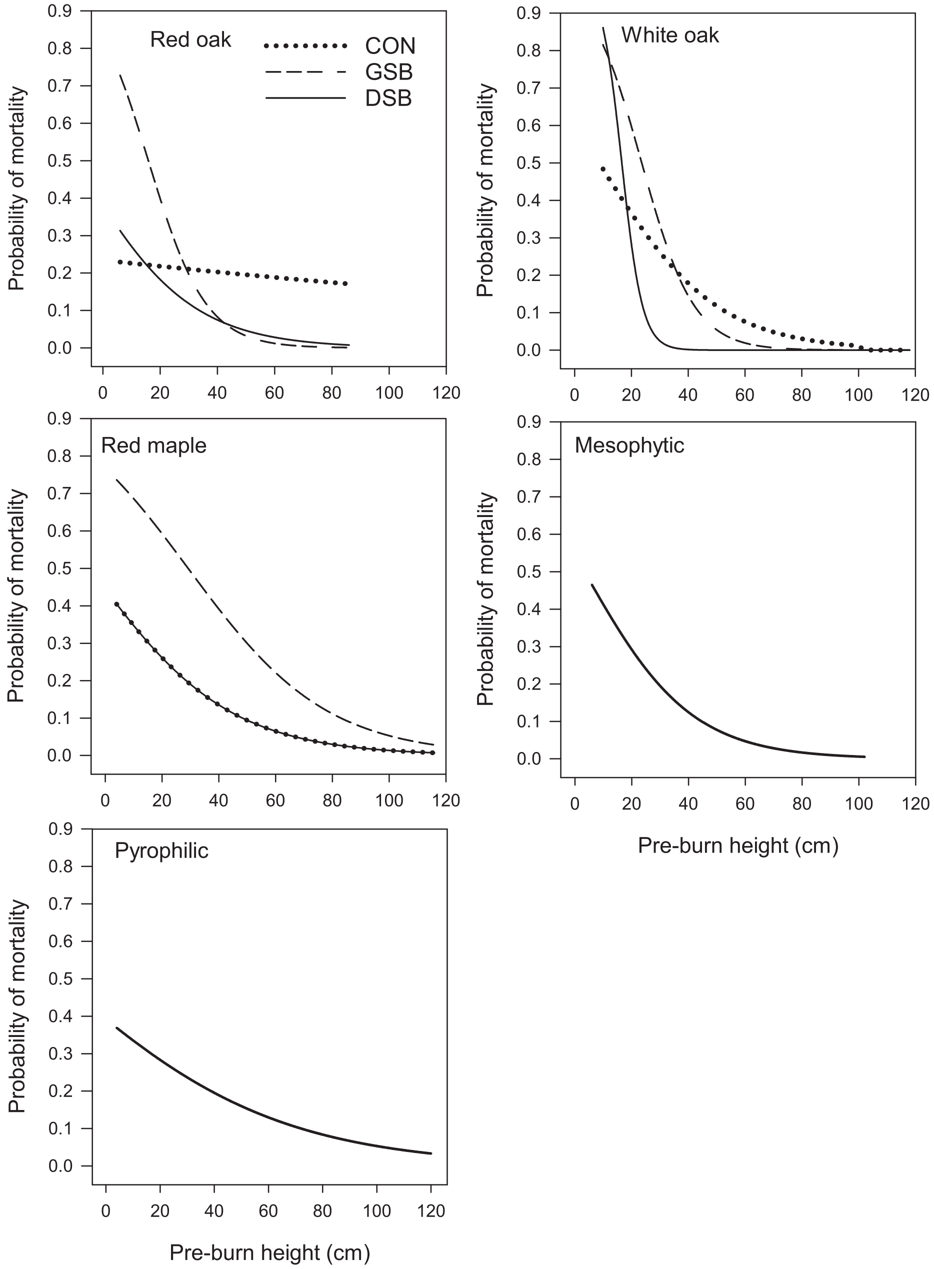

Fig. 6. Probability of individual seedling mortality three years following a prescribed burn modeled using parameter coefficients from the most parsimonious models for each species group (see Table 4). CON = control, GSB = growing-season burn, DSB = dormant-season burn. Parameter coefficients are presented in Table 5.

Table 5
Parameter estimates (standard error) associated with the most parsimonious species-specific models predicting the probability of seedling mortality three years following a single prescribed burn (see Table 4). HGT = pre-burn seedling height (cm), CON = control, DSB = dormant-season burn, GSB = growing-season burn (reference).

	Red oak	White oak	Red maple	Mesophytic	Pyrophilic
Intercept	1.5830 (0.7632)	2.1381 (0.8976)	1.1899 (0.4512)	0.1794 (0.4215)	−0.4400 (0.2472)
Treatment					
CON	−2.7671 (0.9708)	−1.9103 (1.1351)	−1.3182 (0.5223)	–	–
DSB	−2.0629 (0.9492)	1.3369 (1.6587)	−1.4135 (0.5228)	–	–
GSB	–	–	–	–	–
HGT	−0.0997 (0.0402)	−0.1085 (0.0456)	−0.0408 (0.0103)	−0.0532 (0.0231)	−0.0244 (0.0073)
*TRT * HGT*					
CON	0.0951 (0.0461)	0.0599 (0.0537)	–	–	–
DSB	0.0488 (0.0466)	−0.1665(0.1001)	–	–	–
GSB	–	–	–	–	–

effects of early (late March) versus late (early October) growing-season burns on the density of either phyrophilic or pyrophobic seedlings (stems < 1.4 m) and small saplings (stems ≥ 1.4 m and < 7.6 cm dbh) in oak-hickory forests of eastern Tennessee. In contrast, Brose and Van Lear (1998) documented that a single growing-season burn conducted following timber harvest in an upland hardwood forest reduced the abundance and size of fire-sensitive species in the seedling and sapling layer, thereby promoting oak and hickory in the forest understory; their results were still evident 11 years post-treatment (Brose, 2010). In many instances, aggressive sprouting resulting from fire-related damage/top-kill (Arthur et al., 2015), along with continued or increased recruitment of new germinants (Royse et al., 2010) can ameliorate immediate post-burn reductions in seedling and sapling densities. It is likely that periodic burning conducted over long periods, regardless of season, will be required to substantially alter the abundance, size distribution, and composition of the arborescent regeneration layer (Hutchinson et al., 2012a; Iverson et al., 2017).

4.3. Individual seedling dynamics

Mesophytic species, including red maple, possess functional traits (e.g., thin bark, low root:shoot ratio, epigeal germination, meristematic buds often located above the soil surface) that confer susceptibility to fire-related top-kill and mortality. In this study, we found that post-burn seedling mortality was similar among species groups. In contrast, in Missouri, oak and hickory species tended to have lower rates of mortality following annual and periodic fire relative to other pyrophobic species (Fan et al., 2012). In eastern Kentucky, mortality of individual seedlings (stems < 75 cm) three years after a single dormant-season burn, was higher for red maple and species in the white oak group than species in the red oak group and sassafras (*Sassafras albidum*) (Alexander et al., 2008). Interestingly, both Green et al. (2010) and Alexander et al. (2008) found that repeated burning did little to modify mortality trends observed following a single burn in eastern Kentucky, whereas Dey and Hartman (2005) found a significant effect of periodic burning on the probability of survival of various hardwood tree species in Missouri. These incongruities emphasize the differences in response to disturbance of eastern hardwood tree species across the broad range of oak-hickory ecosystems.

Differences in fire intensity and the size distribution of sampled seedlings among studies confound direct comparisons of mortality. However, models that forecast mortality are consistent; the probability of mortality decreases as pre-burn seedling size increases (Dey and Hartman, 2005; Alexander et al., 2008; Fan et al., 2012). Bark thickness, a primary determinant of the ability to withstand fire (Harmon, 1984), increases as seedlings mature (Hoffmann and Solbrig, 2003), conferring increased resistance to both top-kill and mortality. For many species, including oaks, seedling size is positively correlated with belowground biomass (Dey and Parker, 1997), which is related to the ability to re-sprout following top-kill (Hodges and Gardiner, 1992). Because of the propensity to re-sprout, fire-affected individuals often remain a component of the arborescent regeneration layer even after repeated burning (Fan et al., 2012; Arthur et al., 2015; Waldrop et al., 2016).

Although we found no treatment differences in three-year mortality within any species group, we did find that burn season affected the probability of individual seedling mortality for the red oak, white oak, and red maple species groups after controlling for pre-burn seedling size. Results for these three species groups are consistent with other studies in both oak-hickory (Brose and Van Lear, 1998) and longleaf pine (Glitzenstein et al., 1995; Drewa et al., 2002) forest types, suggesting that loss of aboveground biomass during the early growing-season, when root carbohydrates concentrations are low (Kays and Canham, 1991), can cause an increased mortality of arborescent species in the forest understory. Interestingly, seedlings in the red oak group had a lower probability of mortality in DSB and GSB than CON when seedlings exceeded 20 and 40 cm, respectively. Relative to species in the white oak group, those in the red oak group are less tolerant of shade, and often experience higher mortality under closed-canopied conditions (Crow, 1992). In contrast, the probability of red maple mortality was effectively the same in CON and DSB, suggesting one of oaks' main competitors under closed canopied conditions (Lorimer, 1993) may be best controlled with prescribed fire during the growing-season. The higher probability of seedling mortality in both the red and white oak groups observed in this study (particularly following GSB) and elsewhere (Alexander et al., 2008; Dey and Hartman, 2005; Fan et al., 2012) may appear counterproductive to meeting oak restoration goals and objectives in the short-term. However, high probability of mortality ($> 50\%$) in this study was limited to smaller diameter stems. Prevailing thought suggests over a longer time frame, these species, which possess a conservative growth strategy relative to mesophytic competitors, should be favored in response to periodic burning, regardless of burn season (Brose et al., 2013).

With the exception of the white oak and red maple groups, where post-burn height of surviving seedlings was significantly lower than pre-burn in DSB and GSB, prescribed fire, regardless of season, had little effect on absolute seedling height. Post-burn height reductions of re-sprouting hardwood seedlings are common and most pronounced during the initial years after burning (Dey and Hartman, 2005; Fan et al., 2012). Height recovery to pre-burn levels by top-killed and re-sprouting hardwood seedlings can occur with sufficient fire-free periods (Alexander et al., 2008), as re-sprouting hardwood seedlings display high relative growth rates (Kruger and Reich, 1993). The recovery of height beyond pre-burn levels, however, appears to be limited to areas where higher fire intensities cause more severe reductions in canopy cover (Alexander et al., 2008). Repeated burning without concomitant reductions in overstory density and/or fire-free periods can impede long-term height development of hardwood tree species and restrict recruitment into size classes capable of withstanding top-kill and/or mortality following fire (Fan et al., 2012).

5. Conclusions

Although quantitative information related to the effects of burn season on overstory and understory arborescent vegetation is relatively common in longleaf pine forests of the southeastern U.S. (Waldrop et al., 1992; Glitzenstein et al., 1995; Addington et al., 2015), information specific to eastern hardwood forests is largely lacking. Meta-analyses suggesting that burning in the growing-season promotes the establishment, growth, and recruitment of ecologically valuable oak and hickory species are based on relatively few studies, and studies directly comparing the effects of burn season in hardwood forests are largely absent (Brose et al., 2013). Our study is one of only a few experimentally-controlled studies conducted in mature, closed-canopy oak-hickory forest types to test the effects of dormant versus growing-season burning on the structure of arborescent vegetation.

Results of studies are consistent; a single burn applied during the dormant-season results in little to no change in forest structure and composition and is ineffective at achieving specific oak-hickory restoration objectives. Even multiple burns, conducted over a long time period (i.e., 10 years) under closed-canopied stands, cause only very minor, often ephemeral changes in the structure and composition of the overstory, midstory, and arborescent regeneration layers (Hutchinson et al., 2012a; Waldrop et al., 2016; Keyser et al., 2017). Lack of positive effects in the forest understory are likely caused by fire's limited impact on overstory structure and resultant understory light conditions (Chiang et al., 2005; Alexander et al., 2008; Fan et al., 2012).

Evidence from studies in southern pine forest ecosystems (Waldrop et al., 1992) coupled with the limited information available from oak-hickory forests (Barnes and Van Lear, 1998; Brose and Van Lear, 1999; Brose, 2010) suggest burning in the growing-season may be more efficient and effective at causing changes in structure and composition of the arborescent vegetation layers. In this study, we found no effect of burning, regardless of season, on the structure of the subcanopy and overstory strata after three growing-seasons. Similarly, only minor changes in the arborescent vegetation layer were detected following GSB, with the most significant being slight reductions in post-burn height of seedlings in the white oak and red maple groups.

As is the case for dormant-season burns, it is likely that periodic growing-season burns will be required to alter forest structure and reduce the abundance of non-oak and hickory species in the forest understory. Even with repeated burning conducted over long periods of time, studies suggest natural or anthropogenic disturbances that cause mortality of the forest overstory (e.g., partial harvesting, canopy openings due to oak decline and/or windthrow) will be necessary to initiate and sustain meaningful changes in the structure and composition of the arborescent regeneration pool and increase the probability of successful, sustained oak and hickory regeneration and recruitment (Brose, 2010; Hutchinson et al., 2012b; Iverson et al., 2017), regardless of burn season.

Further research is needed on the effects of multiple growing-season fires on structure and composition of oak-hickory forest types. The results of this short-term study suggest that a single growing-season burn is no more effective than a single dormant-season burn at achieving oak and hickory restoration objectives. We suggest that a focus on burn season alone for attaining restoration goals is too simplistic, and ignores the myriad other factors controlling the complex oak and hickory regeneration process (Arthur et al., 2012). More experimentally-designed studies focused on the mechanisms underlying season of burn effects, and across the broad geographic range of eastern oak-hickory forest types, are required to answer relevant questions related to short- and long-term effects that burn season has on stand dynamics of these complex forest ecosystems.

Acknowledgments

This research was initiated by the USDA Forest Service, Southern Research Station, Upland Ecology and Management Research Work Unit in partnership with the Pisgah District of the Pisgah National Forest. We thank Derek Ibarguen, Bill Coates, Patrick Scott, Riva Duncan, and many others for planning and conducting the prescribed burn treatments. Kenneth Frick, Jim Kerzwick, Tracy Roof, Brandy Benz, Jacqui Adams, and Julia Kirschman provided logistical and field support. This paper was written and prepared by USA Government employees on official time, and therefore, is in the public domain and not subject to copyright in the USA.

Conflict of interest

The authors declare that they have no conflict of interest.

References

Addington, R.N., Knapp, B.O., Sorrell, G.G., Elmore, M.L., Wang, G.G., Walker, J.L., 2015. Factors affecting broadleaf woody vegetation in upland pine forests managed for longleaf pine restoration. For. Ecol. Manage. 15, 130–138.

Alexander, H.D., Arthur, M.A., Loftis, D.L., Green, S.R., 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. For. Ecol. Manage. 256, 1021–1030.

Arthur, M.A., Blankenship, B.A., Schorendorfer, A., Loftis, D.L., Alexander, H.D., 2015. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. For. Ecol. Manage. 340, 36–61.

Arthur, M.A., Alexander, H.D., Dey, D.C., Schweitzer, C.J., Loftis, D.L., 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. J. For. 110, 257–266.

Barnes, T.A., Van Lear, D.H., 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. South. J. Appl. For. 22, 138–142.

Blakenship, B.A., Arthur, M.A., 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau Kentucky. For. Ecol. Manage. 225, 134–145.

Brose, P.H., 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. For. Ecol. Manage. 9, 1516–1524.

Brose, P.H., Van Lear, D.H., 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can. J. For. Res. 28, 331–339.

Brose, P.H., Van Lear, D., 1999. Effects of seasonal prescribed fires on residual overstory trees in oak-dominated shelterwood stands. South. J. Appl. For. 23, 88–93.

Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America. For. Sci. 59, 322–334.

Brose, P.H., Dey, D.C., Waldrop, T.A., 2014. The fire-oak literature of eastern North America: synthesis and guidelines. USDA For. Serv. Gen. Tech. Rep. NRS-135. Newtown Square PA. Northern Res. Stat. 98, p.

Burke, M.K., Raynal, D.J., Mitchell, M.J., 1992. Soil nitrogen availability influences seasonal carbon allocation patterns in sugar maple (*Acer saccharum*). Can. J. For. Res. 22, 447–456.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, Heidelberg.

Caldwell, P.V., Miniat, C.F., Elliott, K.J., Swank, W.T., Brantley, S.T., Laseter, S.H., 2016. Declining water yield from forested mountain watersheds in response to climate change and forest mesophication. Glob. Change Biol. 22, 2997–3012.

Chiang, J.M., Arthur, M.A., Blankenship, B.A., 2005. The effect of prescribed fire on gap fraction in an oak forest understory on the Cumberland Plateau. J. Torrey Bot. Soc. 132, 432–441.

Crow, T.R., 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia 91, 192–200.

Cruz, A., Pérez, B., Moreno, J.M., 2003. Resprouting of the Mediterranean-type shrub *Erica australis* with modified lignotuber carbohydrate content. J. Ecol. 91, 348–356.

Delcourt, H.R., Delcourt, P.A., 1997. Pre-columbian native american use of fire on Southern Appalachian landscapes. Conserv. Biol. 11, 1010–1014.

Delcourt, P.A., Delcourt, H.R., Ison, C.R., Sharp, W.E., Gremillion, K.J., 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests, paleoecology of Cliff Palace Pond Kentucky. Am. Antiquity 63, 263–278.

Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. For. Sci. 60, 926–942.

Dey, D.C., Hartman, G., 2005. Returning fire to Ozark highland forest ecosystems: effects on advance regeneration. For. Ecol. Manage. 217, 37–53.

Dey, D.C., Parker, W.D., 1997. Overstory density affects field performance of underplanted red oak (*Quercus rubra* L.) in Ontario. North. J. Appl. For. 14, 120–125.

Dey, D.C., Kabrick, J.M., Schweitzer, C.J., 2017. Silviculture to restore oak savannas and woodlands. J. For. 115, 202–211.

Drewa, P.B., Platt, W.J., Moser, E.B., 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83, 755–767.

Eschtruth, A.K., Cleavitt, N.L., Battles, J.J., Evans, R.A., Fahey, T.J., 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Can. J. For. Res. 36, 1435–1450.

Fan, Z., Ma, Z., Dey, D.C., Roberts, S.D., 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests Missouri. For. Ecol. Manage. 266, 160–269.

Fire Effects Information System (FEIS). USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). < http://www.fs.fed.us/database/feis > .

Glitzenstein, J.S., Platt, W.J., Streng, D.R., 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol. Monogr. 65, 441–476.

Green, S.R., Arthur, M.A., Blankenship, B.A., 2010. Oak and red maple seedling survival and growth following periodic prescribed fire on xeric ridgetops on the cumberland plateau. For. Ecol. Manage. 259, 2256–2266.

Greenberg, C.H., Collins, B.S., McNab, W.H., Miller, D.K., Wein, G.R., 2015a. Introduction to natural disturbances and historic range of variation: Type, frequency, severity, and post-disturbance structure in central hardwood forests. In: In: Greenberg, C.H., Collins, B.S., (Eds.) (Eds.), Natural Disturbances and Historic Range of Variation: Type, Frequency, Severity, and Post-Disturbance Structure in Central Hardwood Forests, USA. Managing Forest Ecosystem Series 32. Springer Publishing, pp. 1–32.

Greenberg, C.H., Weeks, K., Warburton, G.S., 2015b. The historic role of humans and other keystone species in shaping central hardwood forests for disturbance-dependent wildlife. In: In: Greenberg, C.H., Collins (Eds.), B.S. (Eds.), Natural Disturbances and Historic Range of Variation: Type, Frequency, Severity, and Post-Disturbance Structure in Central Hardwood Forests, USA. Managing Forest Ecosystem Series 32. Springer Publishing, pp. 319–354.

Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the historical foundation genus of the east-central United States. Quater. Scie. Rev. 145, 94–103.

Hanberry, B.B., Kabrick, J.M., He, H.S., 2014. Densification and state transition across the Missouri Ozarks landscape. Ecosystems 17, 66–81.

Harmon, M.E., 1984. Survival of trees after low-intensity surface fire in great smoky mountains national park. Ecology 65, 796–802.

Hmielowski, T.L., Robertson, K.M., Platt, W.J., 2014. Influence of season and method of topkill on resprouting characteristics and biomass of *Quercus nigra* saplings from a southeastern U.S. pine-grassland ecosystem. Plant Ecol. 215, 1221–1231.

Hodges, J.D., Gardiner, E.S., 1992. Ecology and physiology of oak regeneration. In: Loftis, D.L., McGee, C., (Eds.), (Eds.), Oak Regeneration: Serious Problems, Practical Recommendations. USDA Gen. Tech. Rep. pp. 54–65.

Hoffmann, W.A., Solbrig, O.T., 2003. The role of topkill in the differential response of savanna woody species to fire. For. Ecol. Manage. 180, 273–286.

Hutchinson, T.F., Yaussy, D.A., Long, R.P., Rebbeck, J., Sutherland, E.K., 2012a. Long-term (13-year) effects of repeated prescribed fires on stand structure and tree regeneration in mixed-oak forests. For. Ecol. Manage. 286, 87–100.

Hutchinson, T.F., Long, R.P., Rebbeck, J., Sutherland, E.K., Yaussy, D.A., 2012b. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. Can. J. For. Res.

42, 303–314.

Hutchinson, T.F., Sutherland, E.K., Yaussy, D.A., 2005. Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio. For. Ecol. Manage. 218, 210–228.

Iverson, L.R., Hutchinson, T.F., Peters, M.P., Yaussy, D.A., 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture. Ecosphere 8, 1–24.

Kays, J.S., Canham, C.D., 1991. Effects of time and frequency of cutting on hardwood root reserved and sprout growth. For. Sci. 37, 425–539.

Keyser, T.L., McDaniel, V.L., Klein, R.N., Drees, D.G., Burton, J.A., Forder, M.M., 2018. Short-term stem mortality of ten deciduous broadleaved species following prescribed burning in upland forests of the southern US. Int. J. Wild. Fire. 27, 42–51.

Keyser, T.L., Arthur, M., Loftis, D.L., 2017. Repeated burning alters the structure and composition of hardwood regeneration in oak-dominated forests of eastern Kentucky USA. For. Ecol. Manage. 393, 1–11.

E.E. Knapp B.L. Estes C.N. Skinner Ecological effects of prescribed fire season: A literature review and synthesis for managers. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-224. Albany, CA. Pacific southwest Research Station. p. 80; 2009.

Kruger, E.L., Reich, P.B., 1993. Coppicing affects growth, root-shoot relations, and ecophysiology of potted *Quercus rubra* seedlings. Physiol. Plantarum 89, 751–760.

C.W. Lafon A.T. Nalto H.D. Grissino-Mayer S.P. Horn T.A. Waldrop. Fire history of the Appalachian Region: A review and synthesis. USDA, Forest Service, Asheville, NC, Gen. Tech. Rep. SRS-219. p. 97; 2017.

Littell, R.C., Henry, P.R., Ammerman, C.B., 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76, 1216–1231.

Loftis, D.L., 1990. Predicting postharvest performance of advance red oak reproduction in the Southern Appalachian. For. Sci. 36, 908–916.

Loftis, D.L., 1983. Regeneration southern Appalachian mixed hardwood stands with the shelterwood method. South. J. Appl. For. 7, 212–217.

Lorimer, C., 1993. Causes of the oak regeneration problem. In: Loftis, D.L., McGee, C.E., (Ed.), (Eds.), Oak Regeneration: Serious problems and practical solutions. USDA, For. Serv., Asheville, NC, Gen. Tech. Rep. pp. 14–39.

McNab, W.H., 2016. A preliminary model of yellow-poplar seedling establishment two years after a growing season prescribed fire in southern Appalachian oak stands. In: Schweitzer, C.J., Clatterbuck, W.K., Oswalt, C.M., (Eds.) (Eds.), USDA For. Serv., Asheville, NC, Gen. Tech. Rep. pp. 682–688.

McNab, W.H., Greenberg, C.H., Berg, E.C., 2004. Landscape distribution and characteristics of large hurricane-related canopy gaps in a Southern Appalachian watershed. For. Ecol. Manage. 196, 435–447.

McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers, toward and encompassing hypothesis of oak forest dynamics across eastern North America. Ecography 34, 244–256.

McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. J. Wildlife Manage. 71, 1717–1728.

Miller, G.W., Kochenderfer, J.N., Fekedulegn, D.B., 2006. Influence of individual reserve trees on nearby reproduction in two-aged Appalachian hardwood stands. For. Ecol. Manage. 224, 241–251.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "Mesophication" of forests in the eastern United States. BioScience 58, 123–138.

Nowacki, G.J., Abrams, M.D., Lorimer, C.G., 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. For. Sci. 36, 276–292.

J.R. Owenby D.S. Ezell. Monthly station normal of temperature, precipitation, and heating and cooling degree days, 1961-1990, North Carolina. Climatography of the United States No. 81, Asheville, NC. US Department of Commerce, National Oceanic and Atmospheric Administration, National Climatic Data Center; 1992.

Robertson, K.M., Hmielowski, T.L., 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern. Oecologia 174, 765–776.

Royse, J., Arthur, M.A., Schorgendorder, A., Loftis, D.L., 2010. Establishment and growth of oak (*Quercus alba*, *Quercus prinus*) seedlings in burned and fire-excluded upland forests on the Cumberland Plateau. For. Ecol. Manage. 260, 502–510.

Simone, S.A., Collins, T.K., Kauffman, G.L., McNab, W.H., Ulrey, C.J., 2005. Ecological zones in the southern Appalachians: first approximation. USDA For. Serv. Res. Pap. SRS-41 41 p.

Thies, W.G., Westlind, D.J., Loewen, M., Brenner, G., 2006. Prediction of delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon. USA. Int. J. Wild. Fire 15, 19–29.

Thomas-Van Gundy, M.A., Nowacki, G.J., 2013. The use of witness trees as pyro-indicators for mapping past fire conditions. For. Ecol. Manage. 304, 333–344.

Vander Yacht, A.L., Barrioz, S.A., Keyser, P.D., Harper, C.A., Buckley, D.S., Buehler, D.A., Applegate, R.D., 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. For. Ecol. Manage. 390, 187–202.

Waldrop, T.A., Hagan, D.L., Simon, D.M., 2016. Repeated application of fuel reduction treatments in the southern Appalachian mountains, USA: implications for achieving management goals. Fire Ecol. 12, 28–47.

Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine-grassland communities in the southeastern United States. For. Ecol. Manage. 47, 195–210.