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Northern red oak regeneration: 25-year results of cutting and prescribed fire in Michigan oak and pine stands

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A R T I C L E I N F O

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A B S T R A C T

Overstory and understory treatments were established in natural oak stands and red pine plantations in Michigan in 1991 to test the hypotheses that (1) oak seedling survival and growth would be greater in pine than oak stands and (2) removal of competitors would enhance oak seedling performance. Late spring prescribed fires were implemented in 2002 and 2008 to investigate their effectiveness in controlling understory red maple. Performance of planted northern red oaks has been monitored since 1991 and the abundance of naturally regenerating oak and red maple seedlings and sprouts in different size classes has been documented since 2001. A subset of oaks has been protected against deer browsing since planting. Results suggest partial competitor removal enhances oak seedling and sprout performance, whereas complete removal increases mortality from browsing and frost. Increases in red maple abundance and decreases in oak abundance were documented after the prescribed fires in 2015. Greater growth and survival of planted oaks was observed in the pine stands, provided they were protected from browsing. Based on these results, the most viable management scenario for maximizing survival and growth of oak seedlings and sprouts in the study region would include protecting oak seedlings from deer in 25% canopy cover shelterwoods in pine plantations. Opportunities exist for developing systems involving alternating rotations and mixtures of oak and pine.

1. Introduction

Increasing recognition of oak (*Quercus* spp.) regeneration problems stimulated several studies, reviews, and conferences focused on identifying causes and potential solutions in the 1980s and early 1990s (Abrams, 1992; Abrams and Nowacki, 1992; Crow, 1988; Laursen and DeBoe, 1991; Loftis and McGee, 1993; Lorimer, 1993, 1985). Of the potential mechanisms underlying regeneration failures, increased competition between oaks and species less adapted to fire such as red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marshall), yellow-poplar (*Liriodendron tulipifera* L.), and American beech (*Fagus grandifolia* Ehrh.) was forwarded as a predominant factor. It was hypothesized that fire exclusion over much of the 20th Century increased the abundance of these competitors throughout the eastern United States (Abrams, 2016, 1992; Crow, 1988; Lorimer, 1993; Nowacki and Abrams, 2008). Oak regeneration failures due to the competitive effects of other hardwoods are thought to be more common on productive sites than on intermediate and poor sites (Loftis and McGee, 1993). Multiple studies established in several states in the 1980s and 1990s focused on reducing overstory and understory competitors through cutting, herbicide application, and prescribed fire (e.g., Brose et al., 2001, 1999a, 1999b; Brose and Van Lear, 1998; Crow, 1988; Loftis, 1990a; Reich et al., 1990; Ross et al., 1986; Will-Wolf, 1991). More recently, McEwan et al. (2011) and Arthur et al. (2012) have pointed out that changes in climate, predators, herbivores, keystone plant species, and land use have also occurred within the same time period as changes in fire regimes and declines in oak regeneration. Deer browsing, late spring frost, and seed predation were also implicated in oak regeneration failures in the

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1990s, but were considered to be aggravating or contributing factors because their importance varied from region to region (Lorimer, 1993). Browsing and frost damage have been addressed in several oak regeneration studies and publications (Marquis et al., 1976; Miller et al., 2017; Thomas-Van Gundy et al., 2014), although competition has remained the primary focus of most projects.

Shared interest in developing techniques for enhancing oak regeneration on the part of the Michigan Department of Natural Resources (DNR) and USDA Forest Service, North Central Forest Experiment Station resulted in support for a long-term, replicated oak regeneration study established in 1991 in northern Lower Michigan (Buckley et al., 1998). The principal aims of this project were to examine the effects of canopy manipulation treatments, understory manipulation treatments, and two prescribed fires on artificial and natural oak regeneration in natural northern red oak (*Quercus rubra* L.) and planted red pine (*Pinus resinosa* Sol. Ex Aiton) stands.

Fossil pollen records indicate long-term co-occurrence of upland oaks and pines in the region, with changes in oak species dominance relative to pines throughout the past 10,000 years (Jacobson, 1979; Webb, 1974). Inventory data collected within the region and additional observations revealed patterns including oak seedlings and saplings in the understory of mature pine stands, and also young pines in the understory of mature oak stands, suggesting a potential for cyclical replacement of oaks and pines (Crow, 1988; Johnson, 1992; Sarnecki, 1990). Based on this evidence and the tendency for oak to follow pine in successional sequences, it was hypothesized that oak regeneration would be enhanced in pine stands relative to oak stands, although the exact mechanisms were unknown. Sarnecki (1990) documented abundant oak regeneration beneath red pine canopies at relatively low levels of canopy cover, suggesting that pines may provide favorable conditions for oak regeneration, while hindering other hardwood competitors. Specific objectives were to (1) test the hypothesis that northern red oak seedlings would be more successful in pine than oak stands, (2) evaluate overstory canopy treatment effects on long-term oak regeneration, (3) evaluate understory treatment effects on long-term oak regeneration, (4) evaluate oak regeneration before and after prescribed fire, and (5) test the hypothesis that woody understory competitors would be reduced with prescribed fire.

2. Materials and methods

2.1. Sampling area

Study sites were established on state forests in southern Roscommon County (84°41′ W, 44°14′ N, elevation 300 m) and southern Crawford County (84°45′ W, 44°31′ N, elevation 400 m) in Michigan. Both counties are within the Grayling Outwash Plain of the Highplains District of the northern Lower Peninsula (Albert, 1995). Soils are characteristic of sandy, mixed, frigid, Alfic Haplorthods developed in pitted outwash. Excavation of soil pits indicated that physical and chemical properties of soils were comparable among sites (Kim et al., 1996). Slopes were ≤5%. Stands utilized in the study were either second-growth natural oak, or unthinned planted red pine stands. The study sites were intermediate in productivity. Site index for northern red oak according to curves for the Lake States region was 17–18 m at a base age of 50 years (Carmean et al., 1989). Site index for red pine was about 17.2 m at age 50, based on curves for red pine in Minnesota (Gevorkiantz, 1957). The oak stands were 88–100 years old and the pine stands were 59–75 years old (Buckley et al., 1998). Deer densities for Roscommon County and Crawford County are estimated at 12–18 deer/km^2 and 6–12 deer/km^2, respectively (Quality Deer Management Association, 2017). Deer population densities between 2006 and 2015 remained stable in Roscommon County (Michigan Department of Natural Resources, 2017a) and were stable, if not increasing in Crawford County (Michigan Department of Natural Resources, 2017b).

In 1991, the herb layer (0–25 cm above ground) was dominated by grasses, sedges, blueberry (*Vaccinium angustifolium* Ait. and *Vaccinium myrtilloides* Michx.), and red maple seedlings. The shrub layer (≥25 cm above ground to stems 2.54 cm in diameter at breast height (dbh)) was predominantly comprised of bracken fern (*Pteridium aquilinum* (L.) Kuhn) and red maple saplings. Witch hazel (*Hamamelis virginiana* L.), beaked hazel (*Corylus cornuta* Marsh.), black cherry (*Prunus serotina* Ehrh.) saplings, and trembling aspen (*Populus tremuloides* Michx.) saplings were also present in the shrub layer. Extensive presettlement forests of eastern white pine (*Pinus strobus* L.), red pine, jack pine (*Pinus banksiana* Lamb.), oak-pine mixtures, and northern hardwoods covered the uplands of Crawford and Roscommon counties (Whitney, 1986). Presettlement stands of large eastern white and red pine on pitted outwash often contained oak in the subcanopy (Whitney, 1986). Following turn of the 20th century logging and repeated burning, extensive areas of both counties were replanted with eastern white pine, red pine, and various mixtures of eastern white, red, and jack pine between 1900 and 1956 (Stone, 1958). Red pine plantations were selected for this study, as natural pine stands of sufficient size and density for experimentation no longer existed in the study region.

2.2. Experimental design

Three replicate oak blocks and three replicate pine blocks measuring 1.74 ha each were subdivided into four 66 × 66 m plots measuring 0.44 ha each. One of four canopy cover treatments (0% residual canopy, 25% residual canopy, 75% residual canopy, or uncut control, hereafter referred to as 0%, 25%, 75%, and 100%, respectively) was randomly assigned to each plot (Buckley et al., 1998). A minimum 20 m-wide buffer zone was established between each treated area and adjacent access roads. Stands receiving canopy cover reduction treatments were cut from fall 1990 to early spring 1991. Partial canopy cover treatments were performed by initially cutting subcanopy trees ≥ 2.54 cm dbh from below, then cutting additional canopy trees as needed to meet the required treatment objective. In all treatments, red maple and suppressed red pine in subordinate canopy positions were cut first. In 0% treatments, all woody plants ≥ 2.54 cm dbh were cut. Soil compaction and understory vegetation disturbance were minimized by restricting logging equipment to the buffer zones. Woody debris was cleared from planting areas by hand.

Four 15 × 15 m understory treatment subplots (0.02 ha each) were arranged in a square pattern at the center of each canopy treatment plot (Buckley et al., 1998), which resulted in an 18 m buffer between understory subplots and the edge of the canopy treatment plot. Four understory treatments were randomly assigned to the understory treatment subplots within each canopy treatment: Shrub Layer Removal (S) (herbs, shrubs, and saplings ≥ 25 cm tall up to 2.54 cm dbh), Herb Layer Removal (H) (herbs, shrubs, and seedlings < 25 cm tall), Litter Removal down to humus layer (L), and Control (C). All treatments were completed with hand tools just prior to planting in 1991 and were maintained periodically from 1992 to 2001. No maintenance of understory treatments occurred between 2001 and 2015.

Northern red oak acorns and nursery seedlings were planted for comparison of treatment effects on seedlings at different stages of development. As outlined by Buckley et al. (1998), all acorns for direct seeding were collected from 20 to 30 dominant trees growing on a range of sites in October of 1990 at the University of Michigan Biological Station (UMBS), located in Cheboygan County, Michigan. Nursery seedlings (2–0) were acquired from Wyman State Tree Nursery in Manistique, Michigan.

Acorns and nursery seedlings were planted 2 m apart on a 10 × 10 m grid within each 15 × 15 m understory treatment plot in late April of 1991. Twenty grid points were randomly selected to receive acorns, 12 were randomly selected to receive nursery seedlings, and four were reserved for related studies (Zhou et al., 1998; Zhou and Sharik, 1997). In total, 5760 acorns and 1152 nursery seedlings were planted. Three acorns were planted at each direct seeding location, 3 cm below the mineral soil surface. Following emergence, seedlings were randomly thinned to one seedling per location. Temporary hardware-cloth (1.27 × 1.27 cm mesh) cages measuring 20 × 20 cm on a side were installed over all direct-seeded locations to exclude seed predators. These temporary cages were removed following seedling emergence in late spring 1991. All nursery seedlings were protected from browsing with 0.45 m diameter × 1.83 m tall cylindrical cages constructed of poultry netting. At the end of the 1991 growing season, six direct-seeded seedlings and six nursery seedlings were selected for permanent caging. These original cages were replaced with new cages in April 2008.

2.3. Fire methods

Heavy development of understory red maple outside of the shrub removal plots by the 2000 remeasurement of the study provided the impetus to investigate the effectiveness of prescribed fire in reducing red maple abundance. Pre-burn assessments suggested that fire treatments could not be implemented under identical conditions across all sites due to varying amounts of precipitation and excluded wind directions. However, when fire treatments were applied, the average wind speeds and relative humidities were nearly uniform for all sites. The goal of both prescribed fires in 2002 and 2008, Fire 1 and Fire 2, hereafter, was to attain strip-head fires with approximately 0.9 m flame lengths so as to top-kill all planted oak seedlings and their competitors on all six blocks. All prescribed fires were implemented a few days after red maple budbreak.

Fire 1 in the oak stands was implemented on 15 May 2002. The nearest weather station recorded 0.15 cm of precipitation two days prior to burning. On-site dry bulb temperature was 18 °C, with an average relative humidity of 34%. Weather station wind speed was recorded at 16 km/h, but mid-flame wind speed averaged only 1.6 km/h. The combination of southwesterly winds and a north-facing slope hindered effective wind speed across oak stands.

Oak stands were burned a second time on 16 May 2008. The nearest weather station recorded a 0.13 cm precipitation event the day of the fire. Weather station temperatures averaged 19 °C, with an average relative humidity of 35%. Westerly winds were measured at 11.2 km/h.

Pine stands were burned for the first time on 21 May 2002. The nearest weather station to pine stands 1 and 2 recorded 0.23 cm precipitation eight days prior to burning. On-site dry bulb temperature averaged 12 °C, with an average relative humidity of 42%. Mid-flame wind speed was from the north-northwest and averaged 2.1 km/h. Pine stand 3 received 0.13 cm of precipitation five days prior to burning. On-site dry bulb temperature averaged 11 °C, with an average relative humidity of 37%. Mid-flame wind speeds for pine stand 3 occurred from the west and averaged 2.6 km/h.

All pine stands were burned a second time on 13 May 2008. The nearest weather station to pine stands 1 and 2 received 2.5 cm of precipitation five days prior to burning. Weather station temperature averaged 18 °C, with an average relative humidity of 41%. Wind speed was recorded at 11.2 km/h from the south. On-site dry bulb temperature averaged 19 °C, with average relative humidity of 45%. On-site winds were recorded from the south-southeast at 6.4 km/h.

2.4. Measurements

Temperature-indicating paints (Tempilaq Paints, LA-CO Industries Inc., 1201 Pratt Boulevard, Elk-Grove Village, IL 60007) were used to quantify relative differences in fire temperature. Eight separate paints calibrated to liquefy at 79°, 149°, 204°, 260°, 316°, 371°, 593°, and 816 °C were painted onto ceramic tiles mounted face down on steel rods 0.6 m above the soil surface in the center of each understory treatment plot.

Total heights were recorded to the nearest 0.5 cm for the tallest stem of each direct-seeded and nursery seedling in 1991, 1992, 1996, 2000, 2001, 2002, 2003, 2006, 2009, and 2015. Planted oak seedling mortality, deer browsing, and frost damage were also recorded in these years. Seedlings were inventoried as dead when no trace of root or shoot could be located, or when live buds or other tissues could not be found along shoots, root collars, or roots. The presence or absence of deer browsing and frost damage was recorded for each individual to calculate the proportion of seedlings impacted in a given treatment. Basal area was estimated with a 10-factor prism. Percent canopy cover was measured with a model c concave spherical crown densiometer (Robert E. Lemmon Forest Densiometers/10175 Pioneer Ave/Rapid City, SD 57702). Four densiometer measurements were taken in each of the four cardinal directions 1 m above the ground at understory treatment plot-centers. An average percent canopy cover was obtained by averaging all calculated canopy cover values within each understory treatment.

Natural regeneration was measured in late-July/early-August of 2001, 2002, 2003, 2006, 2009, and May of 2015. All ramets and genets of woody stems were recorded by species into three size-classes: stems < 25 cm height, stems ≥ 25 cm tall and < 2.54 cm dbh, and stems ≥ 2.54 cm dbh and < 10 cm dbh, hereafter referred to as small, medium, and large stems, respectively. A 1 m^2 quadrat was used to quantify small size-class stems, a 2 m diameter circular plot was used to measure all medium size-class stems, and a 4 m diameter circular plot was used to measure all large size-class stems. A total of four sampling points were established at the vertices of a 6 × 6 m square centered within each understory 15 × 15 m subplot (Hartman et al., 2005). Smaller sampling plots were nested within larger plots at each of the four sampling points. To ensure adequate numbers of stems for statistical analysis, all oak species were pooled into a single category.

2.5. Statistical analysis

Data were analyzed using analysis of variance (ANOVA) models and *F* tests appropriate for split-plot experimental designs. All *F* tests were reported at the $\alpha = 0.05$ significance level. Tukey's Honestly Significant Difference (HSD) with $\alpha = 0.05$ was used for all pair-wise comparisons of canopy composition, and canopy cover treatment means. Separate analyses using reduced models were conducted within canopy composition types when the overall ANOVA indicated statistical canopy composition by canopy cover interactions. Data were arranged by several categories (species, mean heights, caged vs. uncaged) and analyzed separately, but statistical differences were analyzed and are reported across canopy composition and canopy cover treatment. The following ANOVA model was used to examine effects of oak and pine canopy composition, canopy cover, and understory treatments:

$$Y_{i(j)kl} = \mu + \beta_j + \tau_{i(j)} + \gamma_k + \lambda_l + \beta\gamma_{jk} + \beta\lambda_{jl} + \gamma\tau_{i(j)k} + \lambda\tau_{i(j)l} + \gamma\lambda_{kl} + \beta\gamma\lambda_{jkl} + \varepsilon_{i(j)kl}$$

where:

μ = Overall Mean
β_j = Canopy Composition
$\tau_{i(j)}$ = Block (Canopy Composition)
γ_k = Canopy Cover Treatment
λ_l = Understory Treatment
$\beta\gamma_{jk}$ = Canopy Composition x Canopy Cover Treatment
$\beta\lambda_{jl}$ = Canopy Composition x Understory Treatment
$\gamma\tau_{i(j)k}$ = Canopy Cover Treatment x Block (Canopy Composition)
$\lambda\tau_{i(j)l}$ = Understory Treatment x Block (Canopy Composition)
$\gamma\lambda_{kl}$ = Canopy Cover Treatment x Understory Treatment
$\beta\gamma\lambda_{jkl}$ = Canopy Composition x Canopy Cover Treatment x Understory Treatment
$\varepsilon_{i(j)kl}$ = Error term consisting of the interaction $\tau\gamma\lambda_{i(j)kl}$
i = 1, 2, 3
j = 1, 2

Table 1
Basal area and percent canopy cover by canopy treatment within oak and pine stands in 1992 and 2015. Standard errors are in parentheses.

Canopy Cover Treatment (%)	Oak Stands		Pine Stands	
	1992	2015	1992	2015
Basal Area ($m^2 * ha^{-1}$)[a]				
0%	0	10.9 (2.3)	0	1.2 (0.5)
25%	6.1 (2.8)	9.2 (0.8)	8.6 (0.3)	15.7 (1.2)
75%	15.4 (0.8)	20.5 (0.71)	34.3 (2.1)	39.4 (1.6)
100%	34.0 (0.7)	35.8 (1.2)	42.8 (1.4)	44.8 (2.0)
Canopy Cover (%)[b]				
0%	0	56.5 (7.4)	0	9.7 (4.2)
25%	28 (0.7)	65.1 (3.4)	27 (1.2)	44.5 (2.4)
75%	70 (0.6)	67.7 (1.5)	69 (4.0)	66.9 (0.98)
100%	86 (1.5)	73.7 (0.68)	78 (4.2)	67.6 (2.0)

Note: Overstory basal area was measured using a 10 factor prism and canopy cover was measured with a concave spherical densiometer.
[a] $n = 4$.
[b] $n = 16$.

$$k = 1, 2, 3, 4$$
$$l = 1, 2, 3, 4$$

Funding, logistics, and limited personnel precluded the implementation of prescribed fire early on in the study, with the result that controls for a fire treatment were not incorporated in the original design. Therefore, investigation of the effects of fire was limited to comparing the abundance and size of natural and artificial regeneration before and after each prescribed fire. One-tailed t-tests were used to assess paired differences across years between pre- and post-fire planted oak sprout heights and natural regeneration stem densities. All analyses were performed in NCSS 2015.

3. Results

3.1. Canopy cover and basal area

In 1992, cutting treatments resulted in mean canopy cover values that reasonably approximated target values for each treatment (Table 1). Levels of percent full photosynthetically active radiation (PAR) measured one meter above the ground in 1992 were approximately 90%, 65%, 30%, and 10% of full PAR in the 0%, 25% 75%, and 100% canopy cover treatments, respectively, in the oak stands and 95%, 75%, 35%, and 15% of full PAR in the 0%, 25%, 75%, and 100% canopy cover treatments, respectively, in the pine stands (Buckley et al., 1999). By 2015, percent canopy cover had shifted significantly in some treatments since 1990–1991 (Table 1). In 2015, mean percent canopy cover calculated over all canopy treatments was statistically greater in oak stands (67.7%) than in pine stands (47.2%). Basal area increased in all treatments over time (Table 1).

3.2. Fire characteristics

Mean maximum temperature of Fire 2 calculated across all canopy treatments and stand types (108 °C) was statistically higher than that measured in Fire 1 (81 °C; $p = < 0.0001$). Mean temperatures for both fires were statistically higher in pine stands than in oak stands (Fig. 1). In the pine stands, the mean temperature of Fire 2 was 51 °C higher than that of Fire 1 ($p = < 0.0001$). There were no statistical differences ($p = 0.5894$) between Fire 1 and Fire 2 within the oak stands. There were also no statistical differences in fire temperature between canopy cover treatments during Fire 1 in the oak stands, but mean temperature was statistically higher in the 25% canopy treatment than in the 0% treatment during Fire 2. Mean temperatures for 0% canopy cover treatments in pine stands were statistically lower than all other canopy

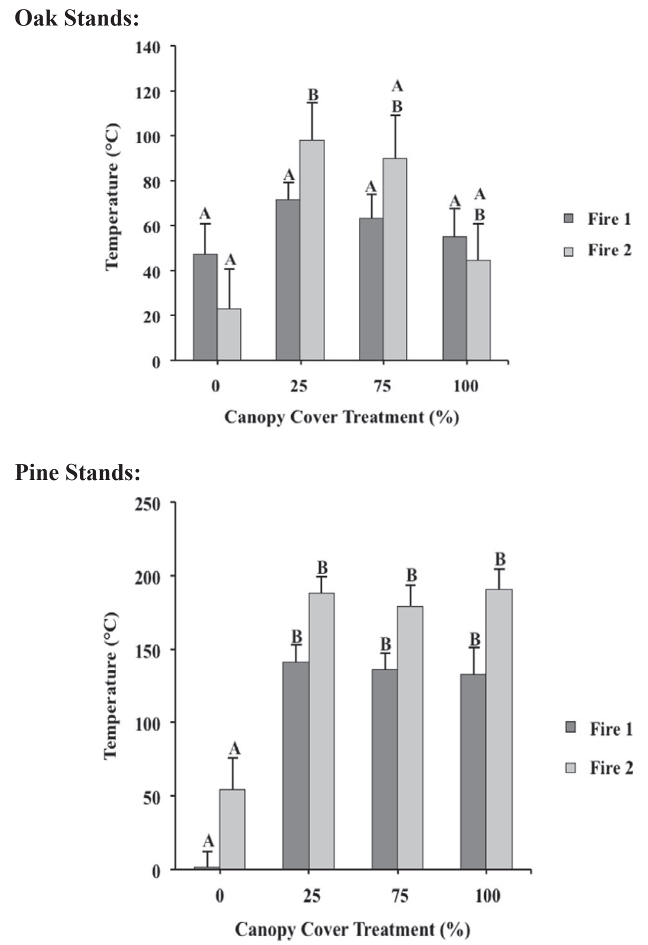

Fig. 1. Mean fire temperature (°C) by fire and canopy cover treatment within oak and pine stand types. Means with the same letter do not differ statistically based on Tukey's HSD (α = 0.05). Within fires, letters indicate statistical differences in fire temperature across canopy cover treatments. Error bars represent one standard error of the mean.

cover treatments during both fires (Fig. 1). It is important to note that these mean fire temperatures are rough estimates due to the temperature increments between the melting points of the temperature indicating paints used. On average, flame lengths observed in the oak stands were 15–31 cm and those in the pine stands were 61–91 cm.

3.3. Planted oak responses between 1991 and 2015

After 25 years, direct seeded and nursery seedlings have suffered significant mortality across treatments (Fig. 2). Oak and pine stand types differed in overall losses, with oak stands having fewer surviving seedlings than pine stands in 2009 ($p < 0.0001$). During the 2015 remeasurement of the study, it was discovered that cages had been removed by unknown individuals in two of the oak block replicates at some time between 2009 and 2015. Therefore, the measurement period of 2009 will be used as an end point for all oak stand variables pertaining to planted oak. Within oak stands in 2009 and pine stands in 2015, understory treatments and planting stock types (direct seeded or nursery seedlings) had no statistical effects and no statistical interaction effects on either long-term seedling survival or growth ($p = 0.3776$ and 0.8101, respectively). As a result, these factors were dropped from the model during further analyses. Mortality within oak stands was statistically similar across canopy cover treatments through time (Fig. 3). In 2009 and 2015, survival of planted seedlings in the 25%, 75%, and 100% canopy cover treatments in the pine stands was statistically greater than in the 0% canopy cover treatment (Figs. 2 and 3).

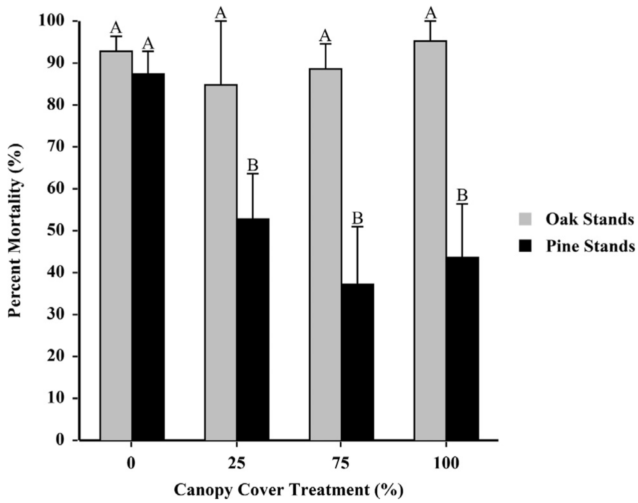

Fig. 2. Percent mortality for planted oaks by canopy cover treatment in oak stands in 2009 and pine stands in 2015. Within stand types, means with the same letter are not statistically different among canopy treatments based on Tukey's HSD (α = 0.05). Error bars represent one standard error of the mean.

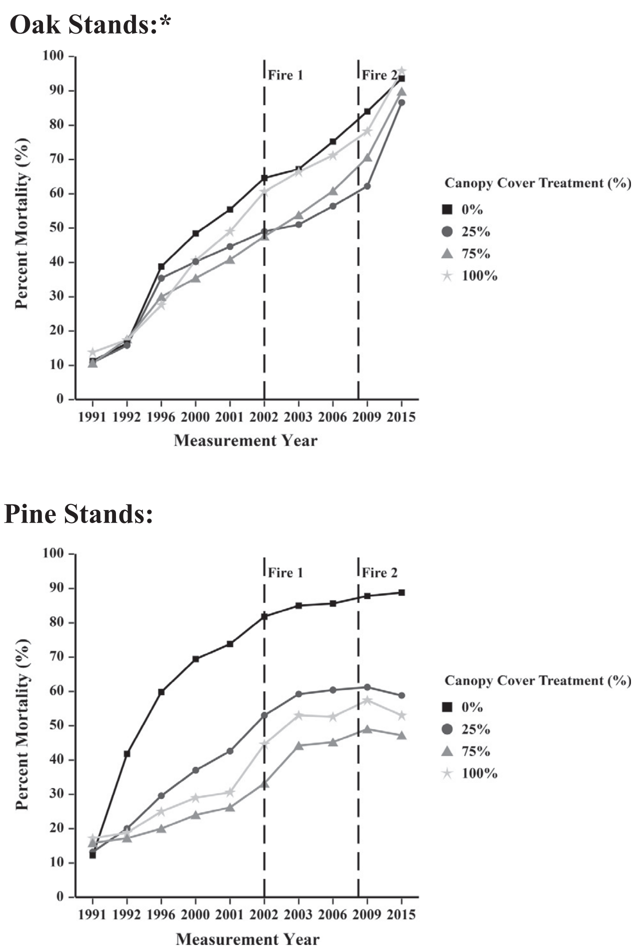

Fig. 3. Percent mortality for planted oaks by stand type, measurement year, and canopy cover treatment. Means are calculated across all other treatment levels. * The caging treatment in two oak blocks was compromised between the 2009 and 2015 measurement periods. Therefore, percent mortality for oaks in the oak stands in 2015 should be interpreted with caution.

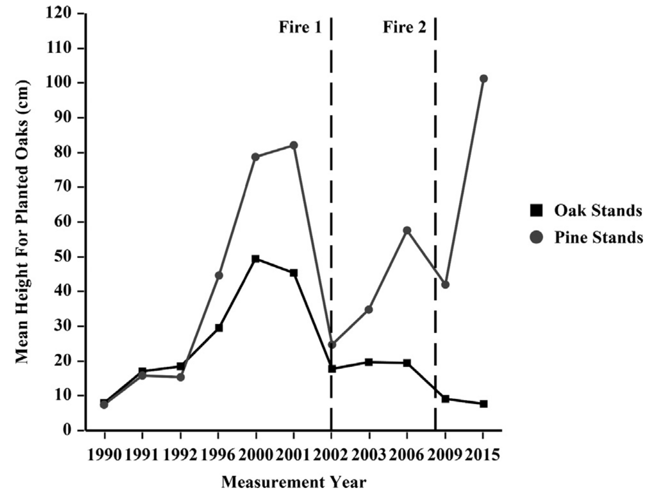

Fig. 4. Mean heights for planted oaks by measurement year and stand type. Means are calculated across all other treatment levels and are for caged seedlings only. Data points for 1990 represent seedling heights just after planting. * The caging treatment in two oak blocks was compromised between the 2009 and 2015 measurement periods. Therefore, mean height growth for oaks in the oak stands in 2015 should be interpreted with caution.

Substantial losses occurred in the 0% canopy cover plots in pine stands during the first few years following planting (Fig. 3).

The mean height of nursery seedlings was 12.96 cm just after planting in 1991. Mean heights of nursery seedlings did not differ between stand type treatments at the end of the first growing season in 1991 (Fig. 4). By 2001, mean heights of planted and caged oaks differed statistically by stand type. Caged oaks had mean heights of 45.32 cm and 82.13 cm in oak and pine stands, respectively (Fig. 4). Post-fire sprout heights in both stand types in 2002 were substantially reduced compared to stem heights before burning in 2001 (Figs. 4 and 5). Heights after burning in 2002 were similar across stand types ($p = 0.0858$). At that time, mean sprout heights in oak and pine stands were 17.72 cm and 24.74 cm, respectively. By 2006, mean heights had increased more in pine stands than in oak stands, with mean sprout heights of 57.49 cm and 19.35 cm, respectively (Fig. 4). Relative to pre-fire heights, post-fire mean heights following the second prescribed fire in 2008 were not reduced as much as those following the first prescribed fire in 2002. Heights for caged oaks differed in 2009 between oak and pine stand types ($p = 0.0053$; Fig. 5). In oak stands, caged oaks had a mean height of 9.21 cm, while those in pine stands averaged 42.02 cm. By 2015, caged oaks within pine stands had regained pre-fire heights with a mean of 101.33 cm (Fig. 5).

Canopy cover treatments had significant effects on mean height growth for caged oaks in both oak and pine stands. Within oak stands, pre-fire heights of caged oaks in 2000 and 2001 were greater in the 0% and 25% canopy cover treatments than in the 75% and 100% treatments ($p = 0.0163$; Fig. 5). However, no differences between canopy cover treatments have been detected within oak stands since that time. Within pine stands, the 25% and 75% canopy cover treatments had greater mean heights of caged seedlings in the pre-fire years of 2000 and 2001 than the 0% and 100% treatments. The same pattern was observed following both fires in 2015 (Fig. 5). Height growth patterns in uncaged seedlings were similar to those in caged seedlings, although all mean heights remained below 30 cm between 1991 and 2015.

3.4. Deer browsing

Averaged over all years, pine stands had a greater percentage of planted oaks browsed by deer than oak stands ($p < 0.0001$). The mean percentage of planted oaks browsed by deer averaged over all years was significantly greater in 0% and 25% canopy cover treatments than in

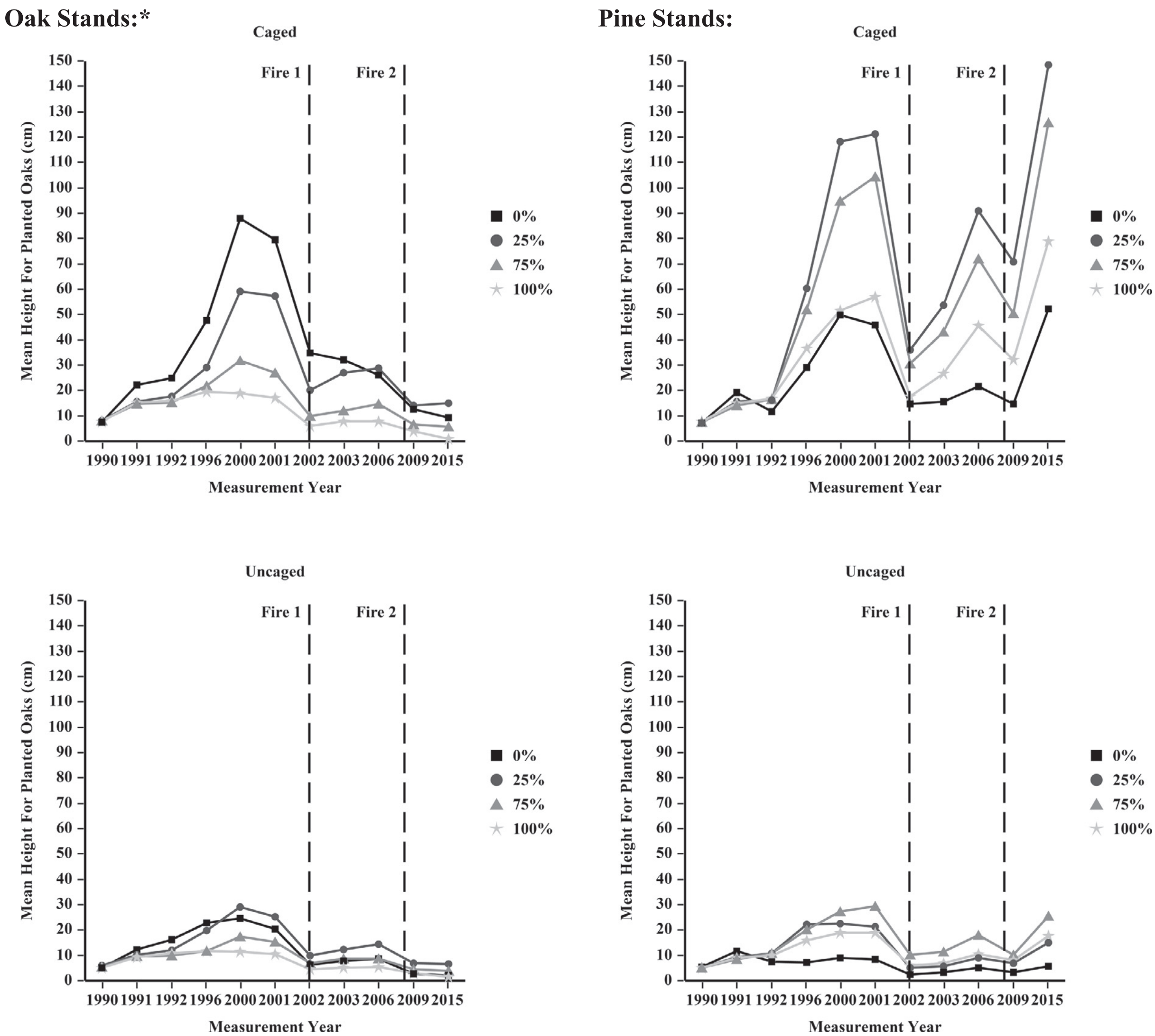

Fig. 5. Mean heights for planted oaks by stand type, caging treatment, canopy cover treatment, and year. Means are calculated across all other treatment levels. Data points for 1990 represent seedling heights just after planting. *The caging treatment in two oak blocks was compromised between the 2009 and the 2015 measurement periods. Therefore, mean height growth for caged oaks in oak stands in 2015 should be interpreted with caution.

the 75% and 100% treatments in oak stands ($p < 0.0001$; Fig. 6). A similar pattern occurred in the pine stands, except that the percentage of planted oaks stems browsed in the 75% canopy cover treatment was statistically similar to that in the 0% and 25% canopy cover treatments. The 75% and 100% canopy cover treatments within oak stands and the 100% canopy cover treatment in pine stands had lower percentages of oak stems browsed across all years than all other canopy treatments (Fig. 6). With respect to specific years, the percentage of planted oaks browsed by deer across all treatment combinations was greater in 2000 (43.0%) than in 2015 (27.6%; $p < 0.0001$). Browsing levels in all other years were statistically similar to those in 2015. Furthermore, mean heights for caged oaks were consistently greater than mean heights for uncaged planted oaks across years (Fig. 5).

3.5. Frost damage

Late spring frost events damaged a significant percentage of planted oaks over the past 25 years (Fig. 7). High percentages of planted oaks damaged by frost were quantified in five (1992, 1996, 2000, 2001, and 2015) of the ten measurement years. Stand type had no significant effect on percentages of seedlings and sprouts sustaining frost damage ($p = 0.1935$). With respect to canopy cover, numbers of oak seedlings and sprouts receiving frost damage were consistently lower in the 75% and 100% treatments than in the 0% and 25% treatments ($p < 0.0001$).

3.6. Natural oak regeneration responses between 2001 and 2015

In oak stands, all size classes of naturally regenerated oak combined comprised a lower relative proportion of all naturally regenerated species combined after two prescribed fires in 2015 (16.17%) than in 2001 before burning (35.92%). In pine stands, naturally regenerated oak in all size classes combined comprised 39.56% of all naturally regenerated species combined across treatments before burning in 2001 (Fig. 8). However, by 2015, the relative proportion of naturally regenerated oak had declined to 27.84%, and red maple surpassed this proportion by 20.80%. Eastern white pine comprised the greatest proportion of naturally regenerated stems within the “Other” category in oak and pine stands across years.

The abundance of naturally regenerated oak in all size classes was greater in oak stands than in pine stands (Table 2). Small size class (< 25 cm height) oak stem densities in oak stands decreased from 2001 to 2015 within 0% and 75% canopy cover treatments (Table 2). No changes in small size class natural oak stems occurred in the 25% and

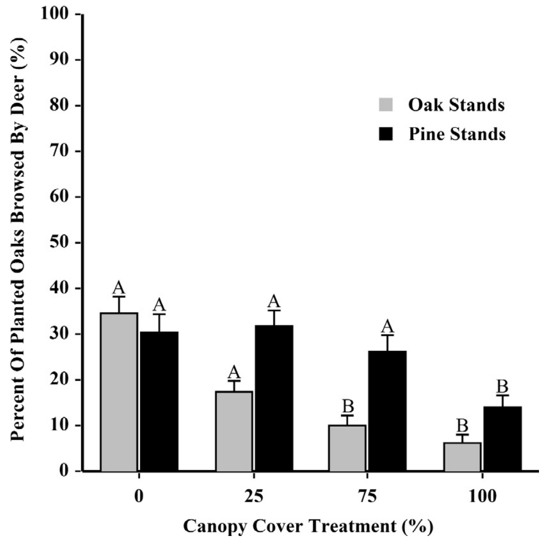

Fig. 6. Mean percentage of uncaged planted oaks browsed by deer (across years) by stand type and canopy cover treatment. Within stand types, means with the same letter are not statistically different among canopy treatments based on Tukey's HSD (α = 0.05). Error bars represent one standard error of the mean.

100% canopy cover treatments in oak stands over the same period (Table 2). No statistical difference in small oak stems was found among canopy cover treatments in oak stands in 2015 ($p = 0.1968$). In pine stands, no statistical difference in small size class, naturally regenerated oak occurred over time within the 0% canopy cover treatment. However, statistically significant declines in the abundance of small size class oak stems were found within the 25%, 75%, and 100% canopy cover treatments between 2001 and 2015 (Table 2). By 2015, canopy cover treatments within pine stands did not differ in the abundance of small natural oak stems ($p = 0.1647$).

Medium size class (stems > 25 cm height and less than 2.54 cm dbh) naturally regenerated oak was more abundant across all canopy cover treatments in all years in oak stands than in pine stands (Table 2). Medium sized oak stem densities in the 25% and 100% canopy cover treatments were statistically lower in 2015 than in 2001 in the oak stands. In contrast, no statistical changes occurred in the 0% and 75% canopy cover treatments in oak stands between 2001 and 2015. In 2015, there were no statistical differences in oak stem densities across canopy cover treatments in the oak stands ($p = 0.2092$). Within pine stands, no statistical difference in the abundance of medium size class natural oak stems occurred within any canopy treatment between 2001 and 2015 (Table 2). However, in 2015 the 75% treatment had statistically more abundant medium size class oak stems than the 0% canopy cover treatment ($p = 0.0417$).

In 2015, large naturally regenerated oak stems (stems > 2.54–10 cm dbh) were limited to the 25% canopy cover treatment in pine stands (Table 2). No statistical changes in the abundance of large oak stems occurred over time within any treatment.

3.7. Red maple regeneration responses between 2001 and 2015

The relative proportion of red maple stems in all size classes before burning in 2001 was greater in oak stands than in pine stands, comprising 51.09% and 27.12% of stems of all species combined, respectively (Fig. 8). The relative proportion of red maple stems in all size classes increased in both oak and pine stands over time. By 2015, after both fires, the proportion of red maple reached 80.87% in oak stands and 48.64% in pine stands.

The density of red maple stems across all stem size classes was greater in oak stands than in red pine plantations before burning in 2001 and after burning in 2015 ($p < 0.0001$; Table 3). In oak stands, small size class (< 25 cm height) red maple densities increased statistically within the 0% and 100% canopy cover treatments from 2001 to 2015 (Table 3). No significant changes in small size class red maple stems were measured over time in the 25% and 75% canopy cover treatments in oak stands. In 2015, the 0% canopy cover treatment had the greatest abundance of small red maple stems in the oak stands ($p < 0.0001$; Table 3). No other differences in small red maple stem densities between canopy cover treatments were observed within oak stands. In pine stands, small red maple stem densities were greater in 2015 after burning than in 2001 before burning in the 100% canopy cover treatment ($p = 0.0164$; Table 3). No statistical differences in small red maple stem densities were detected between 2001 and 2015 in the 0%, 25%, and 75% canopy cover treatments.

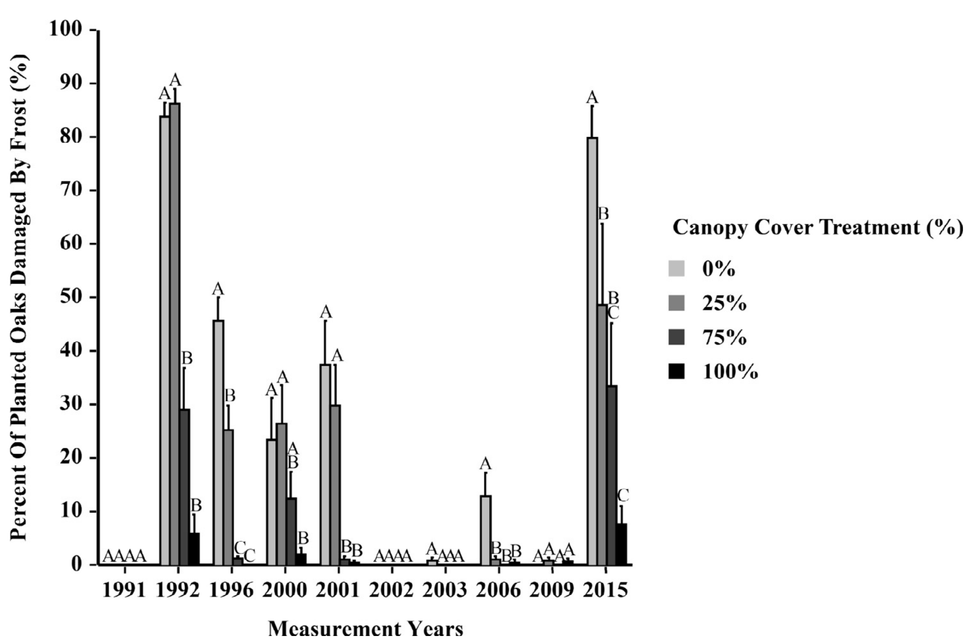

Fig. 7. Percentage of planted oaks damaged by frost by year and canopy cover treatment. Within years, means with the same letter are not statistically different among treatments based on Tukey's HSD (α = 0.05). Error bars represent one standard error of the mean.

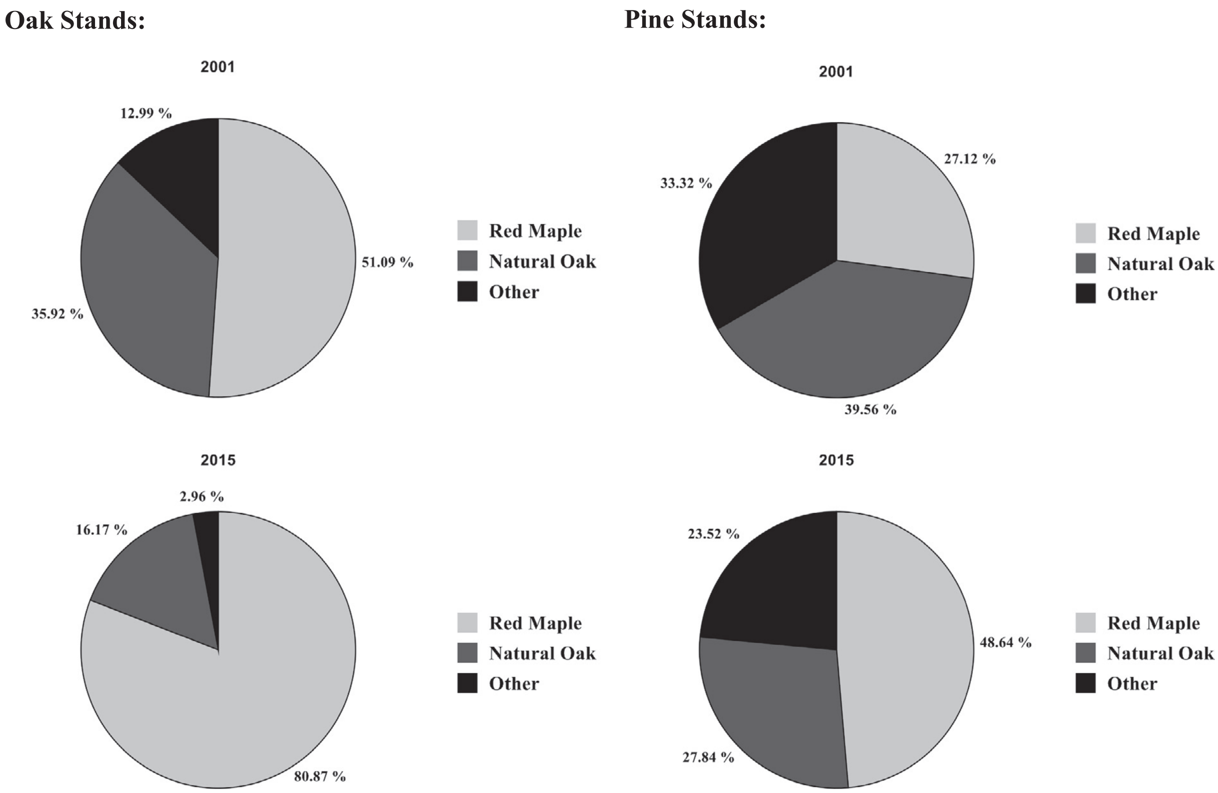

Fig. 8. Relative proportions of naturally regenerated stems of red maple, oak, and other species in all size classes combined in each stand type before prescribed fire in 2001 and after two prescribed fires in 2015. Proportions are calculated over all canopy cover treatments within a given stand type and year.

Similar to the small size class, medium size class red maple stem densities were significantly higher in oak stands than in red pine stands over time ($p < 0.0001$). Within oak stands, the 75% canopy cover treatment had greater medium red maple stem densities after burning in 2015 than in 2001 before burning (Table 3). All other canopy cover treatments within oak stands had statistically similar levels of medium red maple stem densities over time. In 2015, the 25%, 75%, and 100% canopy cover treatments in oak stands had a greater abundance of medium red maple stems than the 0% treatment. In pine stands, a decline in the number of medium red maple stems was measured in the 25% canopy cover treatment (Table 3). In the 0%, 75% and 100% canopy cover treatments in pine stands, medium red maple stem densities

Table 2
Naturally regenerated oak. Stems per hectare by size class, stand type, and canopy cover treatment. Small size class stems are < 25 cm in height, medium stems are ≥ 25 cm tall and < 2.54 cm dbh, and large stems are ≥2.54 cm dbh and < 10 cm dbh. Bold p-values indicate statistical differences between 2001 (before prescribed fire) and 2015 (after two prescribed fires). These values are based on two-tailed t-tests at α = 0.05 significance. N = 48 sampling plots per canopy treatment.

Size Class	Stand Type	Canopy Cover Treatment (%)	2001 (Pre-fire)	2015 (Post-fire)	Difference (2015–2001)	*p-value*
Small	Oak	0	5000.00	1875.00	−3125.00	**0.0058**
		25	7500.00	5000.00	−2500.00	0.1988
		75	9166.67	5000.00	−4166.67	**0.0062**
		100	7083.33	6041.67	−1041.67	0.5639
	Pine	0	625.00	625.00	0.00	1.0000
		25	1250.00	0.00	−1250.00	**0.0127**
		75	3541.67	833.33	−2708.33	**0.0004**
		100	4791.67	1666.67	−3125.00	**0.0121**
Medium	Oak	0	10,610.67	10,345.40	−265.27	0.8719
		25	23,542.42	11,870.68	−11,671.73	**0.0000**
		75	6432.72	4774.80	−1657.92	0.1502
		100	1790.55	5437.97	3647.42	**0.0038**
	Pine	0	1591.60	795.80	−795.80	0.2144
		25	4310.58	2718.98	−1591.60	0.0521
		75	2188.45	3050.57	862.12	0.1803
		100	1657.92	2984.25	1326.33	0.1148
Large	Oak	0	182.37	0.00	−182.37	0.0546
		25	49.74	0.00	−49.74	0.1825
		75	16.58	0.00	−16.58	0.3224
		100	0.00	0.00	0.00	.
	Pine	0	33.16	0.00	−33.16	0.1595
		25	132.63	33.16	−99.47	0.1351
		75	16.58	0.00	−16.58	0.3224
		100	33.16	0.00	−33.16	0.1595

Table 3
Naturally regenerated red maple. Stems per hectare by size class, stand type, and canopy cover treatment. Small size class stems are < 25 cm in height, medium stems are ≥25 cm tall and < 2.54 cm dbh, and large stems are ≥2.54 cm dbh and < 10 cm dbh. Bold p-values indicate statistical differences between 2001 (before prescribed fire) and 2015 (after two prescribed fires). These values are based on two-tailed t-tests at α = 0.05 significance. N = 48 sampling plots per canopy treatment.

Size Class	Stand Type	Canopy Cover Treatment (%)	2001 (Pre-fire)	2015 (Post-fire)	Difference (2015–2001)	*p-value*
Small	Oak	0	2708.33	110,000.00	107,291.67	**0.0011**
		25	5000.00	8125.00	3125.00	0.1043
		75	7708.33	10,416.67	2708.33	0.2079
		100	9791.67	42,291.67	32,500.00	**0.0000**
	Pine	0	208.33	208.33	0.00	1.0000
		25	1041.67	1875.00	833.33	0.3767
		75	1250.00	1250.00	0.00	1.0000
		100	4166.67	16,875.00	12,708.33	**0.0164**
Medium	Oak	0	9350.65	8289.58	−1061.07	0.4341
		25	23,476.10	24,404.53	928.43	0.6507
		75	22,481.35	30,107.77	7626.42	**0.0018**
		100	16,114.95	16,579.17	464.22	0.8250
	Pine	0	66.32	66.32	0.00	1.0000
		25	5902.18	1127.38	−4774.80	**0.0082**
		75	795.80	397.90	−397.90	0.2243
		100	331.58	397.90	66.32	0.7097
Large	Oak	0	2287.85	994.72	−1293.13	**0.0023**
		25	1823.65	547.10	−1276.56	**0.0012**
		75	646.57	66.31	−580.25	**0.0009**
		100	116.05	16.58	−99.47	0.1825
	Pine	0	0.00	0.00	0.00	.
		25	66.31	0.00	−66.31	0.2093
		75	0.00	0.00	0.00	.
		100	0.00	0.00	0.00	.

in 2015 were found to be statistically similar to those in 2001. Medium size class red maple densities did not differ across canopy cover treatments in 2015 in the pine stands ($p = 0.8019$).

Large size class red maple stems were much more abundant in oak stands than pine stands ($p < 0.0001$). Within oak stands, decreases in large red maple abundance were measured between 2001 and 2015 in the 0%, 25%, and 75% canopy cover treatments (Table 3). The abundance of large red maple stems in the 100% canopy cover treatment did not differ statistically from 2001 to 2015. The 0% canopy cover treatment in oak stands had a significantly greater abundance of large size class red maple regeneration ($p = 0.0001$) than all other canopy cover treatments. In pine stands, there was a lack of large red maple regeneration in the 0%, 75%, and 100% canopy cover treatments in both 2001 and 2015. No change occurred in the abundance of large size class red maple stems in the 25% canopy cover treatment from 2001 to 2015 in the pine stands (Table 3). The occurrence of red maple stems in this treatment was the result of stump sprouts persisting from two co-dominant red maple stems originally removed during the 1990–1991 canopy reduction cuts.

4. Discussion

Observed mortality and growth of planted seedlings support the hypothesis that oak regeneration would be enhanced in pine stands relative to oak stands, provided that seedlings were protected from browsing with cages. Heavy mortality of planted seedlings occurred in pine clearcuts in the first years of the study due to deer browsing and frost damage, and browsing was heavier in pine stands than oak stands in most canopy cover treatments. However, long-term results revealed much lower mortality in the 25%, 75%, and 100% canopy cover treatments in pine stands than oak stands. It can be argued that lower mortality of planted seedlings in the pine stands was due to decreased competition for light and other resources. Measurements of PAR early in the study revealed that red pine forests intercepted less incoming PAR than oak forests of equal basal area (Buckley et al., 1999). Patterns in the growth of planted seedlings among canopy types are consistent with greater levels of resources available to planted oaks in pine stands than in oak stands. In terms of natural oak regeneration, the greater abundance of naturally regenerated, medium-sized oak stems in oak than pine stands does not support the hypothesis that oak regeneration would be enhanced in pine stands relative to oak stands. Greater abundance of oak seed sources in oak stands than in pine stands likely contributed to the greater number of oak seedlings in oak stands. Although limited in numbers, growth and long-term survival of naturally regenerated oak stems may be greater in pine stands due to reduced competition with understory red maple, despite heavy deer browsing (Hartman et al., 2005). Our study was not designed to elucidate factors responsible for limited development of understory red maple in the pine stands, but potential factors could include low numbers of red maple seed sources or an inhibitory effect of the thick pine litter on red maple germination and establishment. In all canopy cover treatments, total numbers of natural oak in the medium (≥25 cm tall and < 2.54 cm diameter) size class exceeded the guideline of 1070 seedlings/ha required for adequate future stocking suggested by Sander et al. (1976), but it is important to note that most stems within this size class fell below the minimum 1.37 m height recommended by these authors.

In general, the growth of planted seedlings and the abundance of natural oak regeneration across canopy cover treatments support the contention that removal of competitors should enhance oak regeneration. However, the synergistic effect of late spring frosts and deer browsing were most intense at low levels of canopy cover and tended to override the beneficial effects of competitor removal. Crow (1992) noted a similar pattern in browsing in which greater numbers of seedlings were browsed at lower levels of canopy cover. The contrasting patterns in which the greatest height growth of planted seedlings occurred in the 0% canopy treatment in the oak stands and the least height growth occurred in the 0% canopy treatments in the pine stands may have resulted from more intense frost damage and browsing in pine clearcuts. The lack of hardwood stump sprouts and red maple saplings in pine clearcuts may have provided less protection from late-spring frosts and deer browsing, especially early in the study. The fact that significant impacts of late-spring frosts were noted in five of the ten measurement years suggests that late-spring frosts may play an important role in the dynamics of oak regeneration in the study region. With some exceptions, patterns in the abundance of natural oak seedlings and sprouts across canopy cover treatments resembled those of planted oak survival and growth. Numbers of natural oak stems generally increased with decreasing levels of canopy cover, but the abundance of seedlings in some size classes was depressed in clearcuts. It is likely that late-spring frosts and deer browsing impacted natural seedlings and sprouts in the same ways as planted seedlings.

Most variations of the shelterwood method call for a removal cut to release advanced reproduction stimulated by the establishment cut, often within 3–10 years (Nyland, 2002; Smith et al., 1997). A removal cut has yet to be conducted on the study sites because mean heights have not attained the size required to be competitive (Arend and Scholz, 1969; Johnson et al., 2009; Miller et al., 2017; Sander, 1972; Sander et al., 1976). This was particularly true as sprouts recovered from the two prescribed fires. As of 2015, mean heights of oak sprouts in the 25% and 75% canopy cover treatments in pine stands were approaching sufficient size to support a final removal cut.

Growth and survival of planted oak seedlings was statistically greater in the shrub removal understory treatment early on in the study. Measurements of PAR among treatments at the outset of the study suggested significantly greater PAR in shrub removal plots in oak stands, but no differences in PAR among understory treatments in pine stands, which had far fewer herbs, saplings, and shrubs within the shrub layer. Potentially positive effects of the shrub removal treatment are consistent with the concept that midstory removal should be beneficial to oak regeneration. Other studies have reported mixed results of midstory removal treatments (Clark et al., 2016; Dey et al., 2012; Lockhart et al., 2000; Miller et al., 2004; Motsinger et al., 2010; Parrott et al., 2012). The lack of statistically significant increases in planted oak performance in shrub removal understory treatment plots on the study sites may have been the result of a much stronger effect of the main canopy on resources available to planted oaks than the midstory shrub layer. It is also likely that recolonization of the shrub layer occurred following the cessation of maintenance of the shrub removal treatment in 2001.

The timing of Fire 1 eleven years after the establishment cut on the study sites represents a departure from the 3 to 5 years between cutting and fire recommended for the shelterwood burn technique (Brose et al., 1999b). Additional replicates to allow the early implementation of prescribed fire were initially planned in the study design, but were not established in the field as logistics and resources were insufficient to permit the inclusion of this treatment at the outset of the study. Resources and personnel provided by the Michigan DNR became available in 2001, which, along with the proliferation of understory red maple over ten years, influenced the decision to implement fire in 2002 in all replicates and plots.

Height growth of planted oaks did not appear to be hindered or enhanced by the implementation of prescribed fire in the pine stands. In contrast, the decline observed in height growth of sprouts in the oak stands after Fire 1 may have been due to lower light levels in the oak stands than in the pine stands before and after burning. The lower light levels measured in the oak than pine stands prior to burning (Buckley et al., 1999) may have resulted in lower amounts of stored reserves in oak root systems to support vigorous post-fire resprouting. Again, light levels measured 1 m above the ground in 1992 in the 0%, 25%, 75%, and 100% canopy treatments were approximately 90%, 65%, 30%, and 10% of full PAR in the oak stands and 95%, 75%, 35%, and 15% of full PAR in the pine stands, respectively. In addition, the lack of overstory mortality and red maple resprouting observed in the oak stands after burning would contribute to lower light levels, thereby resulting in less sprout height growth in the oak than in the pine stands. Alexander et al. (2008) observed decreases in canopy cover after prescribed burning in oak-hickory forests in Kentucky, but these effects were limited to one growing season. Heights of post-burn, planted oak sprouts rebounded most rapidly in the 25% and 75% canopy cover treatments in the pine stands and did not rebound in any of the canopy cover treatments in the oak stands. The leveling off of mortality of oak sprouts in all canopy treatments in the pine stands following Fires 1 and 2, compared to the continued increase in oak sprout mortality in oak stands, may have also resulted from lower light levels in the oak stands. PAR was not measured directly in 2015, but rough estimates for the 0%, 25%, 75%, and 100% canopy treatments based on 2015 canopy cover measurements and regression models developed for these sites (Buckley et al., 1999) include 38, 29, 27, and 21% full PAR at 1 m in the oak stands and 89, 53, 30, and 29% full PAR at 1 m in the pine stands, respectively.

Northern red oak is known to have a light compensation point near 2–5% of full sunlight (Gottschalk, 1987; Hanson et al., 1987). Parker and Dey (2008) reported a 2- to 3-fold greater increase in net photosynthesis and leaf conductance to water vapor in northern red oak than sugar maple as light increased from 1 to 2% full sunlight in uncut controls to 25 and 41% sunlight in shelterwoods. Peak growth of northern red oak occurs at 50–70% of full sunlight (Dey et al., 2008; Gottschalk, 1994; Phares, 1971). Red maple, the predominant competitor on the study sites, has been described as a “super-generalist” that exhibits small changes in leaf physiology in response to environmental changes (Abrams, 1998). Gottschalk (1994) reported greater plasticity in leaf weight/leaf area ratio in response to changes in light in red maple than northern red oak, and concluded this may provide red maple with an advantage. The light compensation point for red maple is approximately 2% full PAR (Groninger et al., 1996). Photosynthesis in oaks was found to be up to 50% greater than net photosynthesis in red maple at high light levels (Gilbert et al., 2003).

Although numbers of oak are only one indication of the overall status of oak regeneration on a given site (Brose et al., 2013), the result that the abundance of natural oak stems remained the same or declined in nearly all size classes and treatments indicates that two prescribed fires did not stimulate a net gain in the number of oak stems on the study sites. Several studies involving one or more prescribed fires in other regions on sites with different levels of productivity have documented increases in the abundance of oak stems following fire (e.g., Brose et al., 1999a; Iverson et al., 2008; Keyser et al., 2017; Kruger and Reich, 1997). In contrast, Johnson (1974) documented 58% mortality of small northern red oak seedlings and Alexander et al. (2008) observed 40% mortality of white oak seedlings after one burn. The seedlings in the Johnson (1974) and Alexander et al. (2008) studies were small (0–60 cm tall) and would be comparable to many stems in the small and medium stem categories used in this study.

The lack of a strong, positive, post-fire response in terms of the abundance of naturally regenerated oak stems may have resulted from the time period between the application of canopy cover treatments and prescribed burning. Miller et al. (2017) attributed low survival of natural oak advanced reproduction to application of prescribed fire too soon (two years) after implementation of shelterwood and midstory removal treatments. Based on growth curves for northern red oak seedlings grown in different light environments (Brose and Rebbeck, 2017), application of prescribed fire eleven years after implementation of understory and canopy cover treatments in the oak and pine stands in our study should have provided enough time for natural oak seedlings to reach the minimum size classes (31–61 cm in height and 1.3 cm in diameter) recommended by Brose (2014) and Brose et al. (2014) for supporting ample post-fire sprouting. This is especially true in the 0% and 25% canopy cover treatments, which contained the bulk of natural oak stems in the medium and large size classes in 2001. On the other hand, the window of opportunity to increase the vigor of natural oak regeneration may have been closing by the time prescribed fire was applied, particularly in the case of the second prescribed fire in 2008. Filling in of the main canopy and the concomitant increase in the abundance of understory red maple stems likely combined with deer browsing and frost damage to reduce the ability of natural oak regeneration to establish, resprout, survive, and vigorously grow following the prescribed fires. Similarly important interactions between factors such as fire, deer browsing, and canopy cover have been documented in other regions (Miller et al., 2017; Thomas-Van Gundy et al., 2014).

The net increase observed in the number of red maple stems following two prescribed fires does not support the hypothesis that woody understory competitors would be reduced with prescribed fire. If the prescribed fires resulted in the death of red maple genets (both shoots and root systems), this mortality was overridden by greater gains in numbers resulting from natural reproduction. It was not possible to track the fate of individual stems due to the sampling protocol used for naturally regenerated stems in this study, but it is likely that the germination of new red maple seedlings and sprouts from large and medium size class red maples contributed to the increased abundance of small-size-class red maples following both fires. Similar post-fire patterns have been described in previous studies (e.g., Albrecht and McCarthy, 2006; Arthur et al., 1998; Hutchinson et al., 2005; Iverson et al., 2017; Keyser et al., 2017). Regardless of whether red maple in the large and medium size classes resprouted, the significant decreases in these size classes in several canopy cover treatments suggest that the fires reduced the stature of red maple on the study sites.

The relative stature and size of northern red oak, red maple, and other competitors have an important influence on the outcomes of competition, post-fire sprouting, and regeneration. Current heights, basal diameters, densities of oaks of a particular size, and factors such as site index and overstory density have been used to model probabilities of obtaining different densities and distributions of oak stems attaining a certain height or dominance ranking in the future stand (Dey et al., 1996; Johnson, 1977; Loftis, 1990b). Further, models developed by Larsen et al. (1997) indicate that decreases in overstory density lead to increases in the size and density of oak stems, which has also been observed in the field (Brose and Rebbeck, 2017; Dey and Parker, 1997a). Increased size of oak stems leads to more competitive canopy positions and, up to a point, an increased probability of sprouting vigorously after cutting or fire (Brose et al., 2014; Dey et al., 1996; Johnson, 1977).

The much greater numbers of medium and large red maple compared with the numbers of medium and large natural oak in the oak stands in 2001 indicate that natural oak stems were competing with larger red maple saplings and stump sprouts in many cases. Red maple and other naturally regenerated competitors were not tallied prior to 2001, but it was observed that red maple seedlings, saplings, and stump sprouts were well established throughout the oak stands at the time of planting in 1991. As a result, many of these red maple stems were larger than the planted oaks during their first growing season. In addition to the effects of several years of closed canopy conditions prior to implementation of the canopy treatments and competition with understory red maple, deer browsing and frost damage expanded the gap in size between naturally regenerating oak and red maple stems, particularly in the 0% and 25% canopy treatments. The planting of larger northern red oak nursery seedlings in 1991 would have improved their competitive position relative to red maple and enhanced their ability to vigorously sprout and recover following frost damage, browsing, and prescribed fire (Dey et al., 2008; Dey and Parker, 1997b; Morrissey et al., 2010).

5. Conclusions

Based on the overall results of this study, the most viable management scenario for regenerating oak in the study region would include protecting planted and natural oak seedlings from deer in 25% canopy cover shelterwoods in pine plantations. Although this scenario represents a departure from traditional pine management, the 25-year results of this study suggest that regenerating oak in pine stands may be more feasible than regenerating oak in oak stands. Transitioning pine stands to oak-pine mixtures and eventually oak stands would mimic natural successional patterns observed over most of the eastern U.S. Due to the inherently greater intensity of surface fires and reduced hardwood competition in the understory of pine stands, it is possible that the understories of natural pine stands provided a particularly important niche for oak regeneration in presettlement forests. Underplanting or favoring natural oak regeneration in pine plantations would provide opportunities for the development of silvicultural systems for oak-pine mixtures that would have the added benefit of being more resilient to pests, pathogens, and extreme weather than monocultures (Burton et al., 1992; Hartley, 2002; Kelty, 2006). It would also be possible to design systems involving alternating rotations of pine and oak in which shelterwood harvests would be conducted in pine plantations to regenerate oak stands, followed by clearcutting of the oak stands and planting pine to perpetuate the cycle. The effects of different thinning methods on the performance of northern red oak and other species underplanted in red pine plantations have also been explored (Parker et al., 2001).

As implemented, the two prescribed fires had no clear beneficial effects on oak stems in the pine stands and appeared to be detrimental to planted oaks in the oak stands. Burning 3–5 years after implementation of canopy cover treatments, burning every three years, and burning three or more times may have generated different results. Scheduling the first burn 3–5 years after canopy treatments were applied would have reduced the amount of time understory red maple stems had to grow, and would have also enhanced the advantage of northern red oak over red maple in terms of the innate ability of northern red oak to fix more carbon than red maple at high light levels. Reduced intervals between burns and more burns would reduce the recovery time for red maple sprouts, and magnify the impact of greater allocation to root system growth and stored reserves in northern red oak (Huddle and Pallardy, 1999). Results of some studies involving multiple burns suggest that red maple can eventually be eliminated through incremental reductions in sprout size and the capacity to resprout with each subsequent burn (Arthur et al., 1998; Iverson et al., 2017). Chemical control of red maple stump sprouts just after cutting and greater emphasis on cutting or injecting overstory red maple seed sources in the oak stands would have also improved the competitive status of planted and natural oak stems. Given the ubiquitous distribution of red maple seed sources on the landscape, considerable investments in mechanical, chemical, and prescribed burning control methods will be required to reduce the abundance and competitive effects of this species. In addition to ample red maple seed sources and vigorous red maple resprouting, it is likely that interactions between deer browsing, frost damage, canopy cover, and the vigor of naturally regenerated and uncaged planted oak stems reduced the effectiveness of fire in this study.

The high levels of oak seedling mortality in the 0% and 25% canopy cover treatments early on, the large differences in total height between caged and uncaged oaks, and the interaction between prescribed fire and deer browsing suggest that deer browsing may be the primary factor, rather than an aggravating factor, limiting oak regeneration in the study region. The interactions between factors such as canopy structure, the presence of red maple, browsing, and frost observed in this study highlight the complexity of managing oak regeneration and the potential for changes in the importance of different factors across geographic regions.

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