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Competitive effects of fire-resistant saplings on their fire-sensitive neighbors are greater than the reverse

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Abstract. Although repeated fires are generally thought to reduce competition, direct tests of this hypothesis are rare. Furthermore, recent theory predicts that fires can increase competitive effects of fire-resistant species on fire-sensitive species and thus create stable assemblages dominated by the former. In this study, I quantified competition between saplings of fire-resistant oaks and their fire-sensitive non-oak neighbors in adjacent, repeatedly-burned and unburned 1-ha plots following damage by a tornado that reduced canopy cover to 60%. Using field experiments with established in situ saplings, I tested the hypothesis that competition was greater in an unburned plot than in a repeatedly burned plot by examining both the effects of sapling neighbor identity and experimental sapling neighbor reduction (repeated clipping) on the growth of fire-resistant oak saplings. To test whether competition was increased by fire, I measured diameter growth responses of fire-sensitive non-oaks to repeated clipping and topkill of neighbors by fire. Oaks, which generally had higher diameter:height ratios, were more resistant to topkill than were non-oaks. Although diameter growth of both oaks and non-oaks was greater in the burned than in the unburned plot, growth of oak saplings was not influenced by neighbors in either plot in a year with or without fire. In contrast, competitive effects of non-topkilled saplings (the vast majority of which were oaks) on topkilled non-oaks were significant in the burned plot in 2014. Growth of topkilled non-oak saplings was significantly greater in pairs in which the neighbor had been clipped or topkilled by fire than in pairs in which the neighbor had neither been clipped nor topkilled. Hence, the lower incidence of topkill in oaks in the burned plot after repeated fires increased their competitive effects on their non-oak neighbors in the burned plot. Growth of non-oaks did not increase with oak neighbor reduction in a year without fire. Because avoidance of topkill by fire was positively related to diameter, results suggest that repeated fires could generate a positive feedback between greater fire tolerance by oak saplings and increased competitive effects on their non-oak sapling neighbors.

Key words: competition; disturbance; fire; oak regeneration; *Quercus* spp.; topkill.

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INTRODUCTION

Competition and natural disturbances have traditionally been described as acting in opposition to one another with regard to their effects on species coexistence (Dayton 1971, Connell 1978, Petraitis et al. 1989, Platt and Connell 2003; but see Chesson and Huntly 1997 and Violle et al. 2010 for an alternative viewpoint). Disturbances can cause mortality and thus create gaps, which in turn provide opportunities for recruitment, establishment, or increased growth across a wide array of habitats and environmental conditions (see Walker 2012 for a review). In particular, disturbances such as fire are hypothesized to benefit fire-dependent species by reducing competition from more fire-sensitive species (Lorimer et al. 1994, Midgley 1996, Menges and Hawkes 1998, Brose et al. 1999, Beckage and Stout 2000, Iverson et al. 2008; hereafter, the fire-mediated competition reduction hypothesis). One way in which fire could reduce competition is through significant mortality of established adults of competitive species, subsequently creating opportunities for colonization by weaker competitors (e.g., see Menges and Hawkes 1998). In cases in which fire causes very little mortality, however, interspecific differences in fire-resistance and regrowth following fire may be more important than colonization in determining responses to fire (Whelan 1995, Loehle 2000, Hoffmann et al. 2009, Miller and Chesson 2009, Brewer 2011). Traits that confer fire resistance include thick bark, resprouting from belowground organs and stems, and prolonged storage of resources belowground or in protected aboveground stems (Whelan 1995). High investment in storage and protection in fire-resistant species, however, may reduce growth rate or size, which in turn may place fire-resistant species at a height or growth disadvantage to fire-sensitive species in the absence of fire (Midgley 1996, Hodgkinson 1998, Iverson et al. 2008, Rossatto et al. 2009, Cannon and Brewer 2013). Hence, in the absence of fire, fire-sensitive but competitively superior species displace more fire-resistant species (Nowacki and Abrams 2008, Rossatto et al. 2009). Fires of sufficient intensity or frequency prevent competitive displacement of fire-resistant species by fire-sensitive species (Nowacki and Abrams 2008, Rossatto et al. 2009).

Despite widespread recognition of the potential importance of fire in determining species composition by reducing competition, direct experimental tests of the fire-mediated competition reduction hypothesis are rare (Brewer 1999*b*, Suding 2001). Competitive displacement of fire-resistant species by less resistant species may not occur in the absence of fire if factors other than competition (e.g., differences in longevity, consumers, other disturbances) intervene to influence relative performance of fire-resistant and fire-sensitive species (Meadows and Hodges 1997, Ward et al. 1999, Brewer 2015). Competitive displacement of fire-resistant species by fire-sensitive species also may not occur at relatively unproductive sites due to low growth rates of competitors (Hodges and Gardiner 1993, Cannon and Brewer 2013). In addition, some fire-resistant species have been shown to use phenotypic plasticity (e.g., morphological plasticity in storage vs. growth or reproduction, shade avoidance, seed/bud dormancy) to avoid competitive displacement during years without fire (Brewer 1999, Hinman and Brewer 2007). A direct test of fire-mediated competition reduction requires manipulation of neighbors of fire-resistant species at burned and unburned sites and examining growth or fitness responses of the fire-resistant species (e.g., Brewer 1999).

Although most attention paid to the relationship between disturbance and competition has focused on their opposing effects on species coexistence, there are conditions in which disturbances can increase interspecific competition (Chesson and Huntly 1997, Violle et al. 2010, Brewer 2011). With respect to fire, in particular, several investigators have identified conditions in which fire-generated positive feedbacks (via increased flammability or fire-mediated competitive effects of fire-resistant species) favor stable dominance by fire-resistant species (DeAngelis et al. 1986, Beckage et al. 2009, Brewer 2011). Most ecologists have focused on the negative effects of fire-resistant species on fire-sensitive (strictly speaking, less fire-resistant) species mediated through the production of flammable fuels by the former (Williamson and Black 1981, Rebertus et al. 1989, Bond and Midgley 1995, Thaxton and Platt 2006). An alternative hypothesis, the fire-induced competition hypothesis, predicts that large plants have both a competitive advantage and an advantage in fire-resistance over small plants (Brewer 2011). Such an advantage is possible if at a given size a fire-resistant species recovers from fire more quickly or is more likely to avoid damage by fire than a fire-sensitive neighbor (due to, say, greater belowground storage, more rapid initial growth of resprouts, or thicker bark). The resulting size advantage obtained by fire-resistant species could then allow it to competitive suppress the fire-sensitive species. Hence, fire and competition may act in concert to cause a more rapid loss (and slower recovery) of fire-sensitive species than could be accomplished by fire alone (Brewer 2011). To my knowledge, however, there have been no manipulative experimental tests of fire-induced competitive effects of fire-resistant species on fire-sensitive species.

Competition between fire-resistant oak saplings and fire-sensitive non-oak saplings (e.g., mesophytes, sensu Nowacki and Abrams 2008) in open-canopy, upland oak-dominated forests represents a good system for testing relationships between fire and competition. Oaks tend to have thicker bark than most non-oak saplings, which enables the former to better avoid topkill (Hengst and Dawson 1994). In addition, higher investment in roots in oaks allows them to resprout and grow back more rapidly than non-oak saplings that invest more biomass in stem (Brose and Van Lear 2004). Oaks' high investment in storage roots, however, reduces allocation to stem and the rate of height growth, which in turn may place oaks at a height or growth disadvantage to fire-sensitive species in the absence of fire (Kolb et al. 1990). One hypothesis for the lack of successful regeneration of oaks in upland forests protected from fire throughout the eastern United States is excessive shade and/or competition in the understory of closed-canopy forests (Abrams 1992, Lorimer et al. 1994) combined with intense competition from taller or faster-growing non-oaks in canopy gaps (Brose et al. 1999, Iverson et al. 2008). Although several researchers have suggested that canopy reduction when coupled with repeated prescribed fire could release oak saplings from competition from non-oaks (Brose et al. 1999, Iverson et al. 2008), experimental tests of this hypothesis are lacking. Furthermore, to the extent that these post-fire differences in regrowth between oaks and non-oaks translate into size differences, and thus future differences in susceptibility to topkill, frequent fires could increase the competitive effects of oak saplings on non-oaks (Brewer 2011).

In this study, I quantified competition between saplings of fire-resistant oaks and their fire-sensitive non-oak neighbors in adjacent burned and unburned plots. Using field competition experiments with established in situ saplings, I tested two non-mutually exclusive hypotheses of how fire favors fire-resistant species: Fire-mediated competition reduction and fire-induced competition. Competition experiments were established in two adjacent, large (~1-ha) and environmentally similar plots in an open-canopy (40% canopy gap fraction) forest following tornado damage. One of the plots was subjected to prescribed fire in 2010, 2012, and 2014. The other plot was left unburned throughout the study. If fire reduced competitive effects of non-oaks on oaks, I predicted that the competitive effect of non-oaks on oaks would be greater in the unburned plot than in the burned plot and this difference would increase over time. If fire increased the competitive effects of oaks on non-oaks, I predicted that the greater susceptibility of non-oaks to topkill by fire would put them at a competitive disadvantage to oaks in the burned plot. I further predicted that the fire-induced competitive effect of oaks on non-oaks in the burned plot might not become apparent until there was sufficient accumulation of differences between oaks and non-oaks in the incidence of topkill (and thus size differences). I therefore also tested the hypothesis that differences in topkill between oaks and non-oaks would increase with each successive prescribed fire.

METHODS

Study site

The study was conducted in an upland oak–pine forest within the Tallahatchie Experimental Forest (TEF; the site of long-term monitoring of oak–pine forest dynamics; Surrette et al. 2008, Brewer et al. 2012, Cannon and Brewer 2013). The TEF is located within the northern hilly coastal plains of Mississippi (Holly Springs National Forest within the Greater Yazoo River Watershed, USA; 34.50° N, 89.43° W). Soils in the upland forests are acidic sandy loams and silt loams on the ridges and acidic loamy sands on side slopes and in the hollows (Surrette and Brewer 2008). In the early 1800s, before extensive logging and fire exclusion, open, self-replacing stands of fire-resistant tree species such as *Quercus velutina* Lam., *Q. marilandica* Münchh., *Q. stellata* Wangenh., *Q. falcata* Michx, and *Pinus echinata* Mill. dominated the upland landscape (Surrette et al. 2008). As a result of fire exclusion in the 20th century, second-growth forests are now dominated in the overstory by a mixture of some of the historically dominant upland oak species (but not *Q. marilandica*), pines (mostly *P.*

echinata), some species historically common in floodplains (e.g., *Q. alba* L., *Liquidambar styraciflua* L.), and some species that were common in both uplands and floodplains historically (e.g., *Carya* Nutt. spp., Surrette et al. 2008). The sapling layer in undamaged stands is typically dominated by *Nyssa sylvatica* Marshall, *Carya* spp., *Prunus serotina* Ehrh., *Acer rubrum* L., and *L. styraciflua*, whereas damaged stands with open canopies contain these non-oak species and saplings of various oak species, including the aforementioned and *Quercus coccinea* Münchh. (Cannon and Brewer 2013).

Prescribed burning

Initially, the prescribed fire treatment was replicated at three locations at TEF. However, the canopy environment was conducive to oak sapling recruitment at only one of these locations, namely an area containing two adjacent plots that had been damaged by a tornado in February 2008. The tornado reduced canopy cover to about 45% initially (Brewer et al. 2012), which then recovered to 60% in both plots by 2012 (see *Results* below). Therefore, I established the sapling competition experiment only within the two plots damaged by the tornado, and thus the effect of fire was not truly replicated. Nevertheless, the burned plot was burned repeatedly, first on March 25, 2010 and subsequently on March 29, 2012, and again on April 25, 2014. Details of the fires with respect to environmental conditions (i.e., ambient air temperatures, relative humidity) and fire behavior (i.e., percent coverage, flame lengths) are presented in Appendix A. Although fire behavior varied among years, all monitored saplings were burned by all three fires.

Topkill responses to the 2010, 2012, and 2014 prescribed fires

I contrasted topkill responses of oak and non-oak saplings to the 2010, 2012, and 2014 fires to enable me to specifically examine the competitive effects of non-topkilled stems on topkilled stems (and vice versa) and thus quantify the potential for fire to affect competition through differential topkill of oaks and non-oaks. To examine responses to the 2010 and 2012 fires, I examined saplings (stems greater than 1 m, but less than 10 cm dbh) previously tagged in the Cannon and Brewer (2013) study between 2009 and 2011 within a 10 × 30 m subplot within the burned plot. Although the 2010 fire was patchy (Appendix A), this fire passed through the entire 10 × 30 m subplot in both 2010 and 2012. Hence, no tagged sapling escaped either the 2010 or the 2012 fire. Specifically, I quantified topkill and complete-kill of saplings following the 2010 and 2012 fires. I describe the sampling scheme for the 2014 fire in the next section.

The competition experiment

I tested the fire-mediated competition reduction and fire-mediated competition hypotheses in two complementary steps. First, using pairs of co-occurring saplings, I contrasted the growth of target saplings adjacent to a neighbor of the same species group (i.e., oak target: oak neighbor or non-oak target: non-oak neighbor) with that of target saplings adjacent to a neighbor of a different species group (oak target: non-oak neighbor and vice versa). Second, to quantify the effects of neighboring saplings on the growth of target saplings, I located all neighbors of a specified species group within a 1 m radius (usually not more than one stem), clipped these to the ground, and repeated the clipping at each census (approximately 3 times a year). This procedure kept the neighboring stem as small as possible (typically less than 40 cm tall), thereby dramatically reducing if not eliminating any competitive effect on the target. In several cases, resprouting ceased after three clippings.

In April 2012, four weeks after the 2012 prescribed fire, I located pairs of oak:oak, oak:non-oak, and non-oak:non-oak saplings [stems (or topkilled stems) >1 m but <3 m tall] within 1 m of each other at each plot. I located 16 oak:oak pairs, 28 oak:non-oak pairs, and 16 non-oak:non-oak pairs within each plot. In addition to the 60 pairs, I included all possible pairs of oak:oak, oak:non-oak, and non-oak:non-oak combinations that were previously marked in 2009 in the Cannon and Brewer (2013) study within the 10 × 30 m subplot within the burned plot (described in the previous section, 26 pairs) and within a 10 × 30 subplot previously established by Cannon and Brewer in 2009 in the unburned plot (22 pairs). I knew that these previously marked pairs were saplings that recruited from established seedlings or sprouts following either the 2008 tornado or the 2010 prescribed fire and thus used them as a guide in deciding the appropriate size range for selecting pairs of saplings in 2012 (and 2013; see below). Hence, sapling pairs encountered in 2012 (and 2013) likely were also post-tornado or post 2010 sapling recruits. Of all targets and nearest neighbors encountered (including the 15 pairs per plot first marked in 2013, described below), I identified a total of 22 species (7 oak species and 15 non-oak species) and 384 stems (186 stems in the unburned plot and 198 in the burned plot [Appendix B]).

Beginning in April 2012, I measured height of the tallest stem for each species in a pair and began measuring basal diameter of the largest stem (in terms of basal diameter) in June 2012. For topkilled stems, I made these measurements for the largest topkilled and the largest resprouting stem. For each of the three categories (oak:oak, oak:non-oak, and non-oak:non-oak), I chose approximately half of the pairs at random to be included in the neighbor identity analysis, which therefore did not receive the competition (hereafter, clipping) treatment. I assigned the other half to the clipping treatment. Within each of the two monotypic groups (oak:oak, non-oak:non-oak), I chose one of the two stems at random to be the unclipped target stem. I clipped the remaining stem and all other saplings of the same species group (when present) within a 1-m radius of the target stem. Within the mixed group, I chose the non-oak sapling to be the target sapling and clipped the oak sapling and all other oak saplings within a 1-m radius of the non-oak target sapling. To examine the effects of non-oak neighbor reduction on oaks, in early March 2013, I located 30 additional oak:non-oak pairs within in each plot and randomly assigned 15 of these at each site to a non-oak clipping treatment. I discarded the remaining 15. In the non-oak clipping treatment, the oak sapling was the target sapling, and I clipped the non-oak sapling (along with all other non-oak saplings within a 1-m radius of the oak target).

Because I expected the growth of both oak and non-oak saplings to be limited by overhead shade, I used a spherical concave densiometer to quantify canopy gap fraction above each pair of saplings in the middle of the 2012 growing season (July 2012). I took measurements at 1.5 meters above the ground, but using a densitometer allowed me to easily exclude the effect of the canopy coverage contributed by the saplings themselves.

After the initial measurements in April and June 2012, I conducted additional censuses in July 2012, May 2013, July 2013, September 2013, May 2014, and July 2014 and administered the clipping treatments at each of these censuses. Height was strongly positively correlated with basal diameter in June 2012 as a power function [oaks: height(cm) $= 94.2 \times$ basal diameter(cm)$^{0.66}$, $r^2 = 0.86$, $N = 172$; non-oaks: height(cm) $= 115.2 \times$ basal diameter(cm)$^{0.58}$, $r^2 = 0.77$, $N = 112$]. For this reason and because basal diameter was previously shown to be a good indicator of fire-resistance of oak and non-oak saplings (Cannon and Brewer 2013), I quantified growth by calculating relative change in basal diameter ($\mathrm{rgr}_{\mathrm{diameter}}$). I reported $\mathrm{rgr}_{\mathrm{diameter}}$ for two time intervals, from June 2012 (or March 2013) to September 2013 (hereafter, year 1, an interval during which no fire occurred) and from September 2013 to July 2014 (hereafter, year 2, an interval during which the April 2014 fire occurred). In addition, to determine if oaks were responding to crowding in the unburned plot via phenotypic plasticity in stem elongation, I measured the change in the height to basal diameter ratio from June 2012 to July 2014 for non-topkilled oaks in the burned plot (with either topkilled or clipped neighbors) and in the unburned plot (with and without clipped neighbors). I first log-transformed and then z-transformed both height and basal diameter for 2012 and 2014. The log ratio was the transformed height minus the transformed basal diameter for each year.

Fire-mediated competition reduction predictions

If fire reduced the effects of neighbors on oaks, then, in the burned plot in 2014, the effect of neighbor reduction by clipping on growth of non-topkilled oak saplings would not be significantly different from the effect of neighbors topkilled by fire on oak growth (Fig. 1a). With regard to the effect of neighbor identity, I predicted that a significant competitive effect of non-oaks on oaks in the unburned plot would be indicated by lower $\mathrm{rgr}_{\mathrm{diameter}}$ of oaks in association with non-oak neighbors than with oak

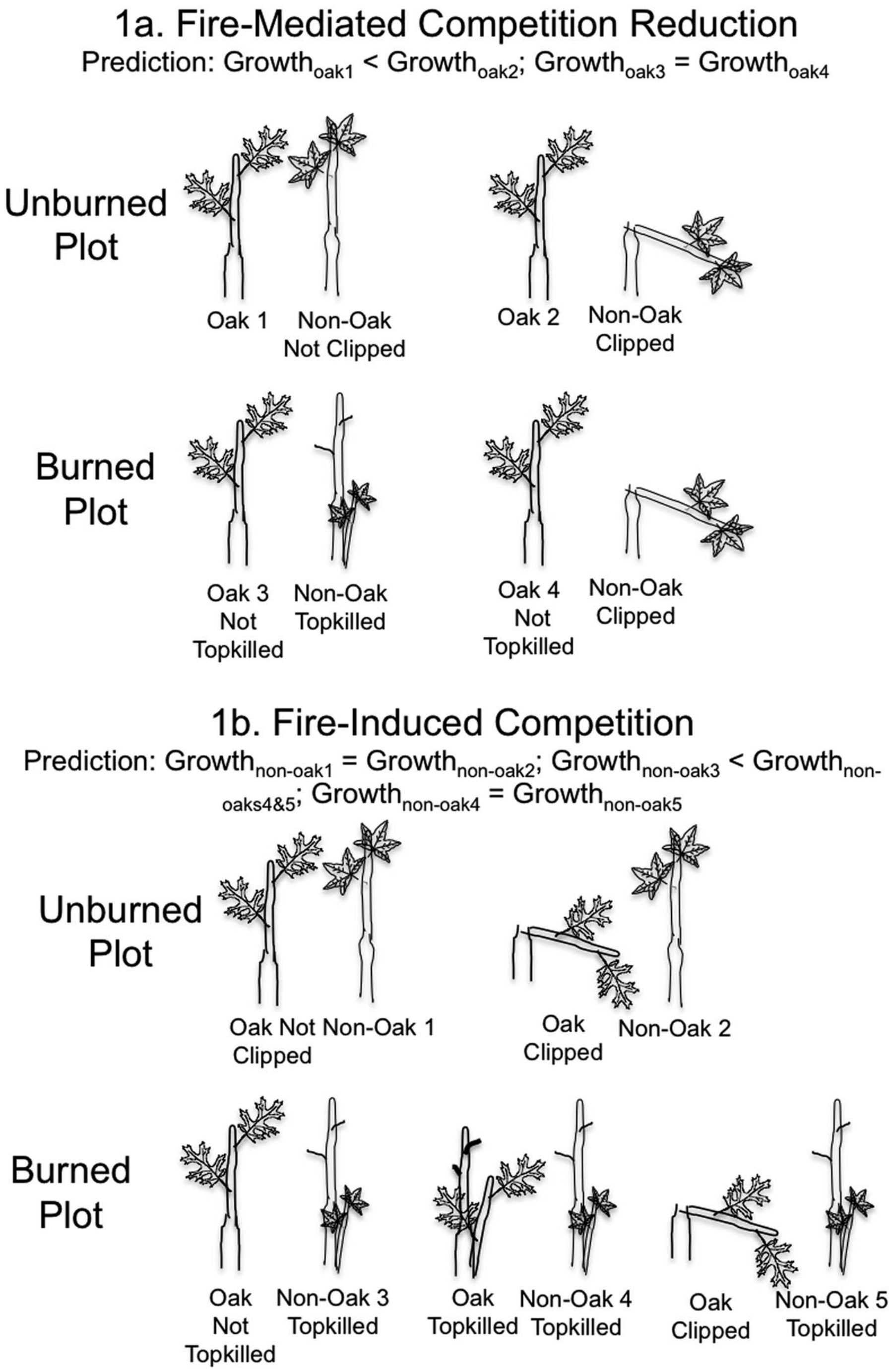

Fig. 1. Predicted growth responses of (a) undamaged oak saplings to reduction of non-oak neighbors in burned and unburned plots, and (b) topkilled non-oak saplings to reduction of oak neighbors in the burned and unburned plots.

neighbors. Evidence of shade avoidance by oaks in the unburned plot would be indicated by a greater increase in height:diameter ratio of oaks from 2012 to 2014 in the unburned plot with neighbors intact than in the unburned plot with neighbors clipped or in the burned plot with neighbors clipped or topkilled.

Fire-induced competition predictions

The hypothesis that fire increased the competitive effects of oaks was examined indirectly by comparing growth responses of topkilled non-oak saplings in the burned plot among samples with (1) clipped neighbors, (2) neighbors topkilled by fire, or (3) neighbors neither clipped nor topkilled by fire. One of the predictions of the fire-induced competition hypothesis is that topkilled saplings would grow more slowly adjacent to saplings that had not been topkilled than those that had been topkilled because of the greater size disadvantage in the former. Therefore, I predicted that growth of topkilled non-oak saplings whose neighbors were topkilled would be greater than that of saplings whose neighbors were neither topkilled nor clipped, but would be equal to that of those whose neighbors were clipped (Fig. 1b). Because significant die-back or topkill of saplings only occurred in the burned plot, I made this comparison only in the burned plot. If oaks were more resistant to topkill than were non-oaks, then fire should give oaks a competitive advantage over non-oaks. As done also for the 2010 and 2012 fires, I therefore determined whether the incidence of topkill following the 2014 fire was greater in non-oaks than oaks, but in contrast to the analysis of the 2010 and 2012 fires, I used both the sapling pairs in the 10 × 30 m subplot [initially marked in the Cannon and Brewer (2013) study] and those pairs located in the larger 1-ha plot in April 2012, but outside the 10 × 30 m subplot. To determine initial growth responses of non-oak saplings to the 2012 fire, I contrasted the relative difference in height between topkilled stems and the tallest resprouting stem in June 2012 among pairs in which the neighbor was either clipped, topkilled, or not clipped or topkilled. To determine whether topkill differentially reduced the competitive effects of oaks and non-oaks on topkilled non-oak target stems, I did two such analyses, one including all pairs (non-oak:non-oak and non-oak:oak) and one including only non-oak:oak pairs.

Statistical analyses

I used a likelihood ratio chi-square test to examine differences between oaks and non-oak in the incidence of topkill (or complete-kill) following 2010, 2012, and 2014 fires in the burned plot. I used a nominal logistic model (multi-source logistic regression) to examine differences between oaks and non-oak in the incidence of topkill, the likelihood of topkill as a function of basal diameter, and the interaction between species group and basal diameter, using data in the burned plot following the 2014 fires.

For the analyses of fire-mediated competition reduction, which included both plots, I analyzed growth responses (the dependent variable) to competition (i.e., either neighbor identity or neighbor reduction), plot (burned vs. unburned), and overhead canopy gap fraction using analysis of covariance. I included canopy gap fraction and its interactions with competition and plot as a covariate of interest. I did separate analyses for each species group (oaks and non-oaks) and for each year (year 1 and year 2). For the analyses of fire-induced competition that included only observations from the burned plot, I did not include canopy gap fraction in the analysis, because it had little influence on growth in this plot. Hence, I examined the effects of neighbor treatment non-oak growth using one-way ANOVA. I analyzed shade avoidance responses of oak saplings to neighbors using one-way repeated measures analysis of variance. I used JMP v. 5.0.1 (SAS, Cary, North Carolina, USA) to do all analyses. Sample sizes were moderately unbalanced among treatment groups for unavoidable reasons as described in Appendix C.

RESULTS

Topkill responses to 2010, 2012, and 2014 fires

As previously found in Cannon and Brewer (2013), the incidence of topkill following the 2010 fire, though slightly lower in oaks than in non-oaks, did not differ significantly between oaks and non-oaks (ratio of topkill to not-topkilled = 80:14 for oaks and 93:11 for non-oaks; likelihood ratio $\chi^2 = 0.83$; $P = 0.36$). In 2012, however, the incidence of topkill was significantly lower in

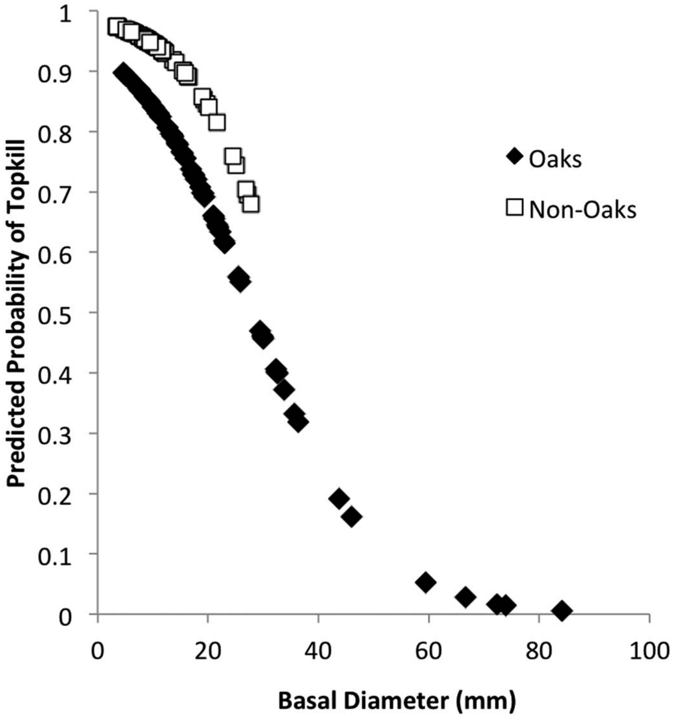

Fig. 2. Logistic regression result showing the predicted probability of topkill of oak and non-oak saplings as a function of basal stem diameter in September 2013, before the 2014 fire.

oaks than in non-oaks in the 10 × 30 m plot (ratio of topkill to not-topkilled = 66:27 for oaks and 88:10 for non-oaks; likelihood ratio $\chi^2 = 9.69$; $P = 0.0019$). Likewise, the incidence of topkill in sapling pairs in 2014 was significantly lower in oaks than in non-oaks (ratio of topkill to not-topkilled = 47:26 for oaks and 57:5 for non-oaks; likelihood ratio $\chi^2 = 15.65$; $P < 0.001$). Furthermore, when the effects of basal diameter and species group were both included in a single logistic model, I found that the advantage that oaks had in terms of avoiding topkill by the 2014 fire was to a large extent due to their greater size (basal diameter; basal diameter likelihood ratio $\chi^2 = 8.59$; $P = 0.0034$; species group likelihood ratio $\chi^2 = 2.99$; $P = 0.084$; Fig. 2). Although most topkilled stems of both species groups resprouted, a small percentage of topkilled stems in each species group did not resprout between 2010 and 2012 (1.1% for oaks and 5.8% for non-oaks).

Fire-mediated competition reduction

There was no evidence of fire-mediated competition reduction. Diameter growth of oak saplings was not influenced by neighbor identity or neighbor reduction in either plot in either year, with or without fire. During year 1 (the interval with no fire, but following the 2012 fire), the growth of oak saplings did not differ with respect to neighbor identity ($\mathrm{rgr}_{\mathrm{diameter}} = 0.37$ yr^{-1} with oak neighbors vs. 0.39 yr^{-1} with non-oak neighbors; neighbor identity $F_{1,54} = 0.05$; $P = 0.88$). In addition, the effect of neighbor identity on oak growth did not differ between the burned and the unburned plot in year 1, and thus there was no neighbor identity by plot interaction ($F_{1,54} = 0.21$; $P = 0.65$). In addition to there being no effect of neighbor identity, neighbor reduction (via repeated clipping) had no significant effect on oak growth in year 1 ($\mathrm{rgr}_{\mathrm{diameter}} = 0.38$ yr^{-1} with unclipped neighbors vs. 0.30 yr^{-1} with clipped neighbors; neighbor reduction $F_{1,100} = 1.99$; $P = 0.16$), nor did its effect vary between plots (neighbor reduction × plot $F_{1,100} = 0.39$; $P = 0.54$; Fig. 3a). The growth of oak saplings (including both topkilled and non-topkilled) was significantly higher in the burned plot than in the unburned plot ($\mathrm{rgr}_{\mathrm{diameter}} = 0.53$ yr^{-1} in the

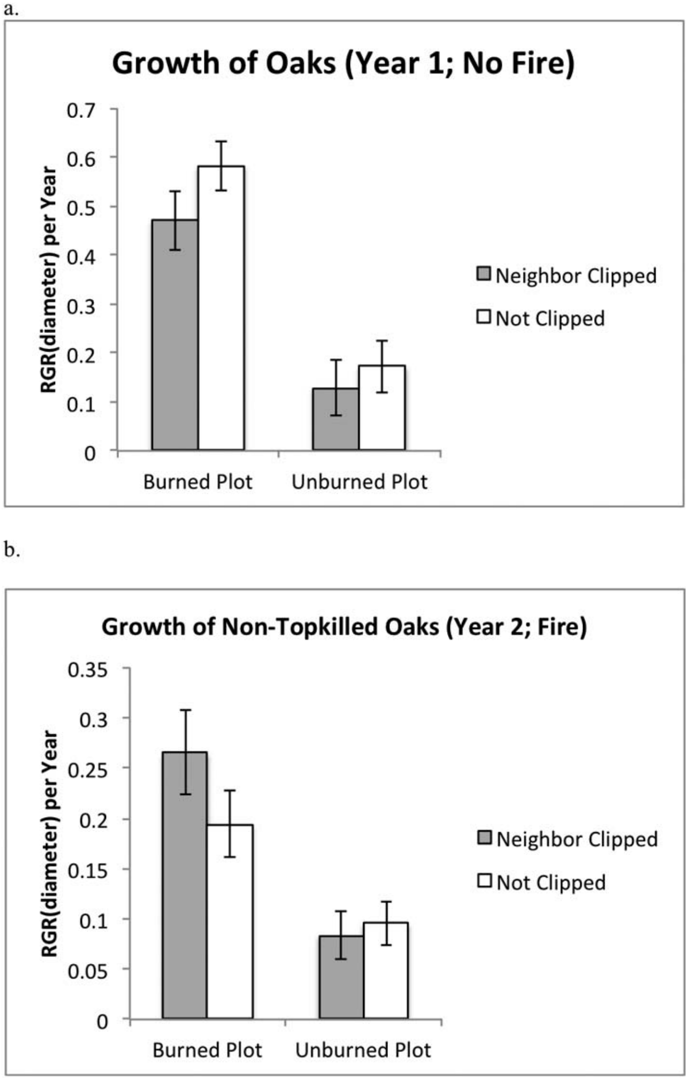

Fig. 3. The effect of neighbor reduction (via repeated clipping) on (a) diameter growth of oak saplings in a year without fire (year 1) and (b) diameter growth of non-topkilled oak saplings in a year with fire (year 2). Values for year 1 are least-squares mean rgr per year ± 1 standard error adjusted for canopy gap fraction. Values for 2 are least-squares mean rgr per year ± 1 standard error. Only the plot effect was statistically significant ($P << 0.001$). Neither neighbor reduction nor its interaction with plot was significant ($P > 0.18$). In year 1, sample sizes from left to right were 25, 31, 24, and 27. Treatment df were 1 for plot, 1 for neighbor reduction, 1 for neighbor reduction × plot interaction, 1 for canopy gap fraction, and 1 for each of the three interactions with canopy gap fraction. Error df = 100. For year 2, sample sizes from left to right were 8, 13, 23, and 28; treatment df = 1 for plot, 1 for neighbor reduction, 1 for the interaction, and 1 for canopy gap fraction; error df = 67. Analyses with type III and type II sums of squares yielded similar results.

burned plot vs. 0.15 yr^{-1} in the unburned plot; plot $F_{1,100} = 46.42$; $P << 0.001$). Neither canopy gap fraction nor any of its interactions with neighbor identity or plot was statistically significant (40.4% ± 4% in the unburned plot vs. 39.1% ± 4.6% in the unburned plot; $P > 0.33$). During year 2 (the interval during which the April 2014 fire occurred), the growth of non-topkilled oak saplings was not significantly affected by neighbor reduction in either the unburned or burned

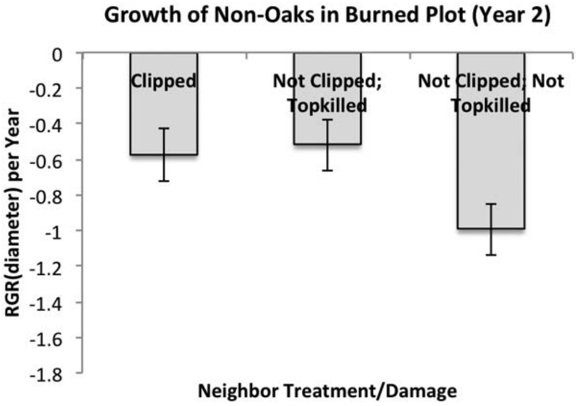

Fig. 4. Differences in relative growth rate of topkilled non-oak saplings in response to neighbor treatment/condition in the burned plot in 2014 (year 2). Values are mean rgr per year ± 1 standard error. Sample sizes from left to right were 14, 18, and 15. Error df = 44.

plot (neighbor reduction $F_{1,67} = 0.84$; $P = 0.36$; neighbor reduction × plot $F_{1,67} = 1.76$; $P = 0.18$; Fig. 3b). As in year 1, growth of non-topkilled oak saplings in year 2 was significantly greater in the burned plot than in the unburned plot ($\text{rgr}_{\text{diameter}} = 0.22\ \text{yr}^{-1}$ in the burned plot vs. $0.09\ \text{yr}^{-1}$ in the unburned plot; plot $F_{1,67} = 20.80$; $P << 0.001$).

Oak saplings did not show unequivocal evidence of a shade avoidance response to the reduction of neighbors between 2012 and 2014. The change in the height:diameter ratio did however vary significantly among unburned, non-topkilled saplings that had neighbors clipped, unburned non-topkilled saplings with intact non-oak neighbors, and burned but not topkilled saplings with neighbors reduced by clipping or fire (year × neighbor treatment $F_{2,61} = 3.19$; $P = 0.048$). The height:diameter ratio increased in the unburned plot (irrespective of whether neighbors were reduced) and decreased in the burned plot (year × neighbor treatment: burned vs. unburned contrast $F_{1,61} = 5.86$; $P = 0.019$). The height:diameter ratio did not increase to a greater extent when neighbors were left intact than when reduced by clipping or topkill (year × neighbor treatment: neighbors reduced v. neighbors not reduced contrast $F_{1,61} = 0.63$; $P = 0.43$).

Fire-induced competition

Growth responses of non-oak saplings to clipping or topkill of neighbors were consistent with a prediction of fire-mediated competition. Fire-induced competitive effects were apparent only after the second fire (2014), but not after the first fire (2012). Following the 2012 fire in June, there was no effect of neighbor reduction (oaks or non-oaks) via either clipping or topkill on the difference in height between topkilled stems and resprouting of non-oaks (neighbor treatment $F_{2,55} = 0.56$; $P = 0.57$). The same was true when I only considered oak neighbors (neighbor treatment $F_{2,41} < 0.01$; $P = 0.99$). In the year without fire (year 1), there was no effect of neighbor identity on growth of non-oaks in the unburned plot (0.12 vs. $0.13\ \text{yr}^{-1}$ for oak and non-oak neighbors, respectively; neighbor identity $F_{1,23} = 0.049$; $P = 0.83$). There were too few observations of non-oak:non-oak pairs in which both individuals were still alive in 2013 to permit a analysis of neighbor identity in the burned plot. Growth of non-oaks did not respond to clipping of oak neighbors either in the unburned plot or the burned plot in year 1 (0.41 vs. $0.43\ \text{yr}^{-1}$ in unclipped and clipped plots, respectively; neighbor treatment $F_{1,70} = 0.80$; $P = 0.79$; neighbor treatment × plot interaction $F_{1,70} = 0.071$; $P = 0.79$). In the burned plot in the year with the 2014 fire (year 2), growth of topkilled non-oak saplings was significantly greater in pairs in which the neighbor had been clipped or topkilled by fire than in pairs in which the neighbor had neither been clipped nor topkilled (neighbor treatment $F_{2,44} = 3.52$; $P = 0.038$; neighbor treatment: topkill or clipped vs. neither topkilled nor clipped contrast $F_{1,44} = 6.79$; $P = 0.012$; neighbor treatment: clipped vs. topkilled contrast $F_{1,44} = 0.09$; $P = 0.77$; Fig. 4).

DISCUSSION

This study represents a rare direct test of differences in competition between burned and unburned areas. I found no evidence of fire-mediated competition reduction in this study. Oak saplings did not show reduced growth in the presence of non-oak sapling neighbors and did not benefit from the experimental reduction (repeated clipping) of non-oak neighbors. Nevertheless, results show that repeated fires can give oaks a competitive advantage over non-oaks by increasing competitive effects of the former on the latter.

One explanation for the lack of competitive effects of non-oaks on oaks is that size differences between non-oaks and oaks in the unburned plot in this study were not sufficient to result in significant competition (Lorimer et al. 1994, Iverson et al. 2008). In contrast to observations in a study at more productive, but compositionally similar, oak-hickory forest sites in Ohio (Iverson et al. 2008), initial heights of oak and non-oak saplings were similar at the beginning of the study in the unburned plot in my study and remained so through July 2014. Both oaks and non-oaks grew faster in the burned plot than in the unburned plot. Except in those cases in which non-topkilled saplings grew alongside topkilled saplings, neither group had an overall diameter growth advantage over the other (Fig. 3a, b). Previous studies have shown that positive effects of sapling thinning on diameter growth were only apparent for individuals at a size disadvantage (Allen and Marquis 1970, Trimble 1974, Lamson and Smith 1978). The lack of variability in height of the sapling community six years after the tornado in the unburned plot indicates that this community had not yet entered the "stem exclusion" phase of post-disturbance stand development (sensu Oliver and Larson 1996). Continued monitoring over time therefore will be required to determine if competitive effects of non-oaks on oaks become apparent after a threshold average tree size is met.

A second possible explanation for the lack of competitive effects of non-oaks on oaks is that oaks could have avoided negative effects of their neighbors in the unburned plot through phenotypic plasticity (i.e., a shade avoidance response; Smith 1982, Schmitt 1987, Brewer 1999, Gilbert et al. 2001). My investigation of changes in the height:diameter ratio of oaks in response to neighbor reduction suggested a possible shade-avoidance response in the unburned plot, but it was not conclusive. The height:diameter ratio of non-topkilled oaks was lower in the burned plot than in the unburned plot in 2012 and decreased significantly between 2012 and 2014 only in the burned plot. However, the height:diameter ratio did not increase to a greater extent when neighbors were left intact than when reduced by clipping in the unburned plot. A possible explanation for these results is that vegetation outside the 1-m-radius neighborhood (to which the clipping treatment was confined) was taller in the unburned plot than in the burned plot, and this difference was sufficient to result in increased diameter growth at the expense of height in the burned plot but not in the unburned plot (Gilbert et al. 2001).

In contrast to the lack of evidence for fire-mediated competition reduction, growth responses of non-oak saplings to clipping or topkill of neighbors were consistent with fire-induced competition (Brewer 2011). I found that growth of topkilled non-oak saplings whose neighbors were either topkilled or clipped was greater than that of saplings whose neighbors were neither topkilled nor clipped (Figs. 1b and 4). Growth of those non-oak saplings whose neighbors were clipped was equal to the growth of saplings whose neighbors were topkilled by fire (Fig. 4). As a group, oak saplings grew back more rapidly following the prescribed fire in 2010 than did non-oaks most likely due to greater root reserves in the former (Cannon and Brewer 2013). Although these post-fire differences in regrowth did not immediately translate into increased competitive effects of oaks on non-oaks, the resulting size differences likely contributed to subsequent differences in susceptibility to topkill in 2012 and 2014. Differences in susceptibility to topkill ultimately gave oaks a size and thus competitive advantage over non-oaks after the 2014 fire. I predict that the advantage that oaks have over non-oaks in avoiding topkill will increase with each successive fire, which in turn will increase the former's competitive effects on the latter. Because fires vary in ways that are not easy to predict, continued monitoring of several fires will be necessary to validate these predictions.

Fire-induced size asymmetry appears to be important in determining competitive interactions between oaks and non-oaks. The obvious and likely effect of size asymmetry is that the taller, non-topkilled oak saplings shaded the much shorter, topkilled non-oak saplings, but I cannot rule out increased competition for water or nutrients. The fire-mediated competition and fire-induced competition hypotheses parallel ideas related to the effects of selective herbivory on competitive interactions (Lubchenco 1978, Louda 1989). Bazely and Jefferies (1986) found that a salt marsh plant species that grew back rapidly from generalist grazing by geese competitively suppressed other species that grew back more slowly. In most studies of selective herbivory, however, the effect on competition has typically been to release ungrazed plants from competition (Belsky 1992, Furbish and Albano 1994, Burger and Louda 1995). Hence, additional studies of disturbance-induced competition mediated by interspecific differences in disturbance-resistance (as opposed to disturbance resilience) are warranted.

To my knowledge, the current study is the first manipulative experimental test of fire-mediated competitive effects of fire-resistant species on fire-sensitive species. The current study focused on interspecific differences in resistance to damage, finding that competitive ability was, itself, a function of disturbance resistance. These findings differ somewhat from those of Violle et al. (2010), who found that severe, mortality-causing disturbances, when combined with competition, caused the extinction of both superior competitors and disturbance-resilient species of protists. The results of this study provide experimental support for a theory of fire-mediated positive feedbacks (DeAngelis et al. 1986, Beckage et al. 2009, Brewer 2011). Synergistic effects of fire and competition might be particularly important in giving fire-resistant species a competitive advantage in systems in which most individuals of both fire-resistant and fire-sensitive species survive fire. The advantages that fire-tolerant tree species have over fire-sensitive species in many systems may result more from differential responses to non-lethal damage than from survival differences. For example, investigations of the savanna-forest boundary in Brazil revealed that the advantage that the more fire-resistant savanna trees had over forest trees in the savanna resulted more from the former's greater ability to avoid topkill than from greater survival of fires per se (Hoffmann et al. 2009). If fire and competition act synergistically, escape of fire-sensitive trees from the "fire trap" (i.e., perpetual topkill, Bond and Midgley 2001) when subjected to fires of moderate intensity may be more difficult than if fire, alone, acts to suppress fire-sensitive species (Brewer 2011).

From the standpoint of managing for oaks, a potential benefit of fire-mediated competition is that complete fire-caused mortality of non-oaks in the vicinity of oaks may not be necessary for oaks to gain a competitive advantage over non-oaks. Following canopy disturbance and a sufficient period of time without fire to allow oaks to build up belowground reserves (Albrecht and McCarthy 2006), frequent fires could result in an accumulation of non-topkilled oaks growing in association with topkilled non-oaks and the concomitant competitive suppression of the latter by the former. Given the lack of competitive effects of non-oaks on oaks in the absence of fire observed in this study, fire-mediated competition could slow the recovery of regrowing non-oaks from each fire and facilitate recruitment of oak saplings into the midstory and ultimately the overstory.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–C are available online: http://dx.doi.org/10.1890/ES15-00116.1.sm