Resprouting potential of oaks and non-oaks in response to repeated mechanical damage

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Abstract

Despite widespread recognition of the importance of resprouting following repeated topkill in promoting fire resistance of saplings, relevant tests are rare. In this study, I developed a “stress test” to examine how the rate of attrition of resprouting ability differed between saplings of fire-resistant oaks and their more fire-sensitive, non-oak hardwood neighbors. Using field experiments with established in situ saplings in open-canopy (60% cover) forest stands, I examined how repeated clipping (two to three times per year over three growing seasons, 2012, 2013, and 2014) affected the incidence of resprouting and the length of the longest resprouting stem. I replicated the clipping treatment in adjacent, repeatedly-burned and unburned 1-ha stands and tested two hypotheses: 1) growth of resprouts following a single clipping was similar to the growth of resprouts following topkill by a spring fire but was greater for oaks than for non-oaks; 2) the growth advantage of resprouts of oaks over that of non-oaks increased over time with repeated clipping. Initial growth responses of resprouting stems to clipping in the unburned stand did not differ significantly from those of resprouting stems to an early spring fire in 2012 but were greater for oaks as a group than for non-oaks. Initial growth rates of resprouting stems after clipping (or fire) in 2012 resulted primarily from species-specific differences in the response to mechanical damage. The initial regrowth advantage of oaks over non-oaks that increased after repeated clippings over three growing seasons. Results suggest that, at least under relatively open canopies, oak saplings potentially have a resprouting advantage over non-oak hardwoods that persists and increases over time when subjected to repeated topkill by fires.

Keywords: clipping, fire, oak regeneration, Quercus spp., repeated fire, sapling, topkill
1. Introduction

Traits that confer fire resistance in woody species include thick bark, resprouting from belowground organs and stems, prolonged storage of resources belowground or in protected aboveground stems, and rapid height growth immediately following fire (Falster and Westoby, 2005; Whelan, 1995). In particular, rapid height growth immediately following fire may give some fire-resistant woody species an advantage over more fire-sensitive species with respect to greater recovery from damage (Brewer, 2015; Cannon and Brewer, 2013; Hodgkinson, 1998; Iverson et al., 2008; Kruger and Reich, 1993a, 1993b; Maguire and Menges, 2011; Midgley, 1996). On the other hand, fire-sensitive species may have higher photosynthetic rates and thus have an intrinsic height growth advantage over fire-resistant species in the absence of fire (Alexander et al. 2008; Rossatto et al. 2009), which in turn may give them a competitive advantage in the absence of frequent fires (Abrams and Nowacki, 1992; Beck and Hooper, 1986; but see Brewer, 2015). Because some fire-sensitive species may respond to a single fire with rapid height growth, however, these species may not be at a height growth disadvantage to more fire-resistant species after a single fire (Alexander et al., 2008; Arthur et al., 1998). Positive responses of resprouters to repeated damage by fire likely requires prolonged storage of resources belowground or in protected aboveground stems (Olano et al., 2006; Reich et al., 1990). The advantage that fire-resistant species have in terms of belowground biomass and/or buds may only accrue in response to repeated damage from fires as these reserves become depleted.

Despite widespread recognition of the importance of resprouting following repeated topkill in promoting fire resistance of saplings, relevant tests are rare. The importance of
belowground reserves in resprouting potential is typically inferred from observations that saplings of species with greater belowground biomass as seedlings typically produce taller or more vigorous resprouting stems after one or multiple fires (Brewer, 2015; Kolb et al., 1990).

Direct tests that relate resprouting potential to belowground biomass and/or buds in saplings, however, are rare, in large part because of the difficulty in obtaining belowground measurements from woody plants that are larger than seedlings (Olano et al. 2006). Furthermore, resprouting performance following fire depends on factors other than belowground biomass and buds, including damage-induced changes in photosynthetic rates (Kruger and Reich, 1993a; b) and fire-related environmental changes that could affect growth rates of the resprouting stems (e.g., increased light and/or nutrients; plant water potential; reduced competition; Kruger and Reich, 1997a; Olano et al. 2006). To disentangle the effects of damage-related changes in photosynthetic rate and fire-related resource fluxes from the effects of repeated biomass loss as drivers of fire resistance in saplings, it is necessary to examine the effects of repeated damage in the absence of fire on resprouting potential.

A contrast of fire-resistant oak saplings and more fire-sensitive non-oak hardwood saplings (e.g., mesophytes, sensu Nowacki and Abrams, 2008) in open-canopy, upland oak-dominated forests represents a good system for understanding the effects of interspecific belowground differences on resprouting potential. Oaks tend to have higher investment in roots, which presumably 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 roots, however, reduces allocation to stem and the intrinsic 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). Furthermore, because height growth of resprouting stems following a single fire depends on many factors beside belowground variables (Kruger and Reich, 1997a, 1997b), oak saplings may not be at a height growth advantage after a single fire (Albrecht and McCarthy, 2006; Alexander et al., 2008; Arthur et al., 1998). The advantage that oak saplings have in terms of extensive belowground biomass or buds may become increasingly apparent after repeated damage, although tests of that hypothesis are lacking.

In this study, I developed a “stress test” to examine interspecific differences in the rate of attrition of resprouting potential between saplings of fire-resistant oaks and those of their more fire-sensitive, non-oak hardwood neighbors in adjacent burned and unburned plots. Using field experiments with established in situ saplings, I examined how repeated clipping (two to three times per year over three growing seasons, 2012, 2013, and 2014) affected the length of the longest resprouting stem. Experimental treatments 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, however, was subjected to prescribed fire in 2010, 2012, and 2014. The other plot was left unburned throughout the study. I used this experimental design to test two hypotheses: 1) growth of resprouts following a single clipping was similar to the growth of resprouts following topkill by a spring fire but was greater for oaks as a group than for non-oaks; 2) the growth advantage of resprouts of oaks over that of non-oaks increased over time with repeated clipping. Support for the first hypothesis was taken as evidence that growth responses of resprouting stems to topkill are affected more by species-related differences in their response to mechanical damage than by heat-related damage or fire-induced environmental changes. Support for the second hypothesis was taken as evidence that the persistence advantage
of oak saplings over non-oak saplings following repeated fires is due in part to a lower rate of attrition of resprouting ability over time in the former.

2. Methods

2.1. 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; Brewer, 2015; Brewer et al., 2012; Cannon and Brewer, 2013; Surrette et al., 2008). The TEF is located within the northern hilly coastal plains of Mississippi (Holly Springs National Forest within the Greater Yazoo River Watershed, U.S.A.; 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).

2.2. *Canopy Damage by a Tornado and Prescribed Burning*

The prescribed fire treatment was replicated at two locations at TEF. However, oak sprouts tend not to gain a fire-mediated advantage over those of non-oaks when the overstory canopy is largely closed (Brewer, 2014; Cannon and Brewer, 2013; Iverson et al., 2008). Therefore, 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. I thus established the clipping experiment only within the two plots damaged by the tornado, and 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. See Brewer (2015) for 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). Although fire behavior varied among years, all monitored saplings were burned by all three fires.

2.3. *The Clipping Experiment*

I examined differential growth responses of resprouting stems following either clipping or fire-induced topkill in 2012 and 2014 (each a fire year). I selected individual saplings between 1 and 3 m tall oaks and non-oak hardwood species roughly in proportion to their frequencies in
each of the two plots. Prior to the March 29 fire in 2012, I selected 25 live individual sapling stems of oaks and 20 live individual saplings of non-oak hardwoods in each of the two plots. In the unburned plot, I selected 7 *Quercus falcata*, 6 *Q. marilandica*, 5 *Q. velutina*, 3 *Q. alba*, 3 *Q. coccinea*, 1 *Q. stellata*, 7 *Acer rubrum*, 5 *Nyssa sylvatica*, 5 *Ulmus alata*, 2 *Prunus serotina*, and 1 *Carya pallida*. 2. In the burned plot, I selected 7 *Q. coccinea*, 6 *Q. velutina*, 5 *Q. falcata*, 4 *Q. alba*, and 3 *Q. marilandica*, 6 *Acer rubrum*, 5 *Nyssa sylvatica*, 3 *Prunus serotina*, 2 *Carya pallida*, and 4 *Ulmus alata*. In the unburned plot, I clipped to the ground each selected stem in early April, late June, and mid September of 2012 and 2013, and in early April and late June of 2014. To ensure equal frequency of topkill in both the unburned and the burned plots, I did not clip the selected stems in the burned plot in April of 2012 nor 2014 (all selected stems had been topkilled by fire in both fire years).

### 2.4. Growth and Survival Measurements, Statistical Analyses and Predictions

Beginning in late June 2012, just before the second clipping treatment in the unburned plot, I measured height of the tallest resprouting stem (if present). A previous study (Brewer, 2015) showed height to be strongly positively correlated with basal diameter as a power function [oaks: height(cm) = 94.2*basal diameter(cm)$^{0.66}$, $r^2 = 0.86$, $N = 172$; non-oaks: height(cm) = 115.2*basal diameter(cm)$^{0.58}$, $r^2 = 0.77$, $N = 112$] and thus a good indicator of size. In addition, in that study, I experimentally demonstrated that height of the tallest resprouting stem was a good indicator of sapling competitive ability (Brewer, 2015). Hypotheses were tested by comparing the growth rates of resprouting stems in the two species groups in the burned plot with those in the unburned plot following one topkill treatment (clipping or fire) from April to
June 2012 and then by examining the reduction in growth from the initial responses following
topkill treatments in 2012, 2013, and 2014. Support for hypothesis 1 was indicated by the lack of
a main effect of plot, such that growth responses were similar between the burned and unburned
plots but differed between species groups (such that oaks as a group had an advantage). Support
for hypothesis 2 was indicated by an increasing advantage of oaks over non-oaks over time with
repeated clipping. Initial responses were quantified using two-way analysis of covariance
(species group and plot as fixed factors). In addition, the initial, pre-treatment stem height was
included as a covariate to account for the influence of initial size on sprout growth. The change
in sprout growth over time was tested by examining growth responses to clipping in July 2014
and subtracting from those the initial growth responses to treatments in April 2012. Analyses of
growth changes were restricted to those stems that survived the initial clipping/fire treatment in
2012. Resprouting stem heights were log-transformed after adding 1 to deal with zeroes
(nonsprouters) and to normalize residuals. In addition to examining changes in growth between
2012 and 2014, species group differences in survival to 2014 were examined using logistic
regression. Analyses were done using the linear models (lm) function and the generalized linear
model (glm) assuming a binomial response in R, version 3.2.4 (The R Foundation for Statistical
Computing, 2016)

3. Results

One oak sapling (Q. alba) was completely killed by the spring 2012 fire, four non-oaks
were killed by the same fire (two saplings of Nyssa sylvatica and two saplings of Ulmus alata),
and two saplings of non-oaks were killed by the clipping treatment in 2012 (one of *Acer rubrum* and one of *Nyssa sylvatica*). Results of this study provided support for the hypothesis that initial growth responses of surviving saplings to damage were unrelated to fire conditions per se but rather were related to species group differences (hypothesis 1). Initial growth responses of resprouting stems between April and late June 2012 did not differ significantly between the burned and the adjacent unburned plots ($F_{1,78}$ (plot) = 0.06; $P = 0.81$). Initial growth responses were greater for oaks as a group than for non-oaks as a group ($F_{1,78}$ (plot) = 22.71; $P << 0.01$; Figs. 1, 2). Nevertheless, initial growth responses to damage varied somewhat among non-oak species. In particular, the initial growth response of *Prunus serotina* to damage was equal to or even greater than those of many of the oak species; Figs. 1, 2). Likewise, although based on relatively few observations, the initial growth response of *Carya pallida* to damage was comparable to those of many of the oak species; Figs. 1, 2). Differences in the initial growth responses between oaks and non-oaks did not vary between the burned and unburned plot ($F_{1,78}$ (species group x plot) = 0.10; $P = 0.76$).

Results also provided support the hypothesis that oaks, as a group, are more tolerant of repeated damage than are non-oak hardwoods. Oaks had an advantage over the non-oaks in terms of growth of resprouting stems after repeated clipping, irrespective of fire. Differences between oaks and non-oaks in the growth responses of resprouting stems were significant following the July 2014 clipping treatments, with oaks tolerating repeated clipping better than non-oaks ($F_{1,78}$ (species group) = 4.48; $P = 0.04$; Figs. 1, 2). Indeed, the majority of non-oak stems failed to resprout (Fig. 2), whereas many oak stems did resprout following clipping in July 2014 (Fig. 1), resulting in differences in survival that approached statistical significance ($z_{78}$ (species group)
= 1.92; \( P = 0.055 \). There was no difference between the burned and the unburned plot with respect to the change in growth between 2012 and 2014 (\( F_{1,78}^{(\text{plot})} = 0.37; \ P = 0.54 \)), nor did species group interact with plot to influence growth response in 2014 (\( F_{1,78}^{(\text{species group x plot})} < 0.01; \ P = 0.96 \)).

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4. Discussion

In this study, I developed a “stress test” to examine how rates of attrition of resprouting potential of saplings differed between fire-resistant oaks and their more fire-sensitive, non-oak hardwood neighbors. Results provide support the hypothesis that oaks, as a group, have an advantage over the non-oaks in terms of growth of resprouting stems after repeated topkill. Resprouting responses to topkill in fire largely reflected species-specific responses to mechanical damage in the spring, rather than a response to environmental changes specifically associated with spring fires in this system (e.g., heat, nutrients, light). Such a response suggests that depletion of belowground reserves and/or buds occurred more rapidly in non-oaks as than it did in oaks as a group. High investment in belowground biomass or buds has been identified as one trait that could give saplings of some fire-resistant tree species an advantage over saplings of more fire-sensitive species with respect to greater recovery from damage (Brose and Van Lear, 2004; Hodgkinson, 1998; Iverson et al., 2008; Midgley, 1996). Tests that relate resprouting potential to belowground biomass and/or buds in saplings, however, are rare, in large part because of the difficulty in obtaining belowground measurements from saplings (Olano et al., 2006). Future work on resprouting potential of oaks and non-oaks should focus directly on the role of belowground reserves and/or buds.
The greater growth response of oaks compared to non-oaks to a single topkill event (from either clipping or spring fire) at the beginning of the study is in general agreement with results of several studies of fire effects on the height growth of resprouting stems (Brose et al., 1999; Cannon and Brewer, 2013; Kruger and Reich, 1997b). Two demonstrated advantages of greater height growth of resprouting stems following damage by fire are a reduced subsequent likelihood of topkill by fire and improved competitive status (Brewer, 2015). Oaks however do not appear to have this regrowth advantage in closed-canopy forests (Alexander et al., 2008; Arthur et al., 1998; Cannon and Brewer, 2013; Iverson et al., 2008) or when the fire occurs immediately after the opening of the canopy (Albrecht and McCarthy, 2006). If oaks depend on belowground reserves to recover from fire, then they may require an open canopy for multiple growing seasons to build the required reserves (Albrecht and McCarthy, 2006). This hypothesis is supported by other studies where oaks responded positively to prescribed fire several years after thinning (Brose et al., 1999; Cannon and Brewer, 2013; Kruger and Reich, 1997b). In the current study, oak saplings had two full growing seasons to increase in size and build up belowground reserves before a fire in 2008, which may have contributed to increased sprout growth.

Although one or two fires may give oaks a sprouting advantage over non-oaks in canopy gaps, the long-term persistence of oaks and attrition of non-oaks depends on how each group responds to repeated fires over time. Not all non-oak species performed more poorly than most oaks to a single clipping or fire. The growth of resprouts of one non-oak species in particular, *Prunus serotina*, was as great or greater than that of most oak species. However, after three growing seasons of repeated clipping, oak saplings as a group performed substantially better than *P. serotina*. The stress test performed here was not intended to simulate an operational, frequent
fire regime. The results do suggest, however, that frequent repeated fires have the potential to give oak saplings a relative persistence advantage over non-oak saplings, including those non-oak species that respond well to a single fire. Frequent fires could be used to alter the species composition of the sprout bank in a way that favors oaks. Such frequent fires could also maintain an open canopy and thus favor desired, shade-sensitive herbaceous vegetation (Brewer, 2016; Brewer et al., 2015). Ultimately, a reduction of fire frequency could be used to allow oak sprouts to escape the fire trap (sensu Bond and Midgley, 2001) and promote oak recruitment to the overstory within canopy gaps (Rebertus and Burns, 1997; Rebertus et al. 1993), as is done in the management of oak savannas (Peterson and Reich, 2001; Rebertus and Burns, 1997).

5. Conclusions

Oaks in forests, woodlands, and savannas of eastern North America are important for their commercial and wildlife value (Johnson et al., 2009), as well as being a base of terrestrial food webs (Tallamy and Shropshire, 2009). Ecologists and land managers have expressed concern over the potential long-term persistence of oaks, given their lack of successful regeneration in forests with closed canopies that have experienced fire exclusion (Nowacki and Abrams, 2008). Repeated fires and open canopies therefore are hypothesized to improve oak regeneration. Results of this study showed that, at least under relatively open canopies, oak saplings have a resprouting advantage over non-oak hardwoods that potentially persists and increases over time when subjected to repeated topkill by fires.
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ecophysiology and community dynamics of central Wisconsin oak forest regeneration.


Figure Legends

Figure 1. Norms of reaction plots of height growth responses of saplings of the five most common oak species after a single clipping (or fire) from April to late June 2012 and multiple clippings (or fire; 8 clippings or 6 clippings and 2 fires over three growing seasons) from late June to September 2014. Values are least squares height corrected for pre-treatment sapling stem height.

Figure 2. Norms of reaction plots of height growth responses of saplings of the five most common non-oak species after a single clipping (or fire) from April to late June 2012 and multiple clippings (or fire; 8 clippings or 6 clippings and 2 fires over three growing seasons) from late June to September 2014. Values are least squares height corrected for pre-treatment sapling stem height.