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RESEARCH ARTICLE

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Effects of Tornado Damage, Prescribed Fire, and Salvage Logging on Natural Oak (*Quercus* spp.) Regeneration in a Xeric Southern USA Coastal Plain Oak and Pine Forest

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ABSTRACT: Due in large part to fire exclusion, many oak-dominated (*Quercus* spp.) forests, woodlands, and savannas throughout eastern North America are being replaced by less diverse forest ecosystems. In the interior coastal plain of the southern United States, these forests are dominated in the mid- and understory by mesophytic species such as *Acer rubrum* L. and *Liquidambar styraciflua* L., which may eventually displace overstory oaks. Oak regeneration has been shown to respond positively to open canopies and prescribed burning. In 2008, a severe tornado damaged previously established study plots in a xeric oak and pine (*Pinus* spp.) forest in northern Mississippi. Some damaged and undamaged plots were treated with prescribed fire in 2010. Additional plots were established in damaged areas, and these plots were salvage-logged. Species composition and growth of saplings were measured to assess the impact of tornado damage and the treatments on oak regeneration. Tornado damage increased overall sapling densities, especially oaks, resulting in increased representation by upland oak species. In burned plots, oak saplings resisted damage and recovered from prescribed fire better than mesophytic saplings. Sapling densities, especially those of oaks, were lower in salvage-logged areas than in damaged areas that were not logged, resulting in greater dominance by saplings of mesophytic species. Results suggest that, on poor soils, oak regeneration requires damaged or thinned canopies and benefits from prescribed burning two years after canopy disturbance. In contrast, natural regeneration of oaks may be incompatible with salvage-logging, especially in areas that receive severe damage from wind.

Index terms: prescribed fire, salvage logging, sapling recruitment, tornado damage

INTRODUCTION

Before European settlement of the eastern United States, low intensity fires maintained oak (*Quercus* spp.) or pine (*Pinus* spp.) dominated forests, woodlands, and savannas across the Midwest and interior South of the United States (Anderson and Bowles 1999; Fralish et al. 1999; Heikens 1999; Brewer 2001; Van Lear 2004). In the twentieth century, fire exclusion enabled fire sensitive, shade tolerant hardwoods to colonize previously fire maintained oak and pine woodlands (Hart et al. 2008; Nowacki and Abrams 2008). These fire-sensitive tree species produced a more closed canopy than the historically open, sparse canopies of oak and oak/pine woodlands (Bowles and McBride 1998), leading to widespread oak and pine regeneration failure and losses of groundcover plant diversity (Abrams 1992; Bowles and McBride 1998). These diverse oak and pine woodlands are now considered rare ecosystems (Anderson and Bowles 1999).

Without fire, oaks are at a competitive disadvantage relative to mesophytes. We define mesophytic species as those tree species that historically only reached canopy tree size in mesic areas such as floodplains, rich soils, or steep ravines. However, with fire suppression, these species are able to reach canopy tree size even on xeric soils. In north Mississippi, such species include *Acer rubrum* L., *Diospyros virginiana* L., *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., *Prunus serotina* Ehrh., and *Ulmus alata* Michx (Surrette et al. 2008). Oaks are at a disadvantage relative to mesophytes for two primary reasons. First, although oaks in closed canopy stands are capable of producing significant numbers of seeds and seedlings, these seedlings are unable to grow when heavily shaded by a dense mesophyte midstory (Lorimer et al. 1994). Second, even if a canopy gap forms and increases light, oak sapling growth is often outpaced by faster growing, mesophyte saplings (Brose et al. 1999; Brewer 2001). Deprived of the open canopy habitat of the oak woodlands and savannas, shade intolerant oak seedlings continually die back and are rarely able to recruit into the canopy and grow to full size (Johnson et al. 2002). When combined with significant current mortality of overstory oaks (Greenberg et al. 2011), the failure of natural oak regeneration could eventually lead to the replacement of fire maintained oak woodlands by dense, closed canopy forests dominated by mesophytic trees (Nowacki and Abrams 2008).

Even with fire, oaks may be at a competitive disadvantage relative to mesophytic species if the latter have grown large enough to avoid damage by fires of moderate intensity (Harmon 1984). Introducing fire in these cases may have little long-term effect on canopy composition and stand density if fire is of low intensity (Arthur et al. 1998;

Elliott and Vose 2005; Hutchinson et al. 2005). A combination of prescribed fire and canopy thinning may be the most efficient means of promoting natural regeneration of oaks (Iverson et al. 2008).

Combinations of thinning and prescribed burns generally promote oak regeneration (Brose et al. 1999; Iverson et al. 2008). The timing of prescribed burning in relation to canopy thinning is crucial, however. Burning stands immediately following canopy thinning may not give oaks an advantage over mesophytes (Albrecht and McCarthy 2006). Brose et al. (1999) used prescribed fire several years after a shelterwood harvest to reduce the abundance of mesophytic seedlings and saplings, giving oak reproduction a competitive advantage in recruiting to the canopy. Using this shelterwood burn method, a mature oak timber stand was harvested and successfully replaced by a younger, oak dominated stand (Brose et al. 1999).

When thinning is not allowed, managers can capitalize on tornado damage to promote oak regeneration. Scheduling a prescribed burn after a natural canopy disturbance may be the only option for promoting oak regeneration in areas where harvest of standing trees is either restricted or impractical. A potential impediment to using delayed prescribed burning after a natural canopy disturbance to regenerate oaks, however, is that many land managers are compelled to act quickly to recover downed merchantable timber and to reduce the risk of insect infestation or wildfire (salvage logging; Lindenmayer and Noss 2006). Salvage logging may cause significant mortality of tree seedlings and saplings because of damage by logs and logging equipment (Zenner et al. 2007). Such losses could be followed by more rapid regrowth by mesophytes and/or increased colonization by efficiently dispersed pioneer tree species that benefit from exposed mineral soils (Foster and Orwig 2006). If so, slower growing and poorer colonizing species such as oaks could be at a disadvantage relative to pioneer tree species.

The main objective of this study was to determine if the destructive effects of tornado damage on upland oak and pine stands could be combined with prescribed fire to increase natural oak regeneration while reducing competition from mesophytic species that have benefited from recent fire exclusion.We also examined whether or not post-storm salvage logging negated the potential benefits of tornado damage to oak regeneration. To accomplish these objectives, we quantified the responses of oak saplings and their potential mesophytic competitors to: (1) tornado damage, (2) prescribed fire, (3) tornado damage+prescribed fire, and (4) tornado damage+salvage logging.

We tested the following hypotheses: (1) Sapling recruitment by most species (oaks and mesophytes) increases with increased canopy removal associated with tornado damage, with the advantage going to the faster growing mesophytes; (2) oak saplings gain a relative height advantage over mesophytes when tornado damage is followed two full growing seasons later by early spring prescribed burning due to greater resistance to top-kill and regrowth of sprouts, and (3) there are fewer total saplings and increased representation by mesophytic and/or pioneer species (e.g., *Pinus taeda* L., *Liquidambar styraciflua*, *Diospyros virginiana*, *Ulmus alata*) following salvage logging in severely damaged areas compared to damaged areas in which no logging occurred.

METHODS

Study site

The study was conducted in an upland hardwood/pine forest within the Tallahatchie Experimental Forest (TEF; the site of long-term monitoring of oak and pine forest dynamics; Aquilani and Brewer 2005; 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, 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). Readily erodible sands are within the top 10 to 30 cm with little or no distinct A horizon overlay silts within the soils studied here (Morris 1981). In the early 1800s, before extensive logging and fire exclusion, open, self-replacing stands of fire-tolerant tree species such as *Quercus velutina* Lam., *Q. marilandica* Münchh., *Q. stellata* Wangenh., *Q. falcata* Michx, and *Pinus echinata* Mill. dominated the upland landscape of this portion of hilly coastal plains (Surrette et al. 2008). As a result of fire exclusion in the twentieth century, second growth stands developed which are now dominated in the overstory by a mixture of some of the upland oak species (but not *Q. marilandica*), pines (mostly *P. echinata*), some species historically common in floodplains (e.g., *Q. alba* L., *L. styraciflua*), and some species that were common in both uplands and floodplains historically (e.g., *Carya* spp., Surrette et al. 2008).

Tornado damage and experimental plots and subplots

In 2003, we established eight 10-m x 30-m plots (in pairs) for determining species composition of groundcover vegetation. All plot pairs were chosen and positioned to meet the following criteria: (1) located on upland soils, (2) contained mature (90+ yr old) trees, (3) burned no more than three times since 1978, preceded by a prolonged period (30+ years) of active fire exclusion, and (4) contained a ridge and a lower slope or hollow. From these long-term plots (Plots 1 – 8; Table 1 and Figure 1), our sampling provided pre-tornado data on canopy cover and sapling composition. After establishment of plots in 2003, Plots 3, 4, 5, and 6 were burned in March 2005, and Plots 1, 2, 7, and 8 were burned in late September/early October of 2004 and 2006.

A tornado struck the area on 5 February 2008 and generated moderate to severe damage in four of the eight plots. Plots 5 and 6 experienced the most damage, with over 70% of stems ≥ 10 cm dbh downed. Plots 7 and 8 experienced moderate damage (10% of trees being snapped or uprooted) but not severe damage. Therefore, to capture severe damage, we established an additional 10-m x 30-m plot adjacent to Plots 7 and 8 (Plot 9; Figure 1) in April 2008. Damage severity was judged by the percentage of downed (but not necessarily dead) canopy trees, which we

Table 1. Treatment, topography, and canopy cover summary for experimental plots.

Plot	Treatment	Topography	Canopy Cover[a]
1	Undamaged	Ridge	90%
2	Undamaged	Slope	89%
3	Fire Only	Ridge	79%
4	Fire Only	Slope	84%
5	Severe Damage + Burn	Ridge	47%
6	Severe Damage + Burn	Slope	45%
7	Moderate Damage	Ridge	75%
8	Moderate Damage	Slope	74%
9	Severe Damage	Midslope	53%
10	Severe Dam. + Logged	Slope	25%
11	Severe Dam. + Logged	Ridge	20%
12	Mod. Dam. + Logged	Ridge	46%
13	Mod. Dam. + Logged	Slope	62%

[a] Canopy cover was measured at peak growing season 2009 with a concave spherical canopy densiometer.

assumed were toppled by the storm, by virtue of sprouting buds, or in the case of pines, by the presence of needles that were present before the storm. Plots 1 – 4 experienced minimal damage (0 to 1% downed trees).

To examine the effects of salvage logging, we established two plots (Plots 10 and 11; Figure 1) just outside a 30 to 50 m buffer surrounding the severely damaged plots 5 and 6, as well as two plots (Plots 12 and 13) outside Plots 7, 8, and 9 in April 2008. These plots were scheduled by the Holly Springs Ranger District staff for salvage timber harvest in June 2008 until the end of 2008. Plots 10 – 13 were established in these areas immediately following timber harvest (before significant colonization of vegetation).

To examine the interaction between damage and prescribed burning, the U.S. Department of Agriculture Forest Service initiated a schedule of biennially prescribed burning of Plots 3, 4, 5, and 6 in early spring 2010. The remaining plots were unburned controls. After all plots were established, we subdivided each plot into eight 5-m x 7.5-m subplots to obtain more detailed and precise estimates of sapling species composition and associated environmental variation (Figure 1).

Prescribed Fires

Due to time constraints, the damaged and undamaged stands were burned one week apart. Damaged plots (Plots 5 and 6) were burned on 25 March 2010. Ambient air temperatures ranged from 22 °C – 24 °C; relative humidity ranged from 30% to 34%. Undamaged plots (Plots 3 and 4) were burned on 1 April 2010. Ambient air temperatures ranged from 23 °C – 27 °C; relative humidity dropped from 36% to 29% over the course of the burn.

The plots represent seven quasi-treatment combinations (Table 1; Figure 1): (1) undamaged, unburned, and not logged (Plots 1 and 2); (2) undamaged+burned (Plots 3 and 4); (3) severely damaged+burned (Plots 5 and 6); (4) moderately damaged, unburned, and not logged (Plots 7 and 8); (5) severely damaged, unburned, and not logged (Plot 9); (6) severely damaged+salvage logged (Plots 10 and 11); and (7) moderately damaged+salvage logged (Plots 12 and 13).

Measurements

Environmental measurements

To verify that tornado damage resulted in a reduction in canopy cover, % canopy cover (averaged across the entire plot) was quantified in 2009 and compared with measurements taken before the tornado in 2006 (Surrette and Brewer 2008). Canopy cover was measured using a concave canopy densiometer and averaging four orthogonal readings within each subplot. In addition, several environmental variables were measured within each subplot to determine which environmental variables were most correlated with differences in sapling species composition. For each subplot, we measured three stable variables which were identified by Famiglietti et al. (1998) to be the most important determinant of soil moisture under dry conditions: (1) elevation relative to the nearest ridge (hereafter, relative elevation), (2) slope aspect, and (3) soil texture. We measured relative elevation trigonometrically using a clinometer and an electronic distance measurer. We measured slope aspect with a compass, and we measured soil texture using a traditional suspension method. Percent soil organic matter was measured using the loss-on-ignition method (Black 1965). We also visually estimated several ground cover variables in fall 2009 including % disturbed soil (plot area containing disturbed soil due to mounds and pits formed near uprooted trees or ruts from machinery disturbance), % leaf litter (plot area covered by litter), % dead crown (plot coverage by dead tree crowns); and in fall 2008, we measured % bare ground (plot coverage by un-vegetated bare soil).

Flame lengths were based on visual estimates made by the Forest Service during the burn. To estimate maximum fire temperature, we constructed aluminum pyrometers using temperature-sensitive paints (Tempilaq G indicating liquids). The paints, rated to indicate maximum temperatures of 79 °C, 121 °C, 163 °C, 204 °C, 246 °C, and 288 °C, were applied in a row to a small aluminum plate (melting point 660 °C) staked 30 cm above ground in each subplot.

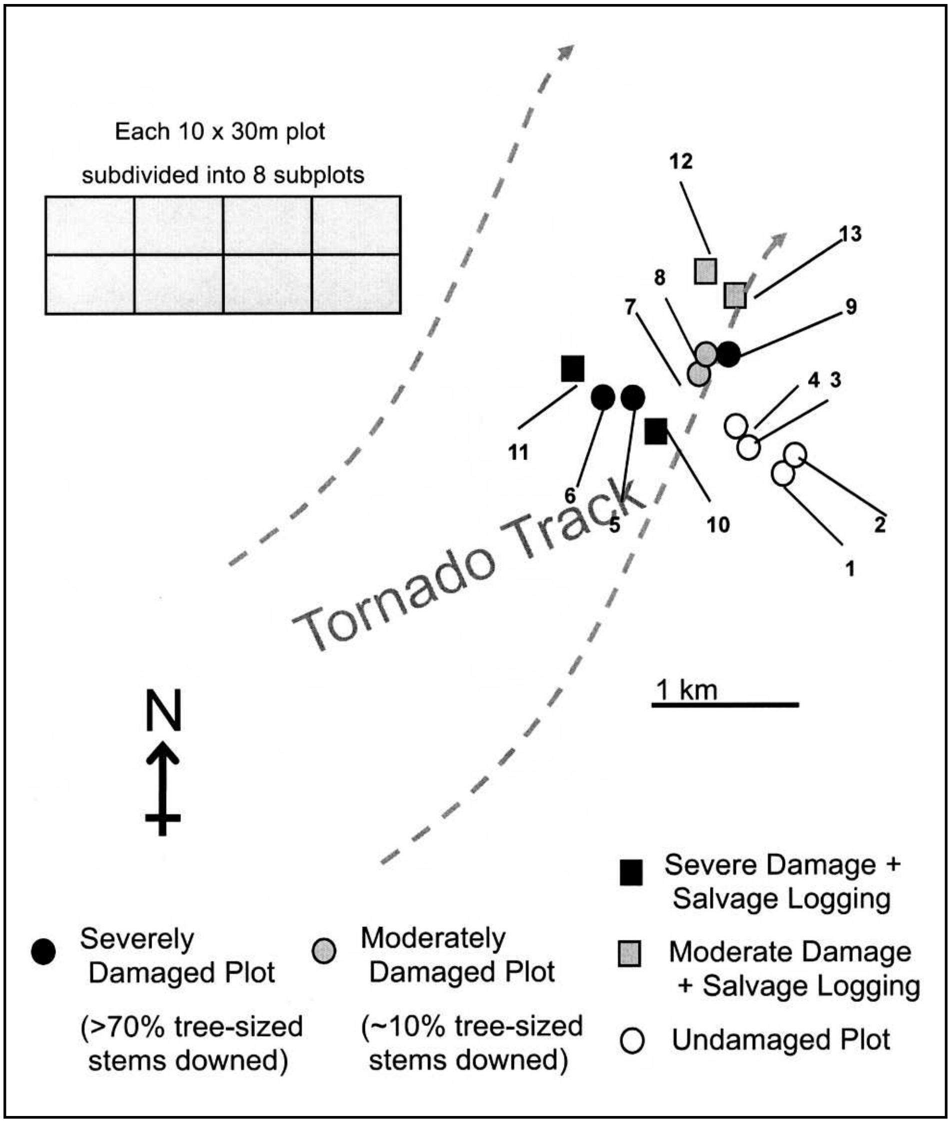

Figure 1. Little Tallahatchie experimental plots located within the Holly Springs National Forest in northern Mississippi. Plots represent combinations of tornado damage, prescribed fire, and salvage logging. Two tornado damaged stands (5 and 6) and two undamaged stands (3 and 4) received prescribed fire. Each 10-m x 30-m plot was subdivided into eight 5-m x 7.5-m subplots. Full plot descriptions are located in Table 1.

Vegetation measurements

We measured the height of each woody sapling (< 10 cm dbh) in 2009 and 2010 and assessed the damage response to prescribed fire in 2010. We compared pre-storm measurements of tall sapling composition with that of the 2009 measurements. We quantified sapling abundances and classified stems into two height classes: short saplings (≥ 1 m tall; < 1.5 m tall) or tall saplings (≥ 1.5 m tall). In August 2010, we measured the height of individual saplings < 2 m tall. We measured the basal diameters of all saplings just after fires with calipers. One growing season after prescribed fires, individual stems were assessed for damage by fire and classified as killed, top-killed (above ground parts killed, but with new basal sprouts from the same rootstock), or partially damaged with epicormic sprouting (i.e., sprouting from the trunk). In addition to overall mortality and resprouting patterns, the number of sprouts and the length of the longest sprout were measured for each top-killed sapling.

Statistical analyses

Sapling species composition and size following tornado damage

True replication of the prescribed fire x tornado damage interaction was not possible in this study because the effects of a single tornado cannot be replicated. Hence, we used a regression approach to analyze the effects of tornado damage on saplings.

We hypothesized that canopy cover would be the most important variable influencing sapling size and composition variation among damaged and undamaged subplots. To evaluate support for this hypothesis, we examined sapling responses to environmental predictors (% canopy cover, relative elevation, slope aspect, soil texture, % soil organic matter, % disturbed soil, % leaf litter, % bare ground) using forward stepwise multiple regression. Separate stepwise regressions were done to examine each of the following response variables: (1) fall 2009 total sapling abundance, (2) fall 2009 short sapling abundance, (3) fall 2009 tall sapling abundance, (4) fall 2009 oak abundance, (5) fall 2009 mesophyte abundance, and (6) the 2009 log abundance ratio of mesophytes to oaks (hereafter, mesophyte dominance) as response variables. When positive, this variable indicates dominance of a subplot by mesophytic saplings; when negative, it indicates dominance by oak saplings. We repeated this analysis of mesophyte dominance using 2010 abundances.

Effects of prescribed burning and sapling basal diameter in severely damaged plots

We evaluated the effects of burning by examining how individual stems responded to damage (i.e., the number and size of resprouting stems) using a combination of regression and ANOVA analyses. To examine which biological factors were important in resistance of saplings to damage from fire, we grouped saplings from burned plots into "damaged" (killed or top-killed+resprouting; n=223) and "undamaged" (slightly damaged or completely undamaged; n=92). We then used forward stepwise logistic regression to evaluate the relative importance of biological factors in increasing resistance to damage. The factors included were stem length, basal diameter, and species group (i.e., mesophyte or upland oak). We also used one-way ANOVA to determine if basal diameter: length ratio differed between mesophytes and upland species (n=247; approximately 70% mesophytes and 30% upland).

To examine patterns of resilience after fire, we used two one-way ANOVAs to determine if resprout number or length differed between upland and mesophytic species (n=221 for resprout number; n=219 for resprout length; approximately 60% mesophyte and 40% upland). We then used Tukey's HSD test (Weiss 2007) to see how each individual species ranked according to resprout number and length. Lastly, we used forward stepwise analysis of covariance to evaluate differences in sprouting between upland oaks and mesophytes, while accounting for size-related covariates (i.e., stem length and basal diameter).

Sapling composition and size following salvage logging

The analyses for logging effects were similar to those described above for tornado damage. In this case, however, we hypothesized that % bare ground and/or soil disturbance would be the most important variables distinguishing sapling densities and composition among subplots within tornado damaged plots that differed with respect to logging.

Meeting assumptions of statistical analyses

In order to meet the assumptions of the statistical analyses used, we transformed both the independent and dependent variables. We used a natural log (+1) transformation for all species abundance data and ratios (sand:silt, mesophytic dominance). All percentage data (canopy cover, % organic matter, % clay, % bare ground, % litter, and % dead crowns) were converted to proportions and arcsine-square root transformed as recommended by Gotelli and Ellison (2004). Slope aspect was converted to radians and then cosine transformed to generate an index of slope exposure (south facing aspects were positive, and north facing aspects were negative). Data were transformed for analyses, but back-transformed for figures. We used leverage plots to display the results of multiple regression because they emphasize the effects of a single predictor variable on the response of interest while accounting for all covariables (Sall 1990). The interpretation of leverage plots is identical to that of typical scatterplots, except that the y axis values represent the residuals of the response variable after accounting for all covariables rather than the raw values.

RESULTS

Sapling composition following tornado damage

The tornado in 2008 reduced canopy cover in the damaged plots from 76.0% in 2006 to 24.7% in 2008. Total sapling abundance in fall 2009 was positively correlated with relative elevation (P=0.01), sand:silt ratio (P< 0.01), and soil disturbance (P=0.01), but it did not respond significantly to reduced canopy cover (P> 0.25). Short sapling abundance in fall 2009 was negatively correlated with canopy cover (P< 0.01) after accounting for the effects of sand:silt ratio (P=0.12), clay (P=0.10), and disturbed soil (P=0.06; Figure 2). These analyses indicate that the increase in saplings after a tornado is primarily from recruitment of seedlings to short saplings.

When examining short oak and mesophytic saplings separately, canopy cover was negatively correlated with upland oak abundance (P< 0.01) after accounting for the effects of slope aspect (P< 0.01) and soil disturbance (P=0.03). Short mesophyte abundance was negatively correlated with canopy cover (P< 0.01) after accounting for the effects of clay content (P=0.01), slope

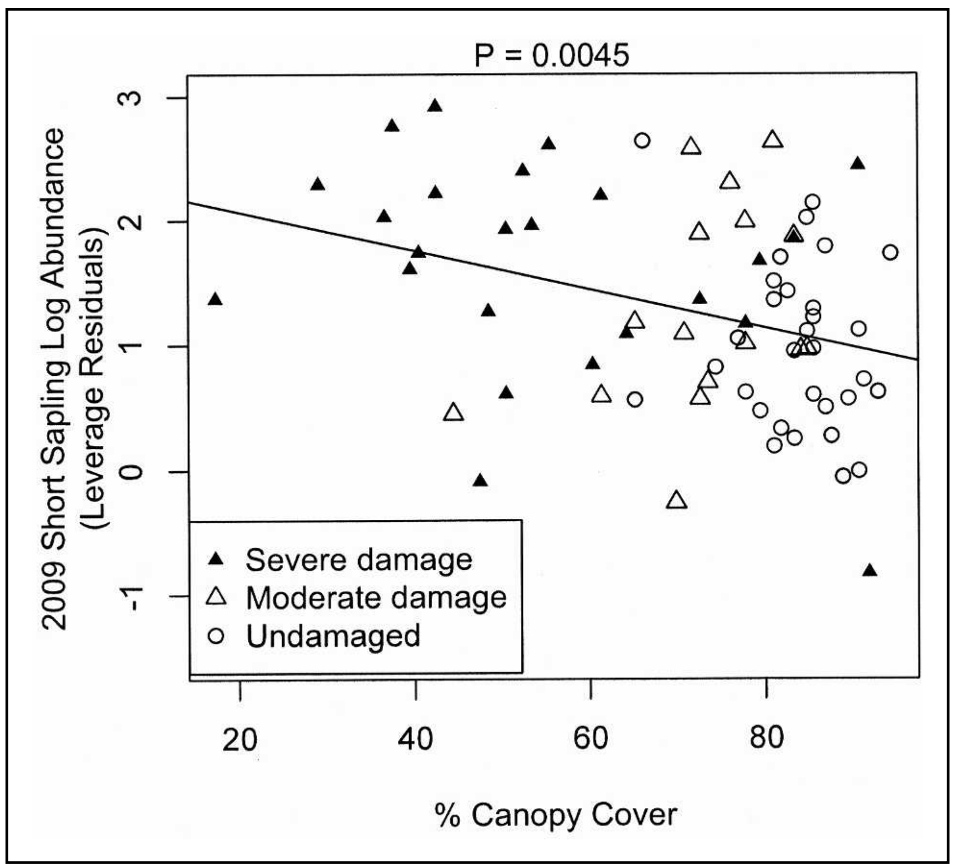

Figure 2. Canopy cover leverage plot of 2009 short sapling density. Values on the y-axis are residuals from a multiple regression of short sapling density against all predictors except canopy cover. Subplots are symbol coded according to tornado damage severity. P-value indicates that slope associated with % canopy cover was significantly different from zero.

aspect (P=0.15), soil disturbance (P=0.11), relative elevation (P=0.19), and sand:silt ratio (P=0.11). This result suggests that both mesophytic and upland oak saplings respond positively to canopy reduction. *Pinus echinata* saplings were too rare to detect any response to canopy cover.

Oaks appeared to benefit more from tornado damage than mesophytic saplings. Among plots with pre storm data, we found that oak abundance increased relative to mesophyte abundance. In 2006, before tornado damage, tall saplings of mesophytes greatly outnumbered those of upland oaks (129 and 30, respectively); but by 2009, mesophyte abundance increased only 19% (to 154 saplings), while oak abundance increased by 80% (to 54 saplings). In 2009, among short saplings, mesophytic dominance was positively correlated with northerly slopes (P< 0.01) after accounting for the effects of elevation (P=0.20), sand:silt ratio (P=0.12), and clay content (P=0.23). By summer 2010, reduced canopy cover was associated with increases in short oak saplings relative to short mesophytes. Canopy cover was significantly correlated with increased mesophytic dominance (P< 0.01; Figure 3) after accounting for sand: silt ratio (P=0.02), dead crown (P=0.15), and soil organic matter (P=0.08). We found similar results when analyzing dominance among total sapling counts.

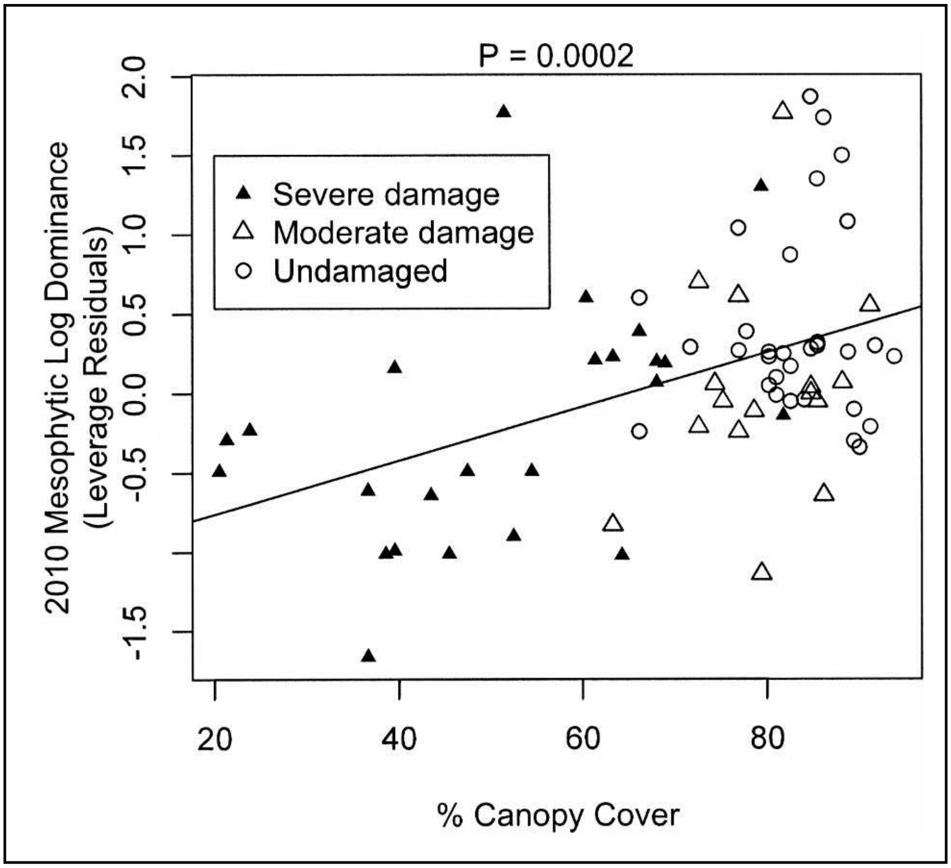

Figure 3. Canopy cover leverage plot of 2010 mesophytic dominance. Values on the y-axis are residuals from a multiple regression of mesophytic dominance against all predictors except canopy cover. Subplots are symbol coded according to tornado damage severity. P-value indicates that slope associated with % canopy cover was significantly different from zero.

Prescribed fire and its effect on saplings

Damaged plots (Plots 5 and 6) contained a heterogeneous fuel supply (a patchy mixture of downed crowns and grass clumps); therefore, flame lengths varied depending on fuel availability, and fires were somewhat patchy. Flames lengths in woody debris ranged from 1.5 – 2.5 m; flame lengths in grassy areas ranged from 0.1 – 1.5 m (J. Walden, Fire Management Specialist, Holly Springs National Forest, pers. comm.). Based on aluminum pyrometer readings, maximum fire temperatures ranged from 79 °C – 660 °C (mean 208 °C; s.e. 47 °C; n=9). In 5 of 16 subplots, fires did not contact the pyrometers, and no reading could be obtained.

Conversely, undamaged plots (Plots 3 and 4) contained a homogeneous fuel supply (an even layer of leaf litter), thus fires were even, with less variation in fire temperatures than damaged plots. Flame lengths ranged from 0.15 – 0.5m (J. Walden, Fire Management Specialist, Holly Springs National Forest, pers. comm.). Fire temperatures ranged from 163 °C – 288 °C (mean 219 °C; s.e. 11 °C; n=16); every pyrometer was contacted by fire.

After prescribed burning on tornado damaged sites, 71% of saplings were either killed or top-killed+resprouting, resulting in much smaller and more numerous stems. The stepwise multiple logistic regression revealed that the probability of top-kill was negatively associated with basal diameter (χ^2=48.31; P< 0.01) and positively associated with pre-fire stem length (χ^2=23.55; P< 0.01). For a given basal diameter, tall species were damaged more severely than short ones. Upland oak species were less susceptible to damage than mesophytic species (χ^2=21.63; P< 0.01). Upland oak saplings had a 50% higher mean basal diameter:length ratio than mesophytic saplings ($F_{1,246}$=74.11; P< 0.01).

Generally, top killed oaks tended to have longer, but fewer, sprouts than mesophytic species (Figure 4); but *Prunus serotina* had unexpectedly long sprouts and *Quercus falcata* had unexpectedly short sprouts (Figure 5). We could not detect differences in sprout number among species (P> 0.05). However, we did detect differences in sprout length among species (P< 0.05; Figure 5). Even after accounting for relationships between sprouting and size-related variables, sprouting differed between upland oaks and mesophytes. The number and length of resprouts varied with the size of saplings. Stepwise analysis of covariance revealed that top-

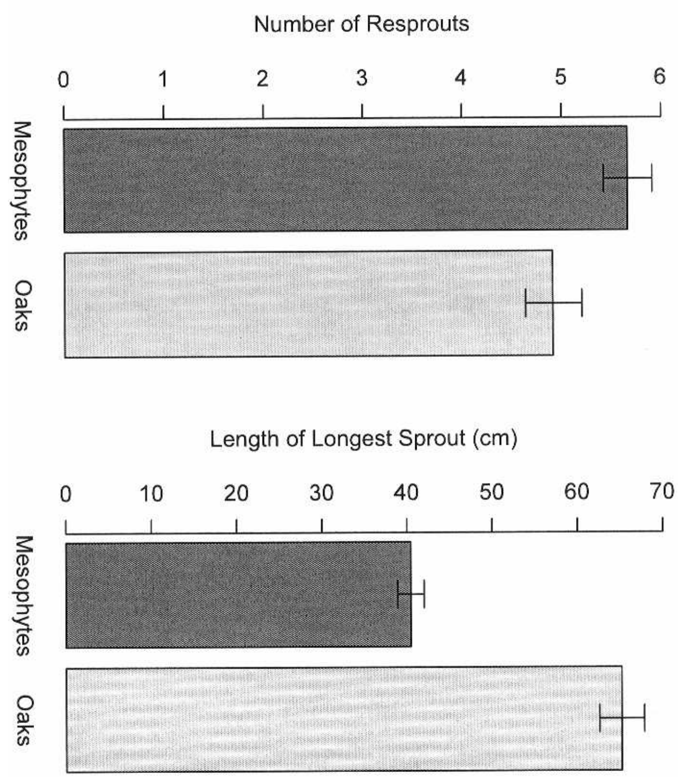

Figure 4. Mean post-fire number of resprouts per sapling and length of the longest sprout for top-killed mesophytic and upland oak saplings. Error bars represent ± 1 standard error of the mean. Data were transformed for analysis, but back-transformed for figures.

killed mesophytes had more sprouts than oaks (P=0.06) after accounting for initial sapling height (P< 0.01). Stepwise analysis of covariance also revealed that top-killed oaks had longer sprouts than mesophytes (P< 0.01) after accounting for the effect of increasing sprout length with basal diameter (P=0.11).

Environmental variation and sapling composition following salvage logging

In June 2008, immediately after salvage logging, damaged stands that had not been salvage logged had a lower % bare ground than moderately damaged+logged stands and severely damaged+logged stands (8.1%, 24.6%, and 64.5%, respectively). These differences were statistically significant (Tukey's HSD; α=0.05). In fall 2009, total sapling abundance decreased with increasing bare ground (P<0.01), after accounting for the effects of sand:silt ratio (P< 0.01). Similarly, in summer 2010, total sapling abundance decreased with increasing bare ground (P< 0.01; Figure 6) after accounting for the effects of sand:silt ratio (P< 0.01) and elevation (P=0.04).

In fall 2009, total upland oak sapling abundance was negatively correlated with % bare ground (P< 0.01) after accounting for the effects of sand:silt ratio (P=0.03) and dead crowns (P=0.01). Total mesophytic sapling abundance was not associated with bare ground but instead increased with sand:silt ratio (P< 0.01) and south facing slopes (P=0.01). Together, these results suggest that salvage logging, through its effects on bare ground, results in lower sapling densities. However, oaks may be impacted more severely than mesophytes.

Among short saplings, mesophytic dominance increased with bare ground (P=0.03; Figure 7) after accounting for the effects of slope aspect (P< 0.01), sand:silt ratio (P=0.04), dead crown (P=0.13), and soil disturbance (P=0.14). The most abundant mesophytic saplings contributing to this dominance were *Acer rubrum*, *Diospyros virginiana*, and *Nyssa sylvatica* Marsh. Similar results were found for summer 2010. These results suggest that salvage logging, with its associated vegetation removal, had a negative impact on upland oak abundance while having no discernable effect on mesophytic saplings.

DISCUSSION

Sapling composition following tornado damage

Results of the current study suggest that oaks of the sapling layer benefited more than mesophytic species in tornado damaged stands with open canopies, with the exception of *Prunus serotina*. In our study, dominance by faster growing mesophytes in 2010 was associated with greater canopy cover. The soils at our site were sandy (mean 61.5% sand; s.e. 1.6%); therefore, we suggest that the relatively nutrient poor loamy sands and sandy loams within the tornado damaged stands in the current study likely reduced the competitive advantage that mesophytic species with higher growth potential would have otherwise had in richer soils. While upland oaks are adapted to the xeric conditions of upland soils, mesophytic species are adapted to the more mesic conditions found in the lowland areas where their distribution was limited historically in north Mississippi (Surrette et al. 2008). In this regard, the findings of this study are in accord with the predictions of those who have argued that the competitive advantage mesophytic species have over oaks following significant canopy reduction depends on soil fertility (Brose et al. 1999; Iverson et al. 2008).

Effects of prescribed fire after tornado damage

Although oaks appeared to benefit from tornado damage even without fire, the hypothesis that oaks would experience an even greater relative advantage over mesophytic species when subjected to tornado damage+prescribed fire was supported. Among damaged saplings, taller and thick-

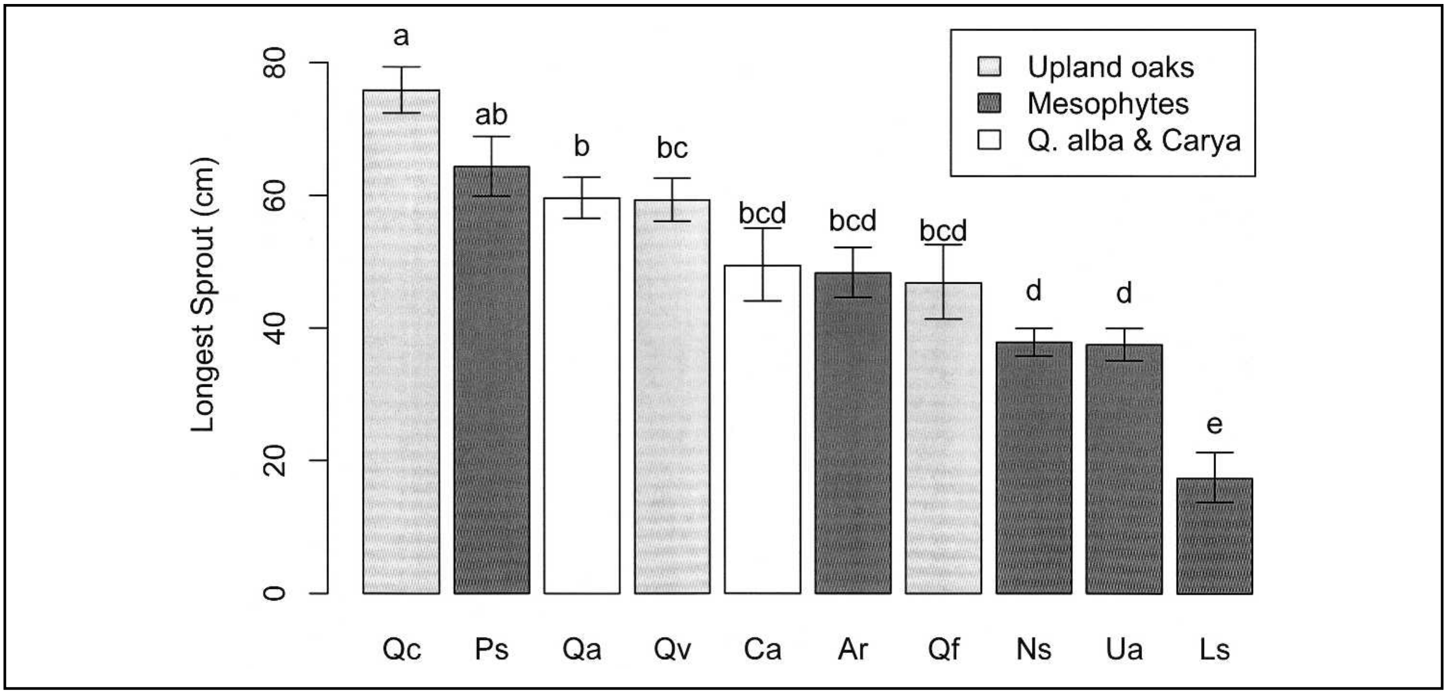

Figure 5. Mean longest sprout length for abundant species. Error bars represent ± 1 standard error of the mean. Species not sharing a letter are significantly different by Tukey's HSD (P< 0.05). Qc = *Quercus coccinea*, Ps = *Prunus serotina*, Qa = *Q. alba*, Qv = *Q. velutina*, Ca = *Carya* spp., Ar = *Acer rubrum*, Qf = *Q. falcata*, Ns = *Nyssa slyvatica*, Ua = *Ulmus alata*, and Ls = *Liquidambar styraciflua.* Data were transformed for analysis, but back-transformed for figures.

er (higher basal diameter) saplings were more likely to resist top-kill. In our study, we waited two full growing seasons after the tornado before implementing the burn treatment. By this time, oak saplings tended to be somewhat stockier than mesophytes (i.e., higher basal diameter to length ratio). This disparity in basal diameter likely contributed to the greater fire resistance among oaks. However, even after accounting for differences in basal diameter, oaks were still more likely to resist damage by fire. This finding indicates that oaks have some other, possibly physiological or structural, characteristics that make them more resistant to damage from fire (e.g., bark thickness or moisture content; Hare 1965). These findings confirm laboratory studies on oak superiority in fire resistance (Huddle and Pallardy 1996).

Upland oaks, as a group, also tended to be more resilient to fire because their longest post-fire sprout tended to be longer than those of mesophytes. Most oak resprouts (with the exception of *Quercus falcata*; Figure 6) were taller than mesophytic resprouts (with the exception of *Prunus serotina*; Figure 6). Because of their taller sprouts, oak saplings may be better poised to outcompete neighboring saplings and recruit to the canopy (Brewer 2011). Although mesophytes tended to have more numerous sprouts after the fire, the difference was statistically significant but not substantial. We hypothesize that these smaller sprouts will rarely recruit to taller size classes because short sprouts are more vulnerable to future fires and more likely to be outcompeted by taller oak sprouts.

Increased resistance and resilience to fire in oaks suggest that prescribed fire may have given oaks an advantage over mesophytic species. These findings appear at odds with the findings of Albrecht and McCarthy (2006), until we consider the amount of time elapsed between thinning and fire treatments. These authors found that prescribed fire combined with thinning did not increase oak seedling densities when burning occurred on the first spring after a dormant season thinning treatment. They suggested that because oaks depend on belowground reserves to recover from fire, the oaks at their sites did not have adequate time to respond to the increased light from thinning treatments and to build the required reserves. This supposition is supported by other studies where oaks responded positively to prescribed fire several years after thinning (Kruger and Reich 1997; Brose and Van Lear 1998). Oak saplings tend to invest most photosynthate to below ground storage (Johnson et al. 2002), and they had two full growing seasons to increase in size and build up belowground reserves before the fire, which may have contributed to increased resistance to top-kill and increased sprout growth. Such differences in resistance and resilience could give oaks a relative height advantage over mesophytes, increasing the chances that these taller oak saplings will eventually recruit to the canopy and result in a stand dominated by upland oaks.

Sapling composition following salvage logging

Salvage logged stands tended to have a higher percentage of bare ground than did unlogged stands, which in turn was associated with logged stands having fewer saplings in both years. Our findings suggest that direct mechanical damage to saplings during salvage logging processes reduces sapling abundances. Our findings contrast

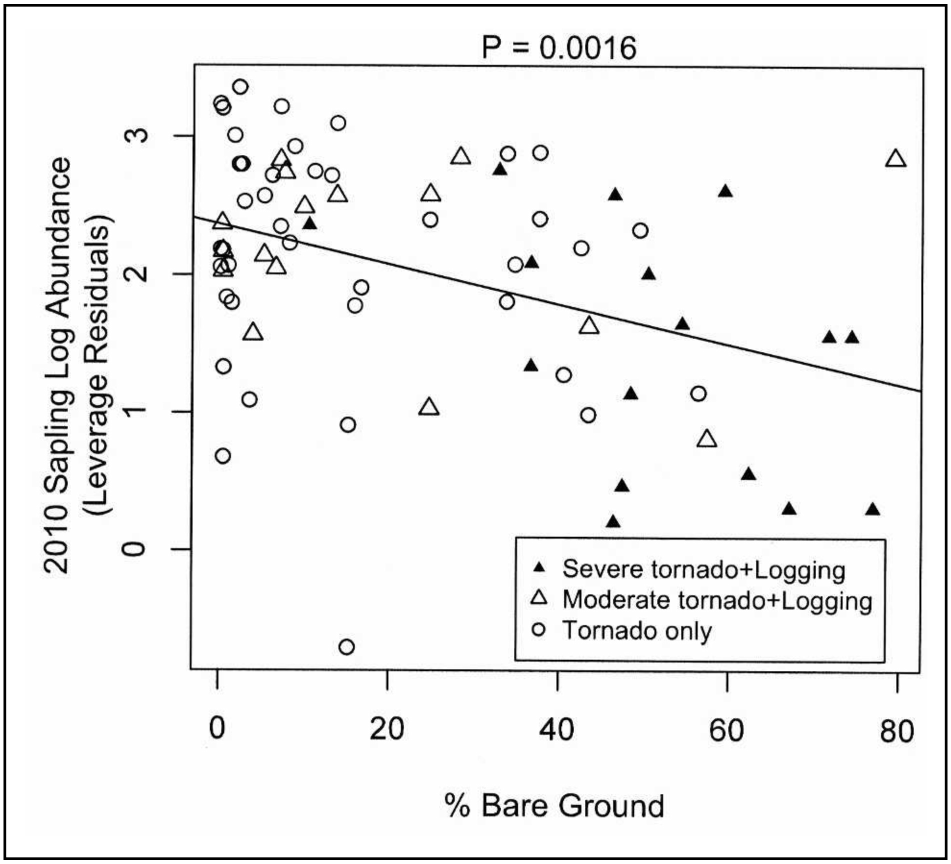

Figure 6. Percent bare ground leverage plot of 2010 sapling density. Values on the y-axis are residuals from a multiple regression of sapling density against all predictors except % bare ground. Subplots are symbol coded according to tornado severity and salvage logging treatments. P-value indicates that slope associated with % canopy cover was significantly different from zero.

with those by previous authors who found that neither sapling nor seedling densities were decreased by post-storm salvage logging (Peterson and Leach 2008a,b). However, these studies evaluated vegetation after moderate severity storms with moderate severity salvage logging, and the authors predicted that after a certain threshold of disturbance, densities may eventually be adversely affected (Peterson and Leach 2008a,b). As expected, our regression approach showed that sapling densities decreased with salvage logging intensity (which in turn was a function of storm damage severity). In a post-harvest aspen (*Populus tremuloides* spp.) forest, Zenner et al. (2007) found reductions in aspen (*Populus tremuloides* spp.) sucker densities along skid trails where harvested logs were being removed. However, since most disturbance was limited to skid trails, these authors found no overall detriment to the productivity of the stand. One explanation of the severe sapling reductions found in our study is that loggers were unable to confine log skidding and soil disturbance to a few designated trails in severely damaged areas, causing mechanical disturbance to a larger portion of the site.

Although our analyses show an overall reduction of saplings in salvage logged plots, it seems that mesophytic dominance of the sapling size class increased with salvage logging severity. Not only were oaks less abundant in salvage logged areas, but they also tended to become proportionately less abundant with salvage logging severity relative to mesophytes. This result suggests that salvage logging decreased oak regeneration and may accelerate displacement by mesophytic species. Our data are consistent with the hypothesis that saplings of most species were impacted by the logging disturbance, but mesophytes were able to regrow more rapidly following logging, which unlike prescribed burning, occurred immediately after the tornado damage. Although widely dispersed pioneer species such as *Pinus taeda* have been shown to exhibit increased seedling recruitment in response to disturbed soil (Schultz 1997), we found no evidence of increased recruitment of this species (saplings or seedlings) in salvage logged areas (this study and Brewer et al., 2012). Hence, our hypothesis that pioneer species would be disproportionately favored because of their superior colonizing ability was not entirely supported. Continued monitoring, however, is needed to properly evaluate this hypothesis.

CONCLUSION

Our study suggests that on poor soils, severe tornado damage by itself, even without fire, may create a light environment beneficial to oak regeneration. Although perhaps not necessary for successful oak regeneration on poor soils, delayed prescribed burning following natural canopy damage could increase the competitive advantage of oak saplings over fast growing mesophytic species. In addition, prescribed burning may be necessary to meet other management goals such as increased herbaceous plant diversity or maintenance of an open canopy, sustained oak regeneration, and reduced fuel loads (Bowles and McBride 1998; Brewer and Rogers 2006; Brewer and Menzel 2009). In contrast to the effects of tornado damage alone or combined with burning, salvage logging following tornado damage on poor soils could put oaks at a disadvantage relative to rapidly growing and/or widely dispersed species (e.g., *Nyssa sylvatica*, *Liquidambar styraciflua*, *Ulmus alata*, and *Liriodendron tulipifera*). Salvage logging and oak regeneration may, therefore, be incompatible on heavily damaged sites. Hence, to promote oak regeneration, salvage logging perhaps should be limited to moderately damaged sites, where the impact on the understory could be minimized.

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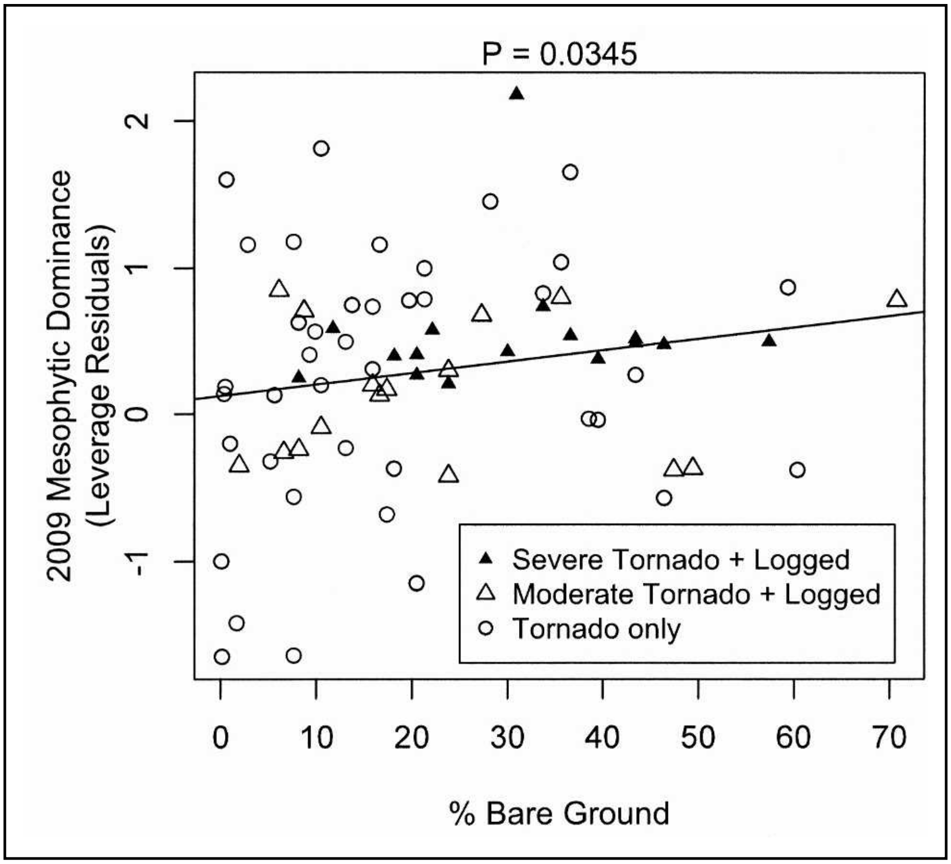

Figure 7. Bare ground leverage plot of 2009 mesophytic dominance. Leverage plots emphasize the effects of a single predictor variable on the response of interest while accounting for all covariables (Sall 1990). Subplots are symbol coded according to the tornado damage severity and logging treatment. P-value indicates that slope associated with % bare ground was significantly different from zero.

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