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Effects of Tornado Damage, Prescribed Fire, and Salvage Logging on Oak (Quercus Spp.) Saplings in Upland Oak Forests in Northern Mississippi

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EFFECTS OF TORNADO DAMAGE, PRESCRIBED FIRE, AND SALVAGE LOGGING ON OAK (*QUERCUS* SPP.) SAPLINGS IN UPLAND OAK FORESTS IN NORTHERN MISSISSIPPI

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ABSTRACT

After European colonization and extensive logging followed by long periods of fire suppression, oak dominated forests, woodlands, and savannahs are being replaced by an unprecedented forest ecosystem. In Mississippi, these new forest systems are dominated in the mid- and understory by mesophytic species such as red maple (*Acer rubrum* L.) and sweetgum (*Liquidambar styraciflua* L.). Partial thinning of trees followed by prescribed fire can regenerate oaks in managed timber stands. A severe tornado occurred on a monitored oak stand in northern Mississippi. Of the damaged plots, some were treated with either prescribed fire or salvage logging or were left alone. I examined the effects of these treatments on oak regeneration. Species composition of saplings was measured to assess the impact of tornado damage and the treatments on sapling regeneration. All saplings, especially oaks, were reduced upon salvage logging which resulted in dominance by mesophytic species. Tornado damage increased all sapling densities, especially oaks, resulting in increased representation by upland oak species. In burned plots, oak saplings resisted and recovered from prescribed fire better than mesophytic saplings, but not enough to gain an overall height advantage. On poor soils, tornado damage alone may be enough to allow the regeneration of oak species without a prescribed fire. Results also indicate that natural regeneration of oaks may be incompatible with salvage logging, especially in areas that receive severe damage from high wind events.

DEDICATION

This work is dedicated to Marianne, without whose unwearying encouragement this work would not have been possible.

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INTRODUCTION

Anthropogenic Decline of Oak Forests

Historically, wildfires maintained oak dominated forests and savannahs which were prevalent across the eastern United States, but due to fire suppression, these fire-maintained ecosystems are disappearing (Abrams 1992, 2003) and are now considered rare ecosystems (Nowacki and Abrams 2008). Some authors have suggested that wildfires—either caused by lightning strikes or intentionally set by Native Americans—would sweep through these areas facilitating the dominance of fire-tolerant oaks in savannahs and woodlands (Pyne 1982, Abrams and Downs 1990, Abrams 1992, Van Lear 2004). These fires maintained oaks and a diverse array of herbaceous plant species and prevented them from being replaced by a less diverse set of shade-tolerant forest species (Nowacki and Abrams 2008). Presently, species that were historically limited to floodplains, hereafter, mesophytic plants, such as sweetgum (*Liquidambar styraciflua* L.), blackgum (*Nyssa slyvatica* Marsh.), and red maple (*Acer rubrum*), are able to replace many oak stands with low-diversity forest ecosystems that have no historical precedent in Mississippi (Brewer 2001).

Native Americans altered the eastern landscape (Whitney 1994), but it was not until European settlement that forest composition and structure were severely altered by substantial logging and destructive, stand-replacing (i.e., not oak-enhancing) fires (Abrams 2003). These dangerous wildfires in the 1920s ushered in fire suppression policies with the Smokey Bear Campaign (Abrams 2003, Nowacki and Abrams 2008). Without fire, an understory dominated by shade-tolerant, fire-intolerant saplings (such as red maple) is poised to replace the oak stands under which they reside (Lorimer 1984). Additionally, if a canopy gap forms allowing more light to reach the forest floor, oaks must still contend with faster-growing, early-successional, and fire-intolerant hardwoods like sweetgum. These mesophtyic species quickly outgrow oaks in canopy gaps (Johnson and Krinard 1983) when there are no fires to "filter" these competitors (*sensu* Surrette et al. 2008). Mature oaks in these stands are producing no shortage of seeds and seedlings, but the shade-intolerant seedlings are unable to grow under the dense understory of plants like red maple (Lorimer et al. 1994), and in open areas they may be quickly outcompeted by sweetgum. Deprived of the open canopy habitat of the fire-maintained oak woodlands and savannahs, these shade-intolerant oak saplings continually die back and are rarely able to recruit into the canopy and grow to full size (Johnson et al. 2002). Instead the once fire-maintained oak forests are failing to regenerate and may eventually be replaced by a dense, closed canopy forest dominated by mesophytic trees (Brewer 2001, Nowacki and Abrams 2008).

Fire-mediated Restoration of Oak Forests

Oak forests are not only disappearing from unmanaged sites; silviculturalists (timber managers) have also had great difficulty regenerating oak stands on fertile, managed land after harvesting (Carvell and Tryon 1961, Clark and Watt 1971, Loftis and McGee 1993, Van Lear 2004). Before harvesting a mature oak stand, silviculturalists must be certain that the forest understory is well stocked with sturdy oak saplings so that when the stand is clear-cut, oaks—

rather than undesirable timber species—will replace the stand (Clark and Watt 1971, Loftis and McGee 1993). When the mature oaks are harvested and the canopy is opened, a large amount of light is able to reach the forest floor. If the oak saplings are better developed than their competitors, they have the potential to bolt up in growth and dominate the canopy until the next clear-cut timber operation. However, without wildfires, it is difficult for oak saplings to dominate the understory on fertile sites because they are quickly outcompeted by faster-growing species (e.g., *Liriodendron tulipifera*; Van Lear 2004). As a result, after harvesting timber on fertile sites, managed oak stands are usually replaced by less desirable timber species (Brose et al. 1999, Nowacki and Abrams 2008).

Even without logging disturbances, many aging unmanaged oak stands are being slowly successionally replaced by shade-tolerant species since the mature oaks in the stand are dying without leaving adequate advance reproduction to replace them (Nowacki and Abrams 2008). Ecologists and silviculturalists across the eastern United States have recognized the role of fire in restoring upland oak forests and have recommended or executed prescribed fires to give oak saplings a competitive advantage over mesophytic species (e.g., Barnes and Van Lear 1998, Dey and Hartman 2004, Hutchinson et al. 2005, Iverson et al. 2008).

In many forests where the mesophytic species have grown to larger size classes (i.e. large saplings and adult trees), they may be large enough to avoid damage from fire (Harmon 1984). Introducing fire in these cases may temporarily change the composition of the seedling and sapling layers, but it may have no long-term effect on canopy composition and stand density. Rather, a combination of prescribed fire and canopy thinning may be required to restore these unprecedented stands to pre-colonial oak forests.

Combining thinning treatments with prescribed burns has been suggested (Hannah 1987) and successfully implemented for restoring oak regeneration (Brose et al. 1999, Iverson et al. 2008). While Iverson et al. (2008) used thinning treatments and two fires to promote oak regeneration, Brose et al. (1999) used thinning treatments in the form of a shelterwood harvest. In the shelterwood method, much of the timber is harvested—opening the canopy—while enough trees are left to shade and protect the desirable seedlings; once they are developed, the remaining mature trees are harvested, and the nursed seedlings regenerate the stand (Helms 1998, Johnson et al. 2002). Several years after the first shelterwood harvest, prescribed fire was used to reduce the abundance of mesophytic seedlings and saplings, giving oak reproduction a competitive advantage in recruiting to the canopy (Brose et al. 1999). Using this shelterwood-burn method, a mature oak timber stand was harvested and successfully replaced by a younger oak-dominated stand.

Using a similar procedure to Brose et al. (1999), the present study seeks to determine whether prescribed fire can be combined with tornado damage (rather than a shelterwood harvest) to act as a filter that curtails regeneration of mesophytic species and at the same time enhances oak regeneration. This study will test the hypothesis that tornado damage can be used as a surrogate for thinning in oak restoration procedures.

This study also seeks to measure how oak regeneration is affected by post-storm logging practices. Instead of using a prescribed fire after natural disasters for restoration objectives, many landowners feel the need to “clean up” after these disasters to recover downed merchantable timber and to reduce the risk of insect infestation or wildfire (Lindenmayer and Noss 2006). The areas are “cleaned” with a process called salvage logging, where downed timber is harvested with heavy machinery after natural disasters like tornados, hurricanes, and wildfires. Rather than simply removing downed logs, salvage logging processes may greatly alter the physical structure, ecosystem processes, community composition, and most importantly, the trajectory of recovery in these stands (Foster et al. 1997, Lindenmayer and Noss 2006). In addition to the effects of tornado damage and prescribed fire on oak regeneration, this study can also assess the poorly understood effects of salvage logging after natural disturbance.

The results of this study will offer an informed procedure for restoring upland oak stands by taking advantage of tornado damage, which may be the only option for opening the canopy in areas where harvest of standing trees is either restricted or impractical. In addition, results will provide information on the unintentional consequences of salvage logging operations in damaged upland oak stands.

OBJECTIVES AND HYPOTHESES

The main objective of this study is to determine if the destructive effects of tornado damage on upland oak stands can be harnessed or combined with prescribed fire to increase natural oak regeneration while reducing competition from off-site mesophytic species that have benefited from recent fire suppression. The study also seeks to determine if post-storm salvage logging negates the potential benefits of tornado damage to oak regeneration. To accomplish these objectives, the study will determine how the abundance of oak saplings and their competitors are affected by 1) tornado damage, 2) prescribed fire, 3) tornado damage combined with prescribed fire, and 4) tornado damage combined with salvage logging. Furthermore, since the tornado-damaged plots differed in damage severity, if the treatments are successful, this study may be able to elucidate what amount of tornado damage is optimal for regenerating upland oak stands (e.g., severe, moderate, or none) and what if any intensity of salvage logging is tolerable for upland oak regeneration.

Tornado Damaged Plots

I hypothesized that in tornado damaged plots, there should be an overall increase in sapling recruitment since more light is reaching the forest floor. However, I expect that the fast-growing, mesophytic species will benefit more from the increased light levels than the slower-growing oaks. Upland oaks allocate more of their resources to underground root reserves rather than vertical growth (Johnson et al. 2002); therefore, they have a slower aboveground growth rate and are likely to be surpassed in height by the mesophytic species.

Tornado Damaged Plots Combined with Prescribed Fire

I hypothesized that oak regeneration would benefit most from prescribed burning in the tornado damaged plots. Specifically, I predicted that oak saplings would gain a relative height advantage over competitors allowing them to be more likely to reach the canopy. Top-kill is the death of the aboveground portion of a plant leaving the belowground portion to resprout. As with previous studies, I predicted probability of mortality by top-kill to decrease as stem diameter increased (Harmon 1984). Additionally, I predicted that oak saplings would be 1) more resistant to being killed and 2) more resilient if top-killed by fire compared to mesophytes of similar size. As the increased light helps to build underground reserves in oaks, and as these reserves facilitate rapid growth after being top-killed by fire (Johnson et al. 2002), it follows that resprouting oaks should have faster growth rates by utilizing their reserves and should gain a height advantage over mesophytic saplings.

Undamaged Plots with Prescribed Fire

In undamaged plots with prescribed fire, I hypothesized that without prescribed fire being coupled with an open canopy associated with tornado damage (and hence, increased light levels), oak root reserves would be smaller and less able to facilitate rapid resprouting after prescribed fires. Therefore, without extra reserves to boost their post-fire growth, I expected oak saplings to be handicapped by slow growth, and I did not expect them to gain a size advantage in the sapling layer after only one burn.

Tornado Damaged and Salvage-logged Plots

In the tornado damaged and salvage-logged plots I expected an overall decrease in saplings and increased representation by mesophytic, pioneer species. I expected that the decrease in saplings would be correlated with logging severity. This decrease in sapling number could be due to damage by logging equipment, scarification of soil, soil compaction, soil desiccation from increased light, or competition from newly established, weedy, herbaceous species. I expected that the original reduction in sapling density caused by salvage logging would be followed by increased colonization by efficiently-dispersed pioneer tree species that benefit from exposed mineral soils such as loblolly pine (*Pinus taeda* L.), sweetgum (*Liquidambar styraciflua* L.), persimmon (*Diospyrus virginiana* L.), and winged elm (*Ulmus alata* Michaux).

METHODS

Parts of the Little Tallahatchie Experimental Forest (the site of long-term monitoring of oak–pine forest dynamics) experienced heavy tornado damage on February 5, 2008. After this natural disturbance, timber removal was initiated in some areas of the forest. The experimental forest is now composed of several tornado-damaged plots, tornado-damaged and salvage-logged plots, and largely undamaged plots. In addition to these disturbances, a few plots received prescribed fire in the spring of 2010. This natural disturbance and subsequent timber operations offer the unique opportunity to observe how two forest management activities—salvage logging and prescribed burning—combine with tornado damage to promote or hinder advanced regeneration of oaks.

Study Site

The upland hardwood–pine forests studied here were located within the northern hilly coastal plains of Mississippi (Holly Springs National Forest and the Tallahatchie Experimental Forest within the Greater Yazoo River Watershed, U.S.A.; 34.50°N, 89.43°W). Soils were 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 within the top 10 to 30 cm overlay silts within the soils studied here (Morris 1981). In the early 1800s, before extensive logging and fire suppression, 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 suppression in the 20th century, second-growth stands developed following extensive logging and currently have approximately twice the stand density of mature stands in the early 1800s (Brewer 2001). Tree species that for the most part were historically restricted to (or that reached tree size primarily within) floodplains (e.g., *Liquidambar styraciflua*, *Acer rubrum*, *Quercus alba* L., and *Nyssa sylvatica*) commonly occur in these upland forests today and dominate the understory (Surrette et al. 2008). These stands are now dominated in the overstory by a mixture of some of the upland oak species (e.g., *Q. velutina*, *Q. stellata*, *Q. falcata*, but not *Q. marilandica*), pines (mostly *P. echinata*), some species historically common in floodplains (e.g., *Q. alba*, *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

Eight 10 x 30 m plots were established in 2003 initially to assess the effects of prescribed burning season on vegetation composition (Figure 1) and initial tree species composition was assessed. On February 5, 2008, six of these plots were damaged by a tornado, and 30–70% of trees ≥10 cm dbh (diameter at breast height, or 1.5 m) were downed; the remaining plots were relatively undamaged (<1% of trees downed). After the tornado, five new plots were established where tornado damage occurred adjacent to plots established in 2003. In four of these new plots, downed timber was salvage logged. As a result, thirteen paired plots (five pairs and a set of three plots) of 10 x 30 m were established in damaged, undamaged, and salvage logged areas on ridges and slopes (and the midslope in the case of the set). The plots represent seven quasi-treatment combinations:

1) severely damaged by the tornado and then treated with prescribed fire in April 2010,
2) not damaged by the tornado but treated with prescribed fire in April 2010,
3) severely damaged by the tornado only; not logged or burned,
4) severely damaged by the tornado followed by salvage logging,
5) moderately damaged by the tornado, but not logged or burned,
6) moderately damaged by the tornado followed by salvage logging, and
7) not damaged by the tornado, not burned, and not logged.

A breakdown of plots, treatments, topography, and tornado damage can be found below (Table 1; Figure 1). Each of the thirteen plots was further subdivided into eight 5 x 7.5 m subplots arranged in two rows of four to aid in measuring vegetation composition and in statistical comparisons (Figure 1).

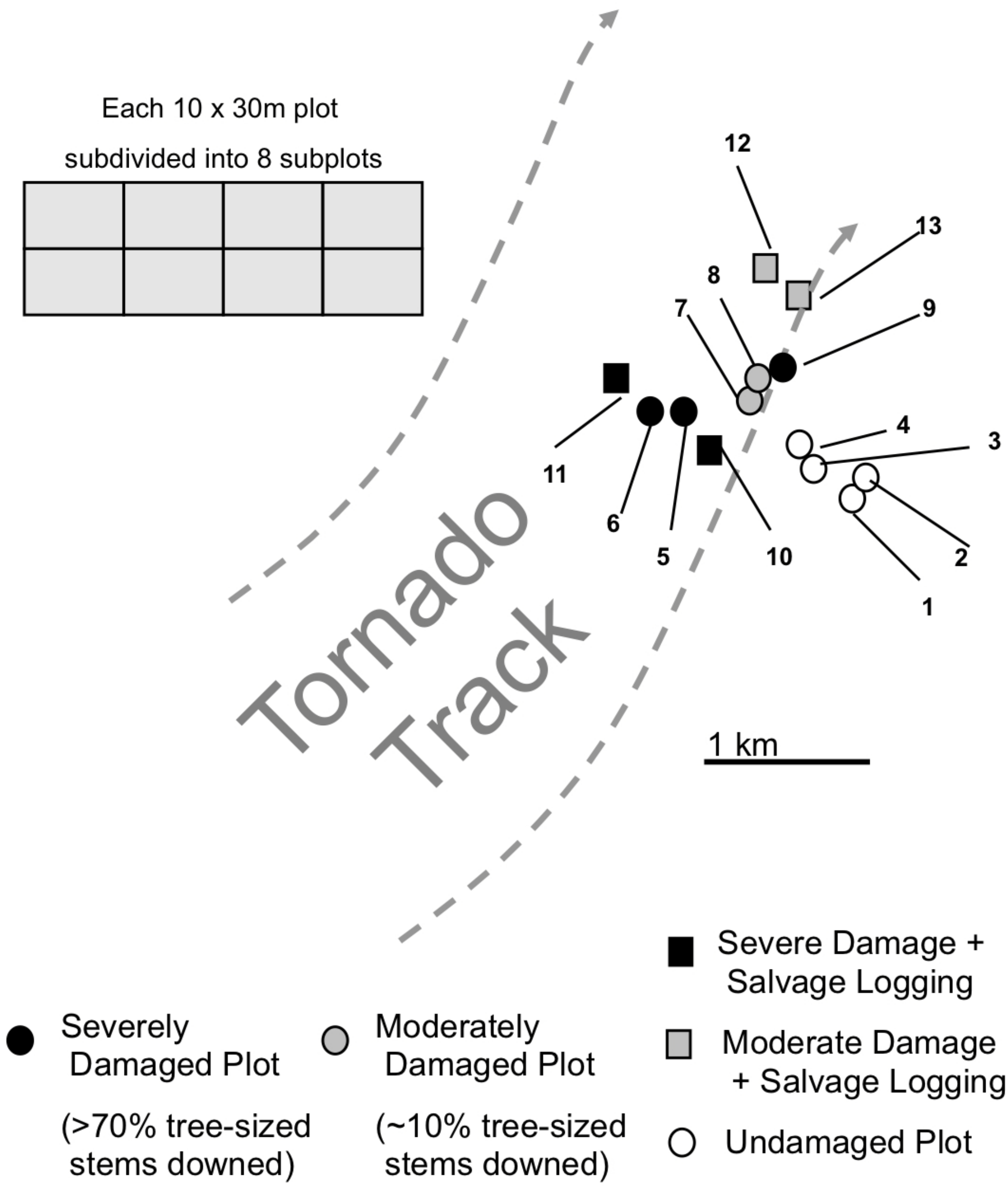

Figure 1. Little Tallahatchie experimental plots located within the Holly Springs National Forest in northern Mississippi. Plots represent combinations of tornado damage, prescribed fire, and salvage logging. Two tornado-damaged stands (5 and 6) and two undamaged stands (3 and 4) received prescribed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

Plot	Treatment	Topography	2005 fire	Canopy Gap Fraction*
1	Undamaged	Ridge	–	10%
2	Undamaged	Slope	–	11%
3	Fire Only	Ridge	+	21%
4	Fire Only	Slope	+	16%
5	Severe Damage + Burn	Ridge	+	53%
6	Severe Damage + Burn	Slope	+	55%
7	Moderate Damage	Ridge	–	25%
8	Moderate Damage	Slope	–	26%
9	Severe Damage	Midslope	–	47%
10	Severe Dam. + Logged	Slope	–	75%
11	Severe Dam. + Logged	Ridge	–	80%
12	Mod. Dam. + Logged	Ridge	–	54%
13	Mod. Dam. + Logged	Slope	–	38%

Table 1. Treatment, topography, burn history, and canopy density summary for experimental plots.

*Canopy density was measured at peak growing season 2009 with a concave spherical canopy densiometer.

Measurements

Environmental measurements

Environmental measurements were used as predictor variables to account for variation in plant communities. They were also used as response variables in the discriminant analysis described below. I 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) relative elevation, 2) slope aspect, and 3) soil texture. A previous study showed that the elevation of a subplot below the nearest ridge (hereafter, relative elevation) was among the best predictors of plant species richness at the sites and thus was included as a covariate (Surrette and Brewer 2008). Relative elevation was determined by measuring slope angle and distance between the nearest point on the ridge and center of the subplot. I used a clinometer to measure the slope angle between a point on the ridge and the center of the subplot. Distances were measured between these points and elevation of each subplot below the closest ridge was calculated trigonometrically. Absolute elevation above sea level was estimated from these measurements of relative elevation by obtaining the elevation of benchmarks with the aid of a GPS unit (x-y coordinates) and a topographic map (z-coordinate). I measured the northerly aspect of each subplot using a compass and a trigonometric conversion (north-facing = 1 and south-facing = -1). Subplots located in sheltered hollows were keyed as having a due north aspect. In each subplot, two points were haphazardly chosen, and a soil core with a volume of 30 cm^3 was taken from both points and pooled for each subplot. I determined the percentage of sand, silt, and clay of samples using a traditional suspension method.

Canopy density was measured by averaging four orthogonal readings from a concave canopy densiometer within each subplot, providing a quantitative long-term measurement of light conditions. Percent soil organic matter was measured using the Loss on Ignition method (Black 1965) on soil cores to help account for differences in soil fertility.

In fall 2009, I estimated several ground cover variables, which were included in the discriminant analysis. I measured the following variables:

1) % disturbed soil: plot area containing disturbed soil due to mounds and pits formed near uprooted trees or ruts from machinery disturbance,

2) % leaf litter: plot coverage by leaf litter,

3) % dead crown: plot coverage by dead tree crowns, and

4) % bare ground: plot coverage by un-vegetated bare soil.

Fire temperature was assessed by using temperature sensitive paints (Tempilaq G indicating liquids). The paints, rated to indicate maximum temperatures of 79, 121, 163, 204, 246, and 288°C, were applied in a row to a small aluminum plate staked 30 cm above ground in each subplot.

Vegetation measurements

I measured the height of each woody sapling in 2009 and 2010 and assessed the damage response to prescribed fire in 2010. I quantified sapling abundances and classified stems into two height classes: short saplings (<10 cm dbh; ≥ 1 m tall; < 1.5 m tall) or tall saplings (<10 cm dbh; ≥ 1.5 m tall). In August 2010, I measured the height of individual saplings <2 m tall. I also measured the height at which new wood began in order to estimate the sapling height at the end of the growing season in 2009. I 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 the fire to determine if the stem was killed (killed with no new growth), 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.

Prescribed Fires

The damaged plots contained a heterogeneous fuel supply (a patchy mixture of downed crowns and grass clumps), while undamaged plots contained a homogeneous fuel supply (an even layer or leaf litter). Further, due to time constraints, the damaged and undamaged stands were burned one week apart creating variation in burn conditions. Thus, fuel and weather differences led to differences in fire characteristics in the damaged and undamaged plots.

In damaged plots (plots 5 and 6) flame temperature and lengths were much more variable than in undamaged plots (plots 3 and 4), and fires were somewhat patchy. Plots 5 and 6 were burned on March 25, 2010. During this burn, ambient temperatures ranged from 22–24°C; relative humidity ranged from 30–34%. Flame lengths varied depending on fuel availability. Flames lengths in woody debris ranged from 1.5–2.5 m; flame lengths in grassy areas ranged from 0.1 to 1.5 m (J. Walden, personal communication). Based on aluminum pyrometer readings, maximum fire temperatures ranged from 79–660°C (mean 208°C; s.e. 47°; n=9). In 5 of 16 subplots, fires did not contact the pyrometers, therefore no reading was obtained.

In undamaged plots fires were even, with less variation in fire temperatures than damaged plots. Plots 3 and 4 were burned on April 1, 2010. During this burn, ambient temperatures ranged from 23–27°C; relative humidity dropped from 36% to 29% over the course of the burn. Flame lengths ranged from 0.15 to 0.5m (J. Walden, personal communication). Fire temperatures ranged from 163–288°C (mean 219°C; s.e. 11°C; n=16); each pyrometer was contacted by fire.

Statistical Analysis

Effects of Tornado Damage on Sapling Species Composition and Size

True replication of the prescribed fire x tornado damage interaction was not possible in this study because the effects of a single tornado could not be truly replicated. Hence, I used a two-step approach to analyze the effects of tornado damage on saplings. First, I used a discriminant analysis with stepwise variable selection (P to enter = 0.25) to examine which of the measured environmental variables were most important in distinguishing the severely damaged, moderately damaged, and undamaged subplots. The damage severity of a plot was assigned based on the percentage of downed (but not necessarily dead) canopy crowns present immediately after the tornado (undamaged: <1%; moderate damage: ~10%; severely damaged: >70%). Since salvage logged plots were anthropogenically disturbed as well as disturbed by the tornado, I excluded these plots from the analysis of the effects of tornado damage. The environmental variables included in the analysis were relative elevation, slope aspect, sand:silt ratio, %clay content, %canopy cover, %dead crown, %leaf litter, and %soil organic matter. I hypothesized that variables such as canopy cover, litter cover, downed crowns, and disturbed soil would be the most important discriminators of groups of subplots that differed with respect to damage severity. In contrast, I hypothesized that variables such as soil texture, organic matter, relative elevation, and aspect would not be important discriminators of tornado damage.

Second, once the significant environmental variables from the discriminant analysis were determined, I used stepwise multiple regression to evaluate how sapling composition and sapling size varied with environmental variation among the subplots. Among the variables that potentially varied significantly among damage categories, I hypothesized that canopy cover would be among the most important predictors of species composition and sapling height.

In order to determine which environmental factors were associated with species composition and size, I used several forward stepwise regressions (P to enter = 0.25) to determine which environmental factors were associated with 1) fall 2009 total sapling density, 2) fall 2009 short sapling density, and 3) fall 2009 tall sapling density. I also used stepwise multiple regression to determine which environmental factors were associated with fall 2009 upland oak abundance and fall 2009 mesophyte abundance. Lastly, to examine variation in the proportional abundance of oaks and mesophytes, I analyzed the log abundance ratio of 2009 mesophytic and oak saplings. When positive, this variable indicated dominance of a subplot by mesophytic saplings; when negative, it indicated dominance by oak saplings. I used forward stepwise regression to determine which factors were correlated with dominance of one species group over another. I repeated this analysis using 2010 abundances.

Effects of Prescribed Burning and Sapling Basal Diameter in Severely Damaged and Undamaged Plots

I evaluated the effects of burning by examining stem level measurements of damage severity and the number and growth of resprouting stems. To examine which biological factors are important in resistance of saplings to damage from fire, I grouped saplings from burned plots into “damaged” (killed or top-killed and resprouting; n=223) and “undamaged” (slightly damaged or completely undamaged; n=92). I then used one-way analysis of variance (ANOVA) to determine if damaged and undamaged saplings differed with respect to length and basal diameter. Next, I used forward stepwise logistic regression (P to enter = 0.25) 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). Lastly, I used one-way ANOVA to determined if mesophytes and upland species differed in basal diameter:length ratio.

Next, I investigated traits of upland and mesophytic species that may be important to resilience after a fire (i.e., resprouting after fire). For these analyses, I used measurements from all saplings top-killed in burned plots. I used one-way ANOVA to determine if upland and mesophytic species differed with respect to resprout number or the length of the longest resprout. I also used Tukey's HSD test (Weiss 2007) to see how species ranked according to resprout number and length. Lastly, I used forward stepwise regression (P to enter = 0.25) to evaluate the relative importance of biological factors in increasing sprout number and length. The factors included were stem length, basal diameter, and species group (i.e., mesophyte or upland oak).

To test the hypothesis that oaks should have a relative advantage after prescribed fire, I used a repeated-measures two-way ANOVA to see if prescribed fire had different effects on upland oaks than on mesophytic species with respect to the final height of stems. For this analysis, I compared pre-fire height in 2009 to the saplings' post-fire height in 2010. For undamaged saplings, the repeated measures were simply the height measurement between years. For top-killed saplings, however, the post-fire measurement was the height of the longest sprout.

Effects of Salvage Logging in Tornado Damaged Plots

The analyses for logging effects were similar to those described above for tornado damage except that I used a Discriminant Analysis to distinguish plots on the basis of salvage logging severity: 1) tornado damaged plots without logging, 2) moderately damaged and logged, and 3) severely damaged and logged plots. Since I was examining the additive effects of logging after tornado damage, I excluded the undamaged stands from this analysis. I hypothesized that variables such as canopy cover, soil disturbance, and bare ground would be the most important discriminators of groups of subplots that differed with respect to salvage logging severity

Second, once the significant environmental variables from the discriminant analysis were determined, I used stepwise multiple regression to examine how post-storm sapling species composition and sapling size varied in response to environmental variation among the subplots. I hypothesized that canopy cover, disturbed soil, and bare ground would be among the most important predictors of species composition and sapling height.

The analysis of the effects of salvage-logging was similar to that of tornado-damaged plots. I used several forward stepwise regressions (P to enter = 0.25) to determine which environmental factors were associated with fall 2009 sapling and summer 2010 sapling densities. To determine if salvage logging affected oaks and mesophytes differently, I used two separate stepwise regressions to determine which environmental factors were associated with fall 2009 upland oak abundance and fall 2009 mesophyte abundance. Lastly, to examine variation in the proportional abundance of oaks and mesophytes, I analyzed the log abundance ratio between 2009 abundance of mesophytic and oak saplings and then repeated this analysis using 2010 abundances.

Meeting assumptions of statistical analyses

In order to meet the assumptions of the statistical analyses used (e.g., normally distributed residuals and homoscedasticity), I transformed both the independent and dependent variables. I used a natural log (+1) transformation for all species abundance data. Ratios (sand:silt, mesophytic dominance) were also natural log transformed. All percentage data (canopy density, %organic matter, %clay %bare ground, %litter, and %dead crowns) were arcsine-square root transformed as recommended for proportions (Gotelli and Ellison 2004). Slope aspect was converted to radians and then cosine transformed to form an index of sheltered slopes (i.e., south-facing aspects were positive, and north-facing aspects were negative). I used the transformed data in all analyses, but to ease interpretation, I present all bar graphs with means and standard errors back-transformed to the original units. Graphical results of multiple regressions are presented as residual leverage plots which emphasize the effects of a single predictor variable on the response of interest while accounting for all covariables (Sall 1990).

RESULTS

Effects of tornado damage on saplings

Determining the important environmental variation distinguishing damage treatments

Discriminant analysis (DA) revealed that reduced canopy cover was the most important indicator of tornado damage. The DA showed that relative elevation ($P<0.01$), slope aspect ($P=0.02$), sand:silt ratio ($P<0.01$), canopy cover ($P<0.01$), %dead crown ($P<0.01$), and %leaf litter ($P<0.01$) were all significant in discriminating damage severity treatments with only 2.8% of subplots misclassified. Two canonical axes (DA axis 1 and DA axis 2; Figure 2) were interpretable and explained 75.5 and 24.5% of the fitted variation, respectively. Furthermore, DA axis 1 successfully categorized the subplots along a damage severity gradient (Figure 2). Canopy cover ($R=0.61$, $P<0.01$), sand:silt ratio ($R=-0.25$, $P=0.03$), and relative elevation ($R=-0.29$, $P=0.02$) were all significantly correlated with DA axis 1 (Figure 2) which indicates that these three variables are the most important measured variables that distinguish a tornado damage severity gradient. Since differences in elevation and sand:silt ratio were unlikely to be changed by tornado damage, these are likely preexisting differences among plots.

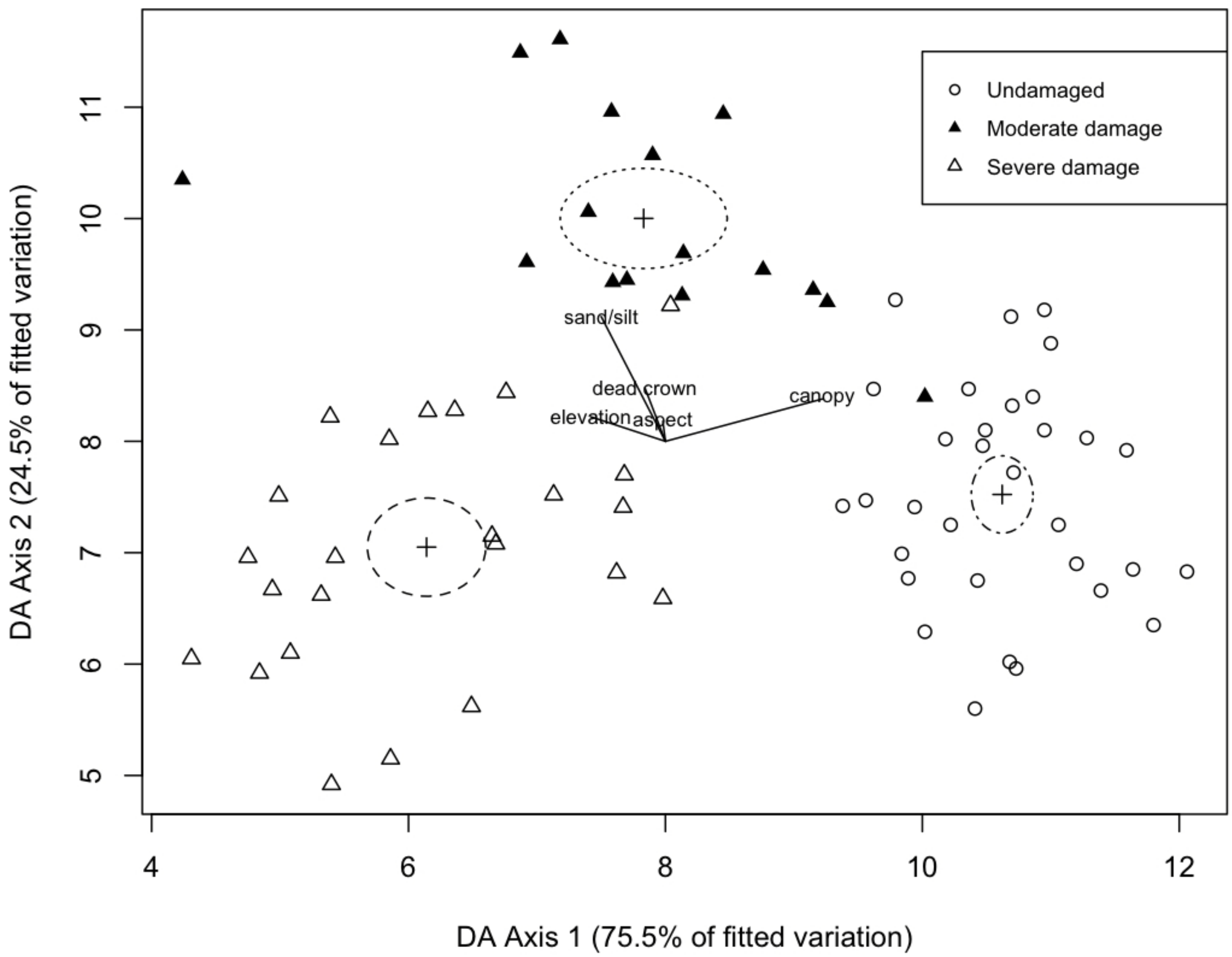

Figure 2. Discriminant Analysis of undamaged, moderately, and severely damaged subplots. Confidence ellipses represent standard errors of axis 1 and axis 2 scores. Vectors represent correlation of environmental variables with DA axes.

Effects of reduced canopy cover on saplings

Total sapling density 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 increased canopy cover. However, short sapling density in fall 2009 decreased with increasing canopy cover (P<0.01; Figure 3) after accounting for the effects of sand:silt ratio (P=0.12), clay (P=0.10), and disturbed soil (P=0.06). I was not able to detect an increase in the number of tall saplings due to recruitment from short saplings. Instead, these analyses indicate that the increase in saplings after a tornado is primarily from recruitment of seedlings to short saplings or from new seedlings that have quickly recruited to short saplings.

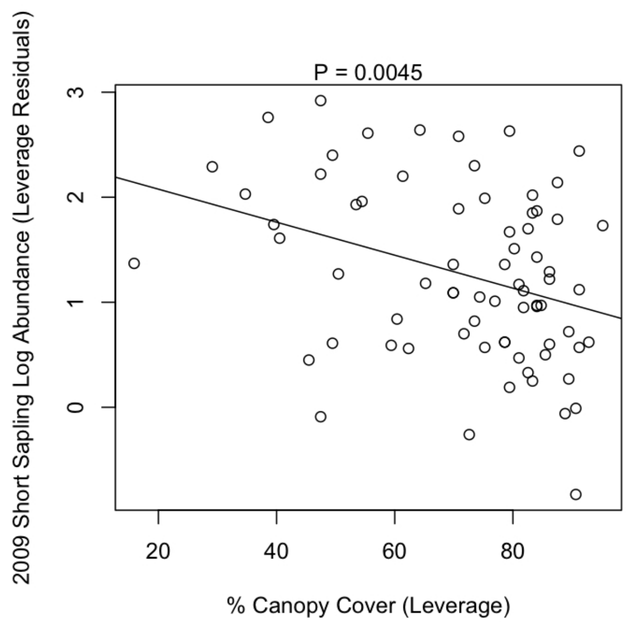

Figure 3. Canopy cover leverage plot of short sapling abundance in 2009.

When examining short oak and mesophytic saplings separately, canopy cover was negatively correlated with upland oak abundance (P<0.01; Figure 4) 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 aspect (P=0.15), soil disturbance (P=0.11), relative elevation (P=0.19), and sand:silt ratio (P=0.11). This suggests that both mesophytic and upland saplings respond positively to canopy reduction.

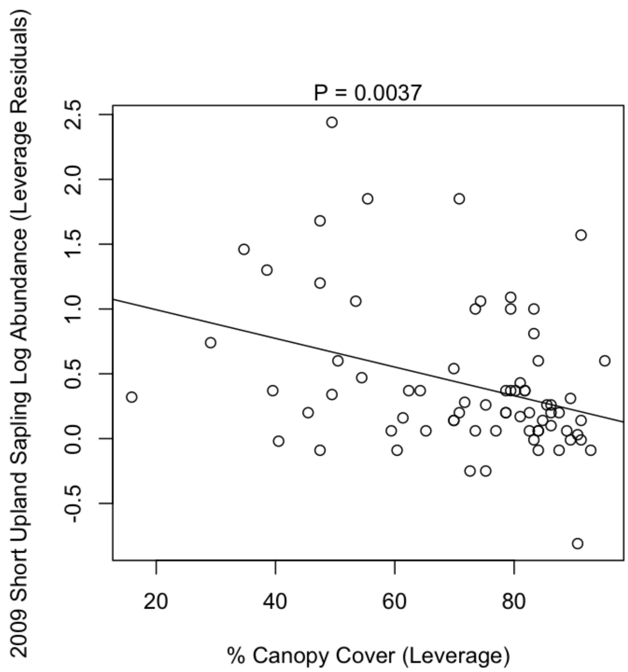

Figure 4. Canopy cover leverage plot of 2009 short upland sapling abundance.

<u>*Effects of reduced canopy on dominance by mesophytic species*</u>

Oaks appeared to benefit more from tornado damage than mesophytic 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, canopy reduction 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 5) after accounting for sand:silt ratio (P=0.02), dead crown (P=0.15), and soil organic matter (P=0.08). I found similar results when analyzing dominance among total sapling counts.

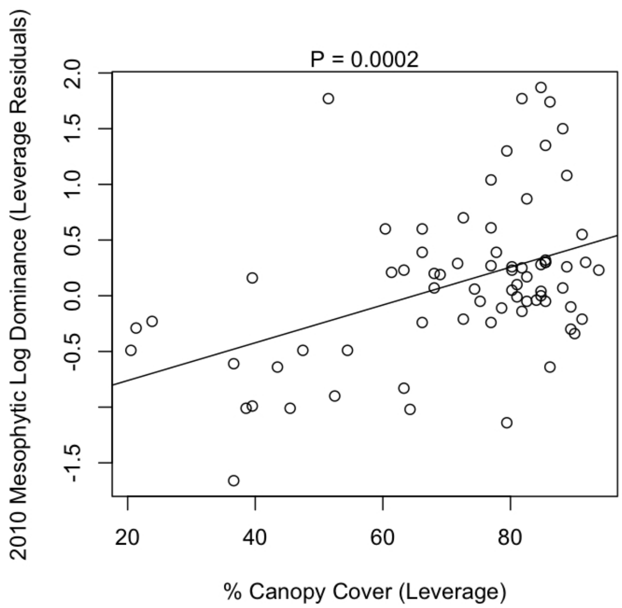

Figure 5. Canopy cover leverage plot of 2010 mesophytic dominance.

Effects of salvage logging on saplings

Determining the important environmental variation distinguishing logging severity

Discriminant analysis (DA) revealed that bare ground was the most important indicator of salvage logging severity, with % bare ground being greatest in the most severely logged stands. The DA showed that relative elevation (P<0.01), slope aspect (P<0.01), sand:silt ratio (P<0.01), soil disturbance (P=0.01), canopy cover (P<0.01), %dead crown (P<0.01) and %bare ground (P<0.01) were all significant in discriminating damage and logging severity treatments with only 5.6% of subplots misclassified. Two canonical axes (DA axis 1 and DA axis 2; Figure 6) were interpretable and explained 93.6 and 6.4% of the fitted variation respectively. Furthermore, DA axis 1 successfully categorized the subplots along a logging severity gradient (Figure 6). Percent bare ground was the only variable significantly correlated with DA axis 1

(R=0.27, P=0.02; Figure 6) which indicates that it is the most important measured variable that differs along a logging severity gradient. Soil disturbance (R=0.34, P<0.01), canopy cover (R=0.65, P<0.01), and %dead crown (R=0.66, P<0.01) were correlated with canonical axis 2, but they did not vary with logging severity (Figure 6).

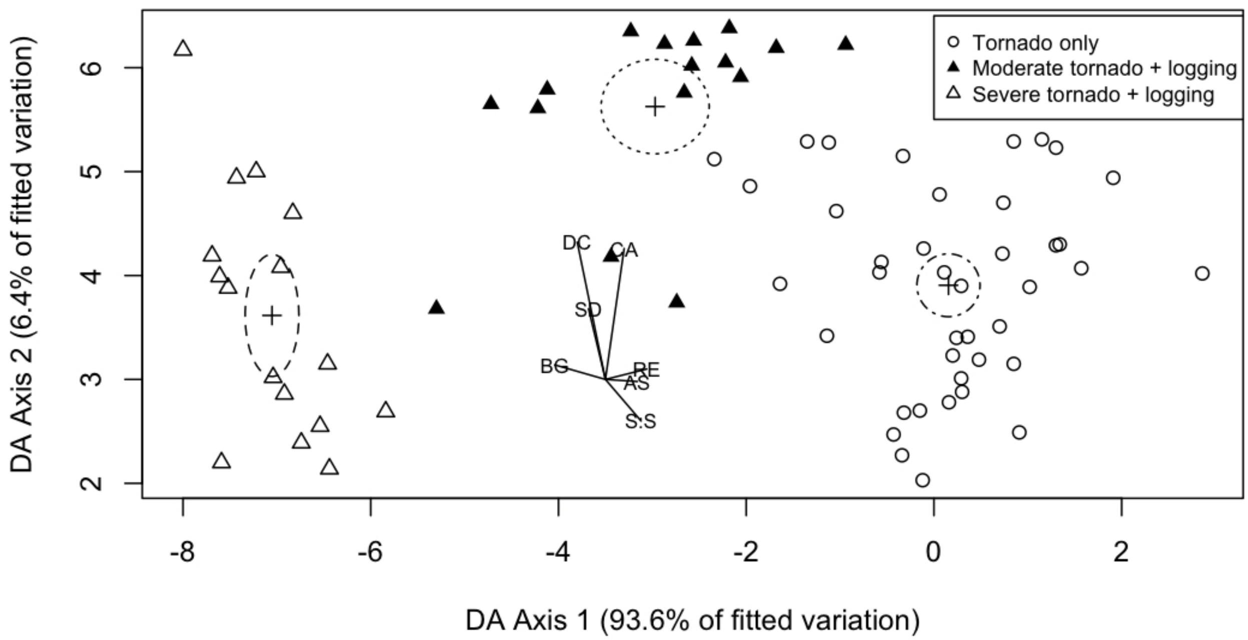

Figure 6. Discriminant Analysis of damaged, moderately damaged and logged, and severely damaged and logged subplots. Confidence ellipses represent standard errors of axis 1 and axis 2 scores. Vectors represent correlation of environmental variables with DA axes. BG=bare ground, SD=soil disturbance, DC=downed crown, CA=canopy cover, RE=relative elevation, AS=aspect, S:S=sand:silt ratio.

Effects of salvage logging disturbance on saplings

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 7) after accounting for the effects of sand:silt ratio (P<0.01) and elevation (P=0.04).

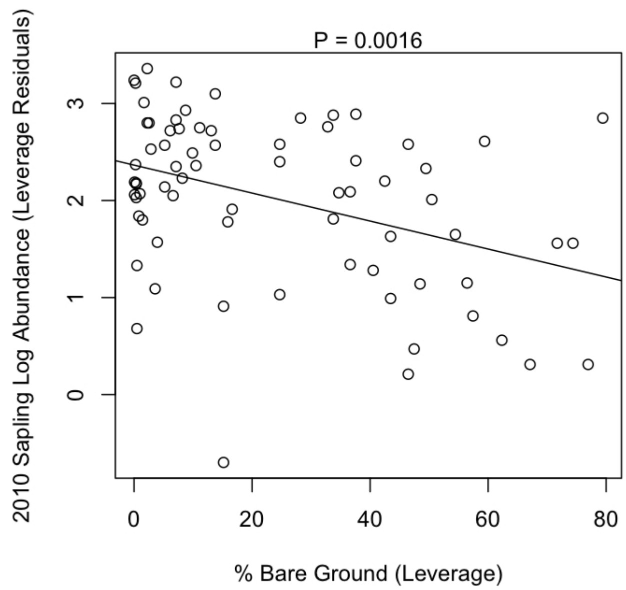

Figure 7. Bare ground leverage plot of 2010 total sapling density.

In fall 2009, total upland sapling abundance decreased with increasing 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, result in lower sapling densities. However, oaks may be impacted more severely than mesophytes.

Effects of salvage logging disturbance on mesophytic dominance

Among short saplings, mesophytic dominance increased with bare ground (P=0.03; Figure 8) 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*, *Diospyrus virginiana*, and *Nyssa sylvatica*.

Similar results were found for summer 2010. These results suggest that salvage logging, with its subsequent vegetation removal, had a negative impact on upland oak abundance while having no discernable effect on mesophytic saplings.

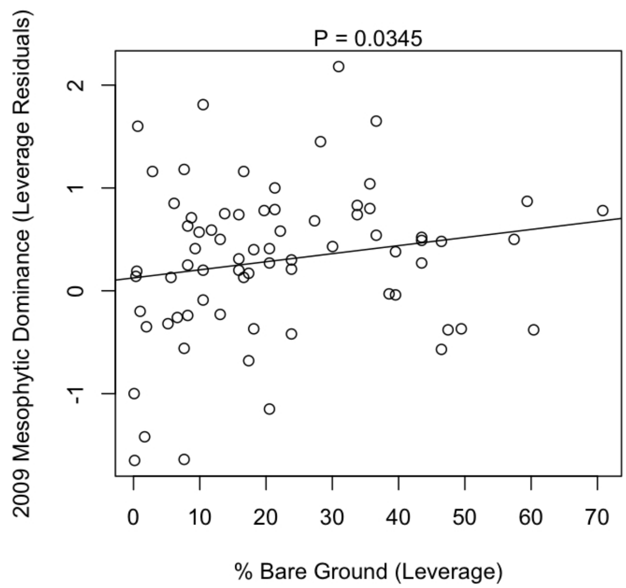

Figure 8. Bare ground leverage plot of 2009 mesophytic dominance.

Effects of prescribed burning on saplings

Biological factors influencing probability of stem damage from fire

After prescribed burning on tornado damaged sites, 71% of saplings were either killed or top-killed and resprouting, resulting in much smaller and more numerous stems. Damaged saplings tended to be shorter ($F_{1,246}$=21.40, P<0.01; Figure 9) and had smaller basal diameters than undamaged saplings ($F_{1,305}$=109.36, P<0.01; Figure 9).

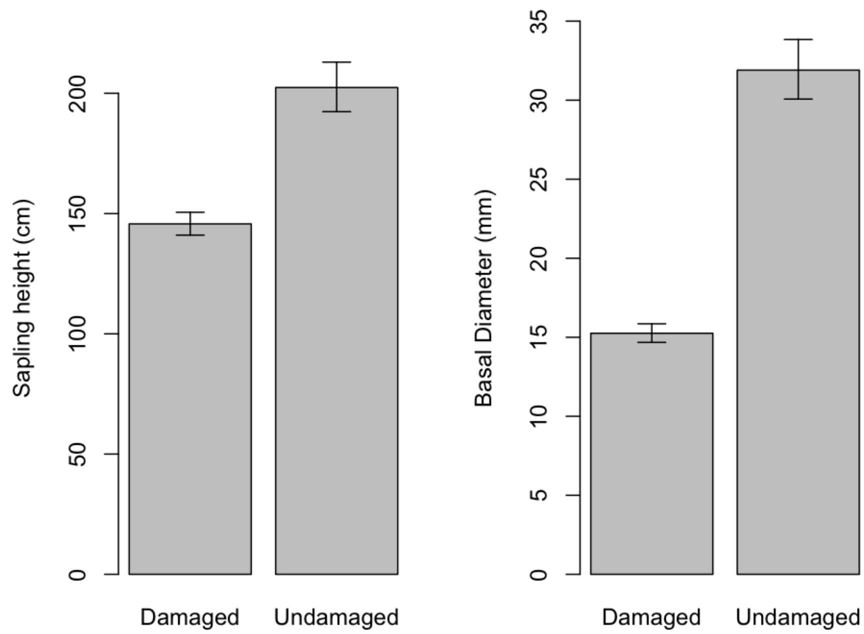

Figure 9. Mean pre-fire height and basal diameter of damaged and undamaged saplings. Error bars represent ± 1 standard error of the mean.

The stepwise logistic regression revealed that basal diameter was negatively correlated to damage susceptibility ($P<0.01$); stem length was positively correlated with damage susceptibility ($P<0.01$); and upland species were less susceptible to damage than mesophytic species ($P<0.01$). The fact that stem length was positively correlated to damage seems to contradict the previous ANOVA (Figure 9). However, since the multiple regression accounts for variation in basal diameter and species group, the regression suggests that for a given basal diameter tall species are damaged more severely than short ones. This suggests that taller and thinner stems (i.e., low basal diameter:length ratio) tend to be killed more often than thicker stems (i.e., high basal diameter:length ratio).

Interestingly, upland oak saplings had a higher mean basal diameter:length ratio than mesophytic saplings ($F_{1,246}=74.11$; $P<0.01$; Figure 10). The fact that upland oaks were less susceptible to fire even after accounting for differences in basal diameter and length suggests that there are other biological factors besides size differences that give upland oaks higher resistance to damage by fire.

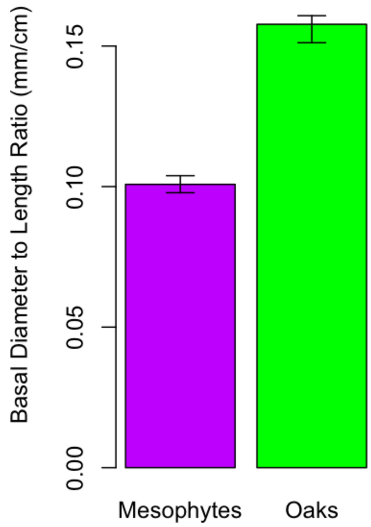

Figure 10. Mean pre-fire basal diameter to length ratio of mesophytic saplings and upland oaks. Error bars represent ± 1 standard error of the mean.

Biological factors influencing resilience of saplings after fire damage

Generally, top-killed oaks tended to have longer sprouts than mesophytic species (Figure 11), but *Prunus serotina* had unexpectedly long sprouts and *Quercus falcata* had unexpectedly short sprouts (Figure 12). One-way ANOVA indicated that mesophytic species tended to sprout more abundantly after a fire ($F_{1,217}$=3.91; P=0.05; Figure 11), but upland oaks tended to have longer sprouts ($F_{1,215}$=70.82; P<0.01; Figure 11). I could not detect differences in sprout number among species (P>0.05). However, I did detect differences in sprout length among species (P<0.05; Figure 11).

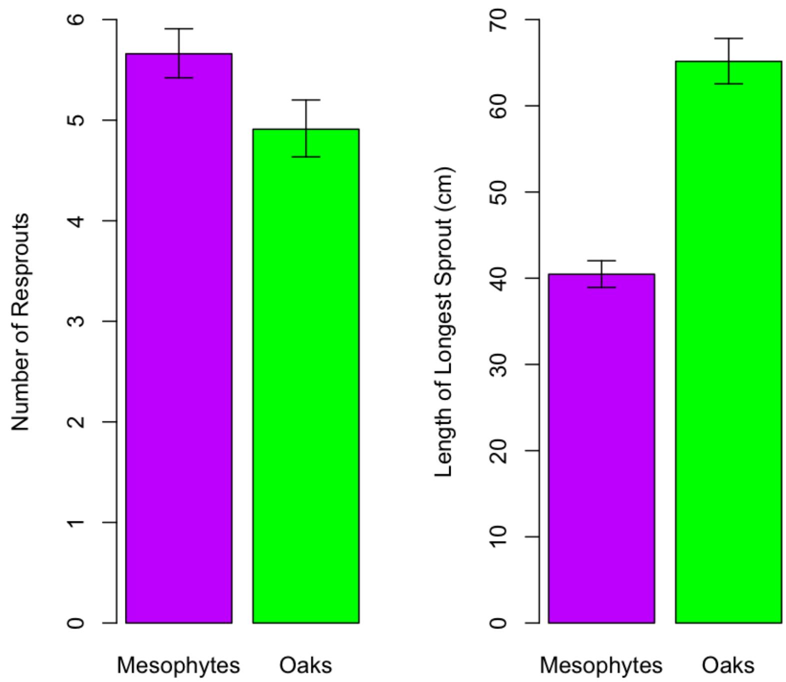

Figure 11. Mean post-fire number of resprouts per sapling and length of the longest sprout for top-killed mesophytic and upland oak saplings. Error bars represent ± 1 standard error of the mean.

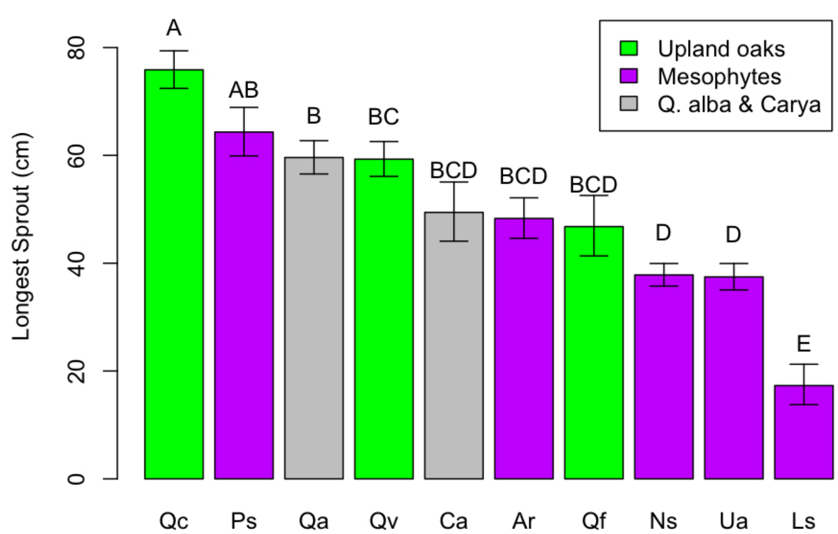

Figure 12. Mean longest sprout length for abundant species. Error bars represent ± 1 standard error of the mean. Species not sharing a letter are significantly different by Tukey's HSD (P<0.05). Qc=*Quercus coccinea*, Ps=*Prunus serotina*, Qa=*Q. alba*, Qv=*Q. velutina*, Ca=*Carya* spp., Ar=*Acer rubrum*, Qf=*Q. falcata*, Ns=*Nyssa slyvatica*, Ua=*Ulmus alata*, and Ls=*Liquidambar styraciflua*.

The number and length of resprouts varied with the size of saplings. Stepwise regression revealed that top-killed mesophytes had more sprouts than oaks ($P=0.06$) after accounting for initial sapling height ($P<0.01$). Stepwise regression 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 ($P=0.11$). The previous analyses of resilience to top-kill were found to be significant only after removing an influential outlier (Cook's d=0.25), which was a very large mesophytic sapling that showed signs of existing damage prior to the prescribed fire and therefore exhibited extremely poor resprouting ability despite its large size.

Fire effects on size dominance of the sapling layer

Upland oak saplings and mesophytic saplings attained similar heights in severely damaged stands with or without fire (Figure 13). Repeated measures ANOVA revealed that the time x species group interaction was significant ($F_{1,261}=5.23$; $P=0.02$). The fire appeared to reduce sapling height in oaks and mesophytic species (due to top-kill and resprouting), as indicated by the significant time x burn interaction ($F_{1,261}=106.06$; $P<0.01$; Figure 13). There was some indication of oak saplings possibly gaining a size advantage over mesophytic saplings as a result of burn (Figure 13), but the time x species group x burn interaction was not statistically significant ($F_{1,261}=0.92$; $P=0.34$). I was not able to examine the effects of fire in undamaged and burned stands due to the low number of oaks found in these stands.

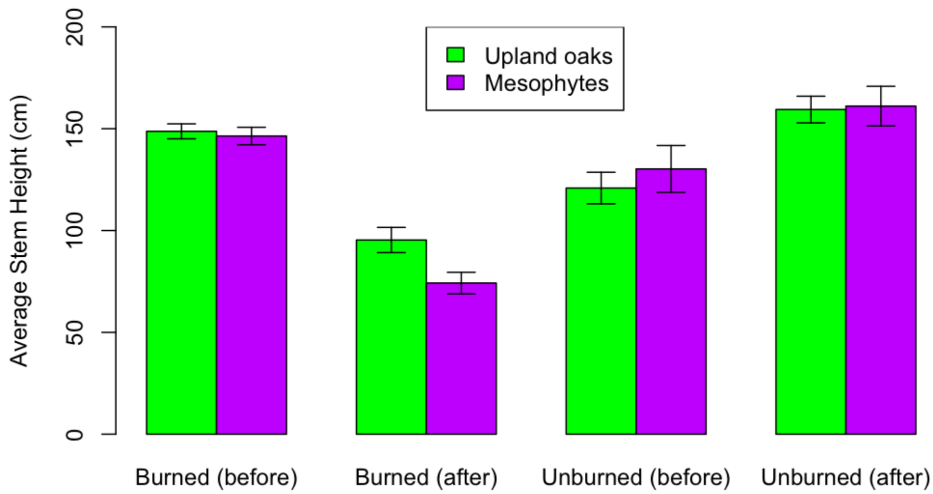

Figure 13. Mean sapling height in severely damaged stands, with and without prescribed fire. Error bars represent ± 1 standard error of the mean.

DISCUSSION

Effects of tornado damage

Stands that differed with respect to tornado damage severity were best distinguished by canopy cover, sand:silt ratio, and elevation. Since differences in sand:silt ratio and elevation were likely pre-existing, a change in canopy cover was the best indicator of a response to tornado damage. That is, low canopy cover was representative of severely damaged stands and high canopy cover characterized undamaged stands. Canopy cover was more important in distinguishing stands than were other potentially important indicators of damage, including percent cover by downed crowns or soil disturbance from uprooted trees.

Results of the current study suggest that oaks of the sapling layer benefited more than mesophytic species in tornado damaged stands with open canopies. This finding does not support the hypothesis that faster growing mesophytic saplings outcompete slower-growing oaks after major openings of the canopy (Abrams 1992, Brose et al. 1999, Albrecht and McCarthy 2006, Iverson et al. 2008). In this study, dominance by faster-growing mesophytes in 2010 was associated with increased canopy cover. I hypothesize 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. The soils at our site were extremely sandy (mean 61.5%; s.e. 1.6%). 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 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 both tornado damage and prescribed fire was supported. I hypothesized that oak reproduction would benefit from prescribed fire because they would be more resistant to top-kill and they would be more resilient if damaged by fire. Among damaged saplings, taller and thicker (higher basal diameter) saplings were more likely to resist top-kill. In the current study, I 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 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 after a fire because their longest post-fire sprout tended to be longer than those of mesophytes. At the species level, oak (with the exception of *Quercus falcata*; Figure 12) resprouts were taller than mesophytic resprouts (with the exception of *Prunus serotina*; Figure 12). Because of their taller sprouts, these saplings may be better poised to outcompete neighboring saplings and recruit to the canopy. Although mesophytes tended to have more numerous sprouts after the fire, the difference was unsubstantial. I speculate that these smaller sprouts will rarely recruit to taller size classes for two reasons: 1) Mesophyte resprouts are shorter and therefore more likely to be damaged by a second prescribed fire, and 2) Because they are shorter, mesophyte resprouts may be more likely to be out-competed for light by the 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 are at odds, however, 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 since 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 build the required reserves. This supposition is supported by other studies where oaks responded positively to prescribed fire several years after thinning (Kruger 1997, Brose and Van Lear 1998). In the present study, the oak stems had two full growing seasons to build up reserves, which may have contributed to increased resistance to top-kill and increased resilience.

These data suggest that at the xeric sites studied here prescribed fire may not be necessary to increase oak regeneration. As expected, the prescribed fire reduced the average height of saplings in severely damaged plots that were burned (Figure 13). This is because many saplings were top-killed and resprout lengths rarely exceeded pre-burn stem lengths. In contrast, in severely damaged plots that were not burned, average sapling lengths increased due to growth following increased light resources (Figure 13). With or without prescribed fire, severe canopy disturbances reduced the size disadvantage that oaks have relative to mesophytic saplings in closed-canopy forests. The severe tornado damage was enough to give oaks a relative height advantage over mesophytes, increasing the chances that these taller oak saplings will eventually recruit to the canopy, regenerating the stand with upland oaks.

Because oaks store much of their photosynthate in belowground structures they tend to have slower growth rates than mesophytic species (Johnson et al. 2002). However, when light becomes available, oaks are able to rapidly convert belowground storage into above ground biomass with a quick flush of growth (Johnson et al. 2002). Despite the fact that oaks are less tolerant of shade, they may grow faster than mesophytes immediately after a disturbance that opens the canopy.

A second factor that could contribute to the reduction in size disadvantage that oaks experienced in the study is soil quality. On poor and xeric soils, a prescribed fire after a severe wind disturbance may be unnecessary if the only management goal is to promote oak regeneration. Other studies attempting to increase oak regeneration by thinning and prescribed fire have been more successful on intermediate or dry sites, while less successful on mesic sites. Huston's (1979) species diversity hypothesis may help explain this phenomenon. The hypothesis predicts that rates of competitive displacement will be lower on infertile soil than on soils of higher fertility (Huston 1979). The reason for this reduction in competitive displacement is because, overall, growth rates are much slower on infertile soil and a disturbance that promotes the growth of less competitive species is likely to occur before a more competitive species has a chance to displace the inferior competitor (Huston 1979). Since overall growth rates at these infertile sites are relatively low, and since oaks may have a temporary flush of rapid growth, a severe natural disturbance such as a tornado may be enough to give oaks a growth advantage over the more competitive mesophytic species, as seen at our sites. Although this study suggests that on xeric sites, prescribed fire may not be necessary to restore oak reproduction, it may still be necessary to meet other management goals such as increased herbaceous plant diversity or maintenance of an open canopy and continual oak reproduction.

Effects of 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 2009 and 2010. Therefore, it is likely that salvage logging, through its effects on increasing bare ground, decreased sapling densities. One hypothesized cause of sapling reduction is that collateral damage from salvage logging processes further reduces canopy cover, which increases solar exposure, desiccates soil, and reduces sapling abundance. Since canopy cover was not correlated with logging severity, I did not find support for this hypothesis. Instead, the analyses suggest it is more likely that direct mechanical disturbance of vegetation by salvage logging processes reduces sapling abundances. Our findings on the effects of salvage logging on sapling densities differ from those found 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 were on 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 predicted, our regression approach suggests that sapling densities decreased with salvage logging intensity. In a post-harvest aspen forest, Zenner et al. (2007) found reductions in aspen 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, causing mechanical disturbance to a larger portion of the damaged site.

Although our analyses suggest an overall reduction of saplings in salvage logged plots, it seems that detriment to saplings with salvage logging was unequal among upland oaks and mesophytic species. While oaks were less abundant with increasing bare ground, mesophytes were not significantly affected. If salvage logging is indeed decreasing sapling densities by mechanical removal from salvaging equipment, it is unlikely that the machinery operators preferred to remove oak saplings over mesophytic saplings. It is more likely that saplings were randomly impacted by the disturbance, and mesophytes were able to recuperate by re-establishment or quick growth from groundcover since they tend to be both superior dispersers and faster growing.

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. The log ratio of mesophyte abundance to upland oak abundance, or “mesophytic dominance” increased with salvage logging intensity. This result suggests that salvage logging is decreasing oak regeneration and actually accelerating displacement by mesophytic species. Other studies on the effects of salvage logging on herbaceous groundcover have shown an increase in ruderal plants at the expense of forest indicators after log removal (Zenner and Berger 2008, Brewer et al. 2011, *in review*)

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. On the other hand, 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. blackgum, sweetgum, winged elm, and yellow poplar). Although perhaps not necessary for successful oak regeneration on poor soils, prescribed burning combined with protection from salvage logging could increase the competitive advantage of oak saplings over fast-growing mesophytic species that would otherwise respond positively to gaps. The upland oaks studied here are best classified as fire-dependent rather than as early-, mid-, or late-seral species. It may be more important for land managers to take advantage of tornado damage of an oak stand as an opportunity to restore a now rare ecosystem. Since global climate change may result in increased natural disasters such as hurricanes and tornados, the usage of post-storm salvage-logging will likely also increase

(Lindenmayer and Noss 2006). Land managers should consider not only the short-term benefits of salvage logging, but also the long-term ecological effects on oak forest regeneration.

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VITA

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