RESEARCH ARTICLE

Temporal Patterns of Oak Mortality in a Southern Appalachian Forest (1991-2006)

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ABSTRACT: The sustainability of eastern oak-dominated forests is threatened by high oak mortality rates and widespread oak regeneration failure, and presents a challenge to natural area managers. We tracked the rate and cause of mortality of 287 mature oak trees of five species for 15 years to determine the temporal patterns and sources of mortality. We observed a 15.3% total mortality rate during the study period. Mortality was due to oak decline (7.3% of trees) and high-intensity wind events (6.6% of trees). Decline-related mortality was gradual, averaging 0.5% annually. Windthrow was episodic, occurring during hurricane-related weather events in 1995 and 2004. Within species, total mortality was disproportionately high for scarlet oak (*Quercus coccinea* Muenchh) (41.2%) compared to other species in the red oak group (13.8% for northern red oak (*Q. rubra* L.); 12.5% for black oak (*Q. velutina* Lam.)) or the white oak group (10.4% for white oak (*Q. alba* L.); 5.7% for chestnut oak (*Q. prinus* L.)). Decline-related mortality was highest for scarlet oak (15.7%) followed by black oak (8.3%), white oak (7.5%), northern red oak (6.9%), and chestnut oak (2.3%). Within the red oak group, the average age of decline-affected and surviving trees did not differ, but average dbh of decline-affected trees was smaller. Decline-affected trees in the white oak group were on average older, but average dbh did not differ from surviving trees. Wind-related mortality also was higher for scarlet oak (21.6%) than for northern red oak (5.2%), black oak (4.2%), white oak (3.0%) or chestnut oak (2.3%). Windthrown red oaks were smaller than survivors, but windthrown trees in the white oak group did not differ in size from survivors. Average age did not differ between windthrown and surviving trees for either group. Oak mortality rates observed in this study, coupled with oak regeneration failure, could result in a substantial reduction in the proportion of mature canopy oaks and change the relative abundance of oak species in southern Appalachian forests over the long-term.

Index terms: mortality patterns, oak decline, oak-dominated forest, oak mortality, windthrow

INTRODUCTION

Upland, mixed-oak (*Quercus* spp.) forests occupy over 50% of the forested land base in the Central Hardwood Region of the United States (Johnson et al. 2002), and oak trees play a critical role in forest ecology and economics of the region. Oak wood products include lumber, pallets, veneer, and pulp and paper (Patterson 2004) and are among the most economically valuable hardwood species (Guyette et al. 2004). Oak trees produce acorns that are a valuable food resource to many wildlife species (Martin et al. 1951) and influence the distribution, recruitment and survival, and behavior of wildlife ranging from migratory birds to black bear (*Ursus americanus*) (McShea and Healy 2002; Rodewald 2003; Clark 2004). Acorns are considered a 'keystone' to biological diversity because of their influence on populations of rodents that are an important prey base for raptors and carnivores, and on populations of white-tailed deer (Odocoileus virginianus) that in turn alter forest structure and composition through browsing (Feldhamer 2002).

Despite their ecological and economic importance, the sustainability of eastern oak-dominated forests is threatened by high mortality rates and widespread regeneration failure, especially on higher quality mesic sites (Loftis and McGee 1993; Dey 2002; Aldrich et al. 2005). Estimates of overall background tree mortality (single-tree death) in old eastern upland hardwood forest ranges from 5%-10% per decade (see Greenberg et al. 1997). Mortality in mature (60-80 year old) second-growth eastern hardwood forest is generally highest in suppressed or smaller, crowded canopy trees; annual mortality rates for larger canopy trees averages 0.5% or less (Lorimer 1989). These estimates of mortality rates were made based on all species within eastern upland hardwood forest. Increased mortality for oaks, especially the red oak group (subgenus *Erythrobalanus*), has been documented in recent decades (Heitzman 2003; Oak et al. 2004). This, coupled with failure to recruit oak seedlings into the forest canopy, could accelerate a shift in species composition away from oak in what is currently oak-dominated eastern upland hardwood forest (Heitzman 2003).

High rates of oak mortality are commonly attributed to "oak decline," a combination of stress factors. Inciting factors include low quality site conditions, drought, defoliating insects, frost, and stand disturbance. Predisposing factors include tree density, physiologic age, soil quality, and topography (Starkey et al. 2004). Contributing factors include pathogens such as the shoe string fungus (*Armillaria mellea*) or bark beetles (Oak et al. 1996) that cause progressive oak crown dieback and mortality (Oak et al. 2004). Oaks such as black oak (*Q. velutina* Lam.) and scarlet oak (*Quercus coccinea* Muenchh), growing on xeric, low quality sites, are especially susceptible to oak decline (Oak et al. 1996). The dominance of mature oaks, the prevalence of low quality sites, and other stress factors across much of the southern United States have caused large areas to be affected by oak decline (Heitzman et al. 2007) and others to remain vulnerable (Oak et al. 2004).

Wind disturbance is another important source of oak mortality in the southern Appalachians. Historical data tracing hurricane paths indicate that hurricane-related windstorms (64-97 km/hr) occur at 1-24 year intervals in the southern Appalachians, causing tree windthrows across 6.8% of the landscape over an estimated 200-year generation span of many eastern forest trees (Greenberg and McNab 1998). McNab et al. (2004) reported that large blowdowns (groups of > 10 windthrown trees; gaps ranging 0.1-3.9 ha) caused by Hurricane Opal in 1995 within the Bent Creek Experimental Forest (BCEF; our study area) were not randomly distributed across the landscape. Large blowdowns occurred at a higher density in watershed basins (1 per 39 ha) than in the surrounding highlands (> 700m elevation; 1 per 192 ha), and were more common on sites with a southeasterly aspect. Red oaks including scarlet, northern red (*Q. rubra* L.), and black oak were disproportionately susceptible to uprooting. Altogether, the basal area of *Quercus* was reduced by 41%-50%, and density (trees/ha) was decreased by 27%-47% within the gaps. In addition to these multiple-tree gaps, individual trees were also uprooted or broken at a high rate during high winds, and scarlet oak accounted for 58% of single windthrown trees (McNab and Greenberg, unpubl. data). Thus, wind-related mortality likely also contributes to an accelerated rate of loss of mature oaks relative to other tree species in the southern Appalachians.

We tracked the rate and cause of mortality of 287 mature, canopy oak trees of five species for 15 years (1991-2006). Our objective was to determine the temporal patterns and sources of mortality and to examine potential differences in mortality rates in relation to tree age, diameter at breast height (dbh), and species. We hypothesized that the sources and rates of mortality would differ between the red oak and white oak (subgenus *Leucobalanus*) groups and that red oak species would be more vulnerable than white oak species to decline- and wind-related mortality. Our study has important implications for the long-term sustainability of eastern oak-dominated ecosystems and natural area management.

METHODS

Study area

The Bent Creek Experimental Forest encompasses a 2500-ha watershed in western North Carolina. Annual precipitation averages 1200 mm and is evenly distributed year round (Owenby and Ezell 1992). Winters are short and mild; summers are long and warm. Elevation ranges from 650-1070 m. Common tree species include scarlet oak, chestnut oak (*Q. prinus* L.), black oak, blackgum (*Nyssa sylvatica* Marshall), sourwood (*Oxydendrum arboreum* (L.) DC), and occasional shortleaf pines (*Pinus echinata* Miller). Tulip poplar (*Liriodendron tulipifera* L.) and northern red oak dominate on moist slopes and coves. Red maple (*Acer rubrum* L.), hickory (*Carya* spp.), dogwood (*Cornus florida* L.,) and white oak (*Q. alba* L.) are common throughout (McNab 1996).

Data collection

We tracked the dates and causes of mortality for 287 mature oak trees of five species from 1991-2006 as part of an ongoing study of acorn production. Sample trees appeared to be healthy when the study was established in 1991. We measured dbh at study establishment and again during 2000 and 2006. Tree condition or mortality was recorded annually during fall acorn collections. We attributed mortality to oak decline if trees died standing; usually death followed years of crown dieback. Death due to uprooting or snapped-off tree boles was considered to be wind-related mortality.

Study species included northern red oak (n=58), scarlet oak (n=51), and black oak (n=24) in the red oak group, and chestnut (n=87) and white oak (n=67) in the white oak group. Study trees were scattered in seven general areas at elevations 650 to 1065 m above sea level throughout the BCEF watershed. Trees were selected randomly and represented a wide range of size classes (14-99 cm dbh at study establishment) and topographic conditions, including aspect, slope position, and percent slope. Most trees were mature and in dominant or codominant (a few were intermediate) crown positions. Trees < 60 years old were not included in our analyses. Although the study was established to quantify acorn production, these long-term data on multiple individual oak trees were also well suited to track temporal patterns of oak mortality.

Age

We took two cores per tree at breast height (if hand-bored) or waist height (if using an Atom Power Borer) during 1998 or 1999. One core was taken from dead trees. Tree cores were stored in labeled plastic straws, and later dried at 65 ºC for 24 hours, mounted on wooden core mounts, surfaced, crossdated, and aged (see Speer et al. 2009 for a detailed methodology). The establishment date was determined by increment core data obtained from the sample trees and defined as the date of innermost ring at breast height (1.37 m above the surface). Trees with severely rotted cores were not included in any of the age-related analyses. Details regarding age of sample trees by species are provided in Figure 1.

Statistical analysis

We used a chi-square analysis using Fisher's exact test for significance to assess differences among oak species in the

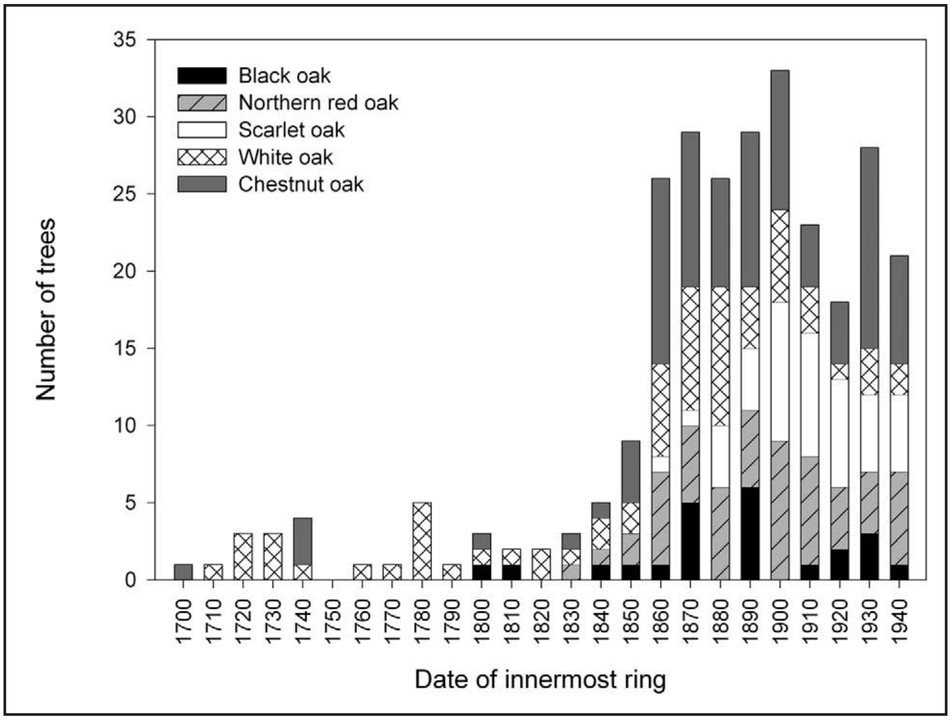

Figure 1. Number of sample trees in each 10-year establishment class. Establishment date was determined by increment core data obtained from the sample trees and defined as the date of innermost ring at breast height (1.37 m above the ground surface).

total proportion of sample trees dying and the proportion dying from decline-related causes or (separately) wind-related causes. We used t-tests to test for differences in dbh and age between the red and white oak subgenera by cause of mortality (oak decline or wind-related mortality). In instances where unequal variances occurred, we used the Satterthwaite method to estimate degrees of freedom. All analyses were performed using SAS/STAT® software, v. 9.1 and were considered significant if $\alpha < 0.05$.

RESULTS

We observed a 15.3% (44 of 287 sample trees) total mortality rate of our sample oak trees on the BCEF during the 15-year study period (Table 1). The chi-square analysis of total mortality (regardless of cause) by species was significant (chi-square, $p<0.0001$) indicating that mortality rate is not independent of species. Within species, total mortality was disproportionately high for scarlet oak (41.2%) compared to other species in the red oak group (13.8% for northern red oak; 12.5% for black oak) or the white oak group (10.4% for white oak; 5.7% for chestnut oak) (Table 1). Most mortality was attributed to oak decline (7.3%) and high-intensity wind (6.6%); the remaining 1.4% was due to lightning strikes or other unidentified occurrences (Table 1). Mortality due to oak decline was relatively gradual, averaging 0.5% annually. In contrast, mortality from windthrow was episodic, with 63% of windthrows occurring in October 1995 and another 37% during September 2004 due to high winds associated with hurricanes Ivan and Frances.

The chi-square analysis of decline-related mortality by species was marginally significant (chi-square, $p=0.0625$), suggesting that mortality rate from decline-related causes is not independent of species. The decline-related mortality rate for the red oak group ($n=133$) was more than double the white oak group ($n=154$) (10.5% versus 4.5%, respectively) over the 15-year study period. Within the red oak group, total decline-related mortality was highest for scarlet oak (15.7%), followed by northern red oak (6.9%) and black oak (8.3%). Within the white oak group, decline-related mortality for white oak was higher for white oak (7.5%) than for chestnut oak (2.3%).

We observed a strong relationship between species and the proportion of individuals affected by wind-related mortality (chi-square, $p<0.0001$). Wind-related mortality was also higher in the red oak group (11.3%) than in the white oak group (2.6%). Within the red oak group, scarlet oak incurred the highest wind-related mortality (21.6%), followed by northern red oak (5.2%) and black oak (4.2%). Wind-related mortality

Table 1. Total sample size and number and percent of mature oak trees experiencing decline- and wind-related mortality between 1991 and 2006 at the Bent Creek Experimental Forest, Asheville, NC.

		Cause of Mortality			
Species	Sample size	Decline	Windthrow	Other	Total
Red oak group					
Northern red oak	58	4 (6.9%)	3 (5.2%)	1 (1.7%)	8 (13.8%)
Scarlet oak	51	8 (15.7%)	11 (21.6%)	2 (3.9%)	21 (41.2%)
Black oak	24	2 (8.3%)	1 (4.2%)	0 (0%)	3 (12.5%)
Total	133	14 (10.5%)	15 (11.3%)	3 (2.3%)	32 (24.1%)
White oak group					
White oak	67	5 (7.5%)	2 (3%)	0 (0%)	7 (10.4%)
Chestnut oak	87	2 (2.3%)	2 (2.3%)	1 (1.1%)	5 (5.7%)
Total	154	7 (4.5%)	4 (2.6%)	1 (0.6%)	12 (7.8%)
Total oaks	287	21 (7.3%)	19 (6.6%)	4 (1.4%)	44 (15.3%)

was also relatively low for both white oak (3.0%) and chestnut oak (2.3%).

Tree age of windthrown trees averaged 102 years for the red oak group and 131 years for the white oak group, and mean age did not differ between live and dead trees in either group ($p > 0.05$) (Figure 2). Windthrown individuals were significantly smaller (45 cm dbh) than survivors (61 cm dbh) in the red oak group ($p=0.0017$), but average dbh did not differ between live (54 cm dbh) and windthrown (57 cm dbh) trees in the white oak group ($p=0.8164$) (Figure 3a).

Trees within the white oak group that died of decline-related causes were, on average, older (187 years) than live trees (138 years) ($p=0.0390$). In contrast, trees in the red oak group that died of decline-related causes were, on average, the same age as live trees (average of 108 years; $p=0.3384$). In the red oak group, the average dbh of survivors was 30% greater than the dbh of trees that died of decline-related causes ($p=0.0063$). In contrast, the dbh of trees in the white oak group did not differ between live trees and trees that died of decline-related causes ($p=0.0549$), and averaged 62 cm (Figure 3b).

DISCUSSION

Our study indicates that mature oak trees in the southern Appalachians are experiencing a high mortality rate that can be attributed to two major sources – gradual decline (7.3% of study trees) and windthrow, which is episodic but contributed to nearly half of total oak mortality during our 15-year study period (6.6% of trees). These two sources combined resulted in an annual oak mortality rate of 1%.

Death due to oak decline occurred over several years and resulted in a relatively constant "background" mortality rate averaging about 0.5% annually (for all oak species) during our study period (1991-2006). However, the decline-related mortality rate was more than twice as high in the red oak group as in the white oak group. Within the red oak group, scarlet oak experienced the highest percentage of decline-related mortality, followed by black and northern red oak. Within the white oak group, decline-related mortality was higher for white oak than for chestnut oak. Oak decline-associated mortality in our study area was mild compared to mortality rates in severely impacted areas of southeast Missouri and northern Arkansas, where the basal area and density of overstory red oak species were reduced by nearly 80% beginning around 1999 (Heitzman 2003). Other studies of oak decline in the Ozark Highlands of Missouri and northern Arkansas show that decline-related mortality rates of red oak species are four to six times higher than white oak species, and are likely exacerbated by red oak borer (*Enaphalodes Rufulus* (Haldeman)) (e.g., Heitzman 2003; Shifley et al. 2006). Clinton et al. (1993) reported that oak decline-related mortality, exacerbated by drought, affected 2% of the southern Appalachian mixed-oak forest area in the Coweeta basin in 1988. Most gaps were created by the death of large oaks, predominantly scarlet oak. Our study also indicates that the red oak group, particularly scarlet oak, is more susceptible to the combination of edaphic and biological factors contributing to crown dieback and eventual mortality.

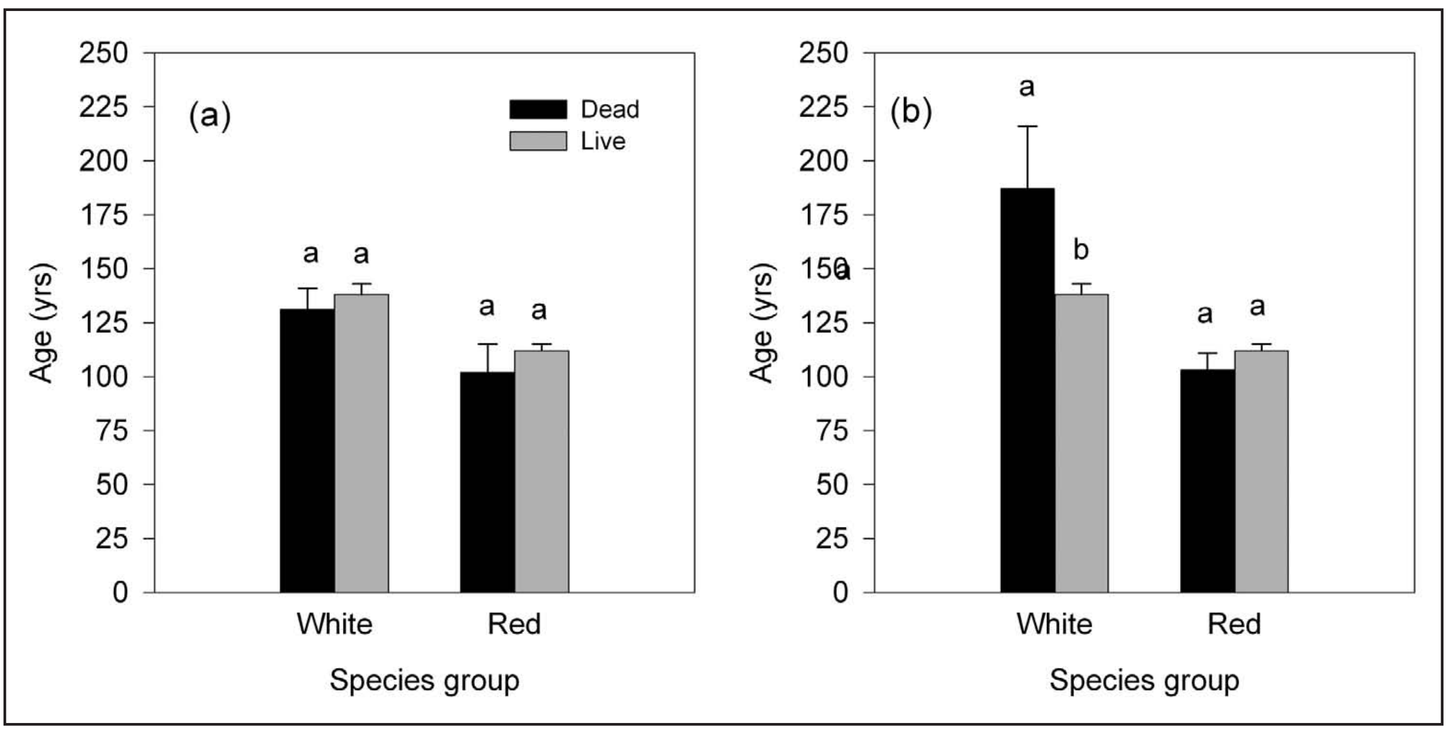

Figure 2. Mean age ±SE of live trees and trees affected by (a) wind–related mortality and (b) decline–related mortality in the red and white oak species groups at the Bent Creek Experimental Forest, Asheville, N.C. Means followed by the same letter within a species group are not significantly different.

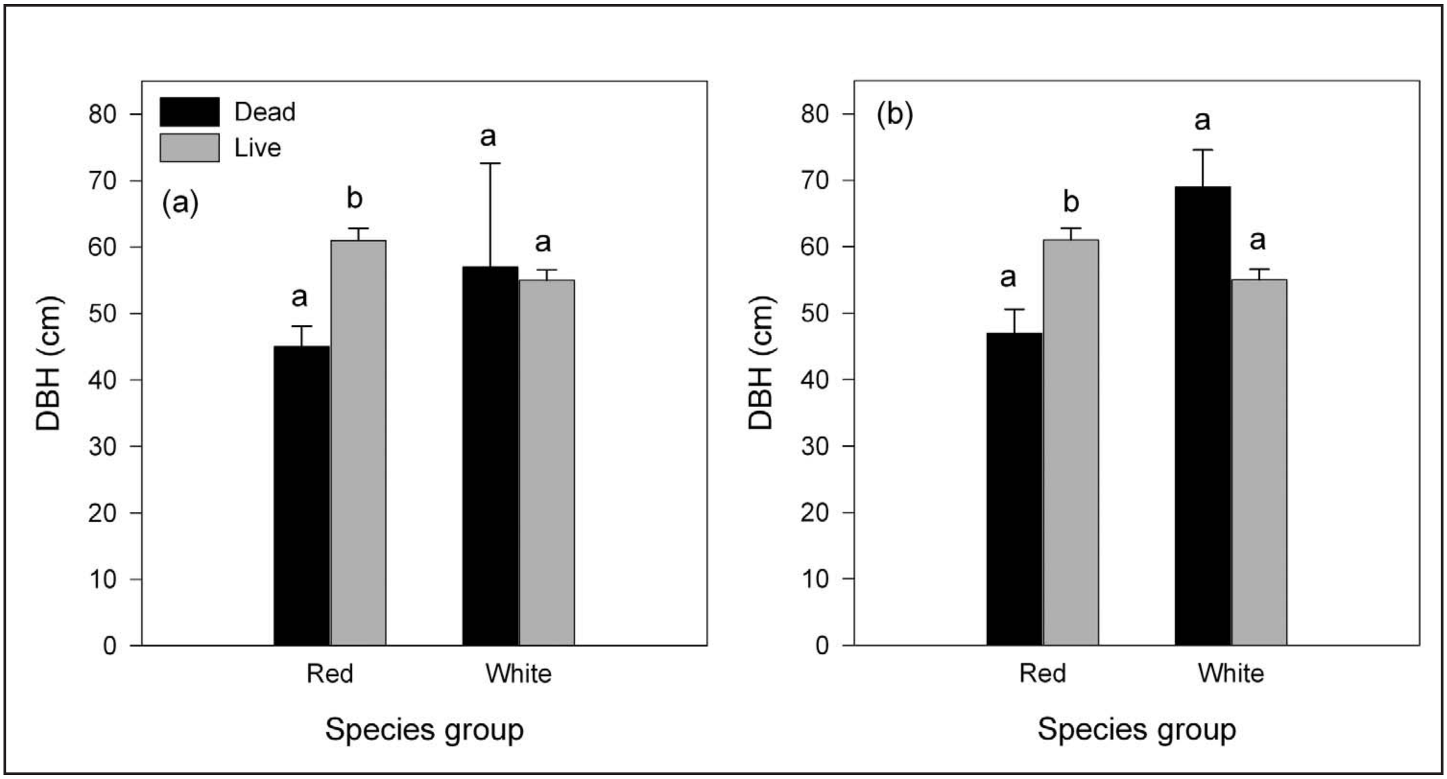

Figure 3. Mean diameter at breast height (dbh) (cm) ±SE of live trees and trees affected by (a) wind–related mortality and (b) decline–related mortality in the red and white oak species groups at the Bent Creek Experimental Forest, Asheville, N.C. Means followed by the same letter within a species group are not significantly different.

In contrast, oak mortality from windthrow occurred predominantly during two or three high wind events. High winds associated with Hurricane Opal in October 1995 resulted in the death of 63% of the windthrown sample trees: Hurricanes Ivan and Frances, both in September 2004, caused mortality of an additional 37% of the windthrown sample trees. Wind and high levels of precipitation associated with remnants of subtropical hurricanes affect forests of the southern Appalachian Mountains at approximately 1-24 year intervals (Boose et al. 1994; Greenberg and McNab 1998). These wind events resulted in pulses of mortality that added to an already high mortality rate from oak decline and senescence.

Oak trees in the red oak group were also more susceptible to windthrow than oaks in the white oak group. Within the red oak group, scarlet oak was disproportionately susceptible to windthrow, followed by black and northern red oak. In the white oak group, both chestnut and white oak were equally affected by wind-related mortality. Oak decline was not noted for most of the windthrown trees, but may have nonetheless predisposed them to uprooting during high wind events. Greenberg and McNab (1998) reported that the basal area of *Quercus* spp. was reduced by 41%-50%, and density decreased by 27%-47% in five large, incomplete gaps created by downbursts of wind during Hurricane Opal at the BCEF; red oaks (scarlet, black, and northern red oak) were disproportionately more susceptible to windthrow than white oaks.

Most oak trees within our sample were established in or after 1860 (< 146 years old). Only trees in the white oak group established before 1800 (one chestnut oak was established in 1700; one white oak was established in 1710); we had no trees in the red oak group established before 1800, suggesting that red oak species are shorter lived (Shifley et al. 2006). Among the red oak group, the oldest black oak was established in 1800 (206 years old); the oldest northern red oak was established in 1830 (176 years old), and the oldest scarlet oak was established in 1860 (146 years old).

In our study, the age of mature canopy oaks did not appear to affect mortality rates due to windthrow. Similarly, age was not a factor in decline-related mortality in the red oak group. Within the white oak group, however, a positive relationship between age and decline-related mortality was observed with decline-affected trees averaging 49 years older than survivors. Windthrown trees within the red oak group were, on average, smaller in diameter than their surviving counterparts. In contrast, the mean diameter of windthrown and surviving trees within the white oak group did not differ. Several studies report a positive relationship between dbh and susceptibility to uprooting of hardwood trees (e.g., Foster 1988; Gresham et al. 1991). Peterson and Pickett (1995) found intermediate dbh size classes to uproot. Greenberg and McNab (1998) reported that more large-diameter individuals were uprooted than smaller-diameter trees of many hardwood species. However, they found no relationship between dbh and windthrow of scarlet, black, and northern red oak, whereas more large-diameter white oaks and chestnut oaks were windthrown than their smaller-diameter counterparts (Greenberg and McNab 1998).

Within our study area, oaks compose approximately 26% of forest trees > 10 cm dbh, including 9.4% in the red oak group and 16.8% in the white oak group (McNab, unpubl. data). Our study focused on oaks, and did not include mortality rates for all forest tree species. However, Lorimer (1989) reported a 0.5% annual mortality rates for mature canopy trees (all species combined) in eastern upland hardwood forest. Our results indicate that in our study area, oak mortality is at least double the average turnover rate of mature forest trees (all species combined) in general (1% versus 0.5%, respectively) (Lorimer 1989). Because our study area is oak-dominated, this estimate is likely conservative (e.g., 1% mortality of oaks alone, which compose 26% of trees in the forest).

The disproportionately high mortality of red oaks, and scarlet oak in particular, suggests that oak mortality is not uniform across the southern Appalachian landscape but is greater on low quality sites such as xeric ridgetops and where scarlet oaks are also most abundant (Oak et al. 1996). Higher mortality in lower quality xeric sites could be offset by oak regeneration, which is more problematic on the higher quality mesic sites (Dey 2002). Oak mortality rates observed in this study, coupled with oak regeneration failure, could result in a substantial reduction in the proportion of mature canopy oaks and change the relative abundance of oak species in southern Appalachian forests over the long-term, and represents a challenge in sustainable management of oak-dominated natural areas.

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