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The role of environmental factors in oak decline and mortality in the Ozark Highlands

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Abstract

Oak decline is a chronic problem in Missouri Ozark forests. Red oak group species are most susceptible and decline is reportedly more severe on droughty, nutrient-poor sites. However, it was not clear whether greater decline severity was caused by poor site conditions or is simply due to the greater abundance of red oak group species found on poorer sites. We conducted this study to determine whether oak decline severity in oak-dominated Missouri Ozark forests is related to factors strongly influencing site quality including soil, landform position, and slope-aspect. We monitored the survival of 6606 dominant or co-dominant oak trees for 10 years and surveyed crown dieback on more than 1995 oak trees during a single year to determine if mortality and the presence of decline symptoms were related to site factors. Analysis confirmed that red oak group species had more crown dieback and greater mortality than did white oak group species. We also found greater red oak mortality on upper slope positions and where soils were gravelly and low in base cations. However, the abundance of red oaks was also greater in these same locations. Further analysis showed that if the initial abundance of red oaks was included as a covariate in the model, the site factors no longer were significant effects related to oak mortality. Moreover, we found that frequency of oaks exhibiting crown dieback was the same or sometimes greater on high quality sites. These findings show that red oak mortality is more prevalent on droughty and nutrient-deficient sites because red oak group species are more abundant there. Rather than simply predisposing oaks to decline, droughty and nutrient-deficient site conditions most likely favored the establishment and growth of red oaks following the extensive logging during the early 1900s. The extensive oak decline occurring on droughty and nutrient-deficient soils today appears to due to the high abundance of mature red oak group species on these sites.
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Keywords: Site factors; Oak decline; Oak mortality; Missouri Ozark forests

1. Introduction

Oak decline is the most widespread problem plaguing oaks (Starkey and Oak, 1989a). For more than a century, it has been observed periodically throughout North America and Europe wherever oaks are prominent. It develops when oaks are under physiologic stress and subsequently attacked by pathogens such as root diseases or insects (Kessler, 1989; Starkey et al., 1989; Jung et al., 2000). Drought is most commonly cited as the stress that triggers decline episodes, however, injuries caused by frost, ice, or wind and insect defoliation can also cause decline (Kessler, 1989; Starkey et al., 1989; Rosson, 2004).

Since the 1970s, oak decline has been a chronic problem throughout the Missouri Ozarks (Law and Gott, 1987). Widespread episodes of decline generally have followed periods of drought. Red oak group species (*Quercus* section *Lobatae*) have been particularly susceptible, especially those that are physiologically mature growing on droughty, nutrient-poor sites such as on ridges or south-facing slopes and on soils that are shallow or rocky (Starkey and Oak, 1989a). High mortality of red oak group species in Missouri Ozark forests has been associated with Armillaria root disease (Bruhn et al., 2000).

Kabrick et al. (2004a) found that the mortality rate for mature canopy dominant and co-dominant red oak group species to be about 10 times greater than for canopy dominant and co-dominant white oak group species in Missouri Ozark forests. Moreover, cumulative red oak mortality was greater on upper slope positions than on lower slopes and upland waterways (Kabrick et al., 2004b). However, red oaks were

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also more abundant on upper slopes so it was not clear whether greater decline severity was caused by poor site conditions or simply was due to the greater abundance of red oak group species found on poorer sites. These findings have important implications for determining whether site variables are important for inclusion in models that forecast where oak decline events will occur and for prioritizing where management for mitigating oak decline should be done.

We conducted this study to determine whether oak decline severity is related to site conditions and if there was proportionally greater oak mortality on poorer sites. The objectives were to evaluate the incidence of oak crown dieback and mortality in relation to the key site factors of soil, landform position, and aspect, to determine their role in perpetuating oak decline.

2. Methods

We used data from the Missouri Ozark Forest Ecosystem Project (MOFEP). MOFEP is a long-term study to quantify the effects of forest management on upland oak systems (Brookshire and Shifley, 1997; Shifley and Brookshire, 2000; Shifley and Kabrick, 2002). The study consists of nine sites ranging in size from 314 to 516 ha, primarily within the Current River Oak Forest Breaks and the Current River Oak-Pine Woodland Hills landtype associations of the Ozark Highlands (Nigh and Schroder, 2002). The Current River Oak Forest Breaks has narrow ridges and steep sideslopes with relief of 90–140 m, which exposes three sedimentary bedrock formations: Roubidoux and Gasconade (both Ordivician age), and Eminence (Cambrian age). The Current River Oak-Pine Hills has broad ridges with relief <90 m and exposes only the Roubidoux and Gasconade bedrock formations. The underlying bedrock strongly influenced the physical and chemical properties of the soils. Soils derived from parent materials of the Roubidoux formation and the upper portion of the Gasconade formation comprise highly weathered and very gravelly pedisediments and primarily are classified Ultisols (Typic Paleudults and Typic Hapludults). Soils derived from parent materials of the lower portion of the Gasconade formation and from the Eminence formation comprise gravelly pedisediments overlying gravel-free clayey pedisediments and residuum and primarily are classified Alfisols (Typic Paleudalfs and Typic Hapludalfs). Soils in upland waterways formed in gravelly alluvium derived from the underlying bedrock formations and adjacent soils and are primarily classified Entisols (Mollic Udifluvents) or Alfisols (Mollic Hapludalfs) (Meinert et al., 1997; Kabrick et al., 2000).

There are 648 permanent 0.2-ha vegetation plots distributed roughly equally among the nine MOFEP sites. Since 1992, these permanent plots have been re-inventoried approximately every three years to document the condition of woody vegetation (Jensen, 2000). Characteristics recorded for each tree include species, diameter at breast height (dbh), or size class for trees <4 cm dbh, and status (e.g., live, dead, den, cut, blow-down), and crown class (e.g., dominant, co-dominant, intermediate, suppressed). Trees >11 cm dbh are tagged so their growth can be monitored. Site index was determined in 1995 using one to five suitable co-dominant or dominant trees located outside of but adjacent to each of the permanent vegetation plots. Site index was estimated for each species using height, age at dbh, and published site index equations for the Missouri Ozarks (Nash, 1963; McQuilkin, 1974).

Data from permanent vegetation plots showed that when the study was initiated, the forests were second growth and fully stocked (*sensu* Gingrich, 1967) and that 68% of the canopy dominant and co-dominant trees were 45–65 years old. Oaks were the dominant trees and four oak species, white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), and post oak (*Q. stellata* Wangenh.) comprised 71% of the basal area (Kabrick et al., 2004b). Other oaks found at MOFEP included chinkapin oak (*Q. muehlenbergii* Engelm.), blackjack oak (*Q. marilandica* Muench.), Shumard oak (*Q. shumardii* Buckl.), and northern red oak (*Q. rubra* L.), but in combination they comprised only 1% of the basal area. Shortleaf pine (*Pinus echinata* Mill.) (8%), pignut hickory [*Carya glabra* (Mill.) Sweet] (4%), black hickory (*C. texana* Buckl.) (4%), mockernut hickory (*C. tomentosa* Poir. Nutt.) (4%), flowering dogwood (*Cornus florida* L.) (3%), and blackgum (*Nyssa sylvatica* Marsh.) (2%) also were in the study area.

For this study we selected a subset of 205 of the 648 permanent vegetation plots that were internally uniform with respect to site factors of interest and had not received harvest treatments during the course of MOFEP and for more than 40 years prior to its initiation in 1990. We limited our analyses to canopy dominant and co-dominant white oak group species (white oak and post oak) and red oak group species (scarlet oak and black oak) $\geq$11 cm dbh during the initial inventory completed in 1992 (n = 6606 trees). To determine mortality for each species group, we calculated the basal area (per hectare basis) that died between the end of the first inventory completed in 1992 and the last inventory completed in 2002. To estimate crown dieback, we surveyed a random selection of one to five canopy dominant or co-dominant trees each from the red oak and white oak groups in the two hundred and five 0.2-ha plots (n = 1995 trees) in 2002 when the incidence of oak decline was particularly acute. For each tree, crown dieback was estimated by class (none = less than 5%; slight = 5–33%; moderate = 34–66%; severe > 66%).

Site factors were derived from a detailed landscape-scale soil mapping project conducted on MOFEP in 1994–1995 (Meinert et al., 1997; Kabrick et al., 2000). This included characterizing geomorphology, geology, and soil characteristics of each permanent MOFEP vegetation plot. Laboratory data generated from 117 soil excavations were correlated to the soil mapping units. Detailed information about the soil mapping and soil characterization can be found in Meinert et al. (1997) and Kabrick et al. (2000). From the subset of MOFEP plots that we selected, we organized the site information so that we could examine the effects of landforms, soils, and slope-aspect on the abundance, cumulative mortality, and crown dieback of oaks.

The landforms that we examined included upland waterways, backslopes, benches, shoulder slopes and summits

Table 1
Landforms included in the study

Landform	Description
Backslope	The landscape position that forms the steepest inclined surface and principle element of many hillslopes. Slopes > 20%. Contains sideslope, noseslope and headslope components
Bench	A narrow, nearly level to slightly sloping platform breaking the slope continuity. Typically occurs on backslope positions in the Ozarks where underlying bedrock is more resistant to weathering than layers above or below. Slopes 0–20%
Shoulder	The landscape position that forms the upper most inclined surface near the top of a hillslope. It is commonly convex in shape and comprises the transition from summit to backslope. Slopes 8–20%
Summit	The topographically highest hillslope position of a hillslope profile and exhibiting a nearly level surface. Slopes 0–8%
Upland waterway	The land bordering small-order streams that is subject to inundation under floodstage conditions. Slopes 0–4%

(Table 1). We examined landforms because they control the movement of water across the landscape surface as well as within the soil, potentially affecting water supply. Slope-aspect classes include protected (slopes > 20% and azimuths of 316–135°) and exposed (slopes > 20% and azimuths of 136–315°). Slope-aspect strongly influences evaporative demand and is thereby an important consideration for evaluating moisture stress. We allocated the soils into seven soil groups representing distinctly different combinations of physical and chemical properties, parent materials, underlying bedrock formation, and/or taxonomic classifications reflecting different capacities to supply water, base cations, or both (Tables 2 and 3).

We examined the initial abundance and cumulative mortality (occurring over a 10-year period) of the two oak species groups among landforms, soil groups, and by slope-aspect class with analysis of variance using the general linear models procedure (SAS version 9.1, SAS Institute, Inc., Cary, NC, USA). Because some soil groups occur on a single landform (e.g., soil groups 1 and 2 occur exclusively on upland waterways, group 6 occur only on benches), we examined the effects of soil groups separately within three landforms: (1) upland waterways, (2) backslopes and shoulders, and (3) benches. For significant effects ($\alpha = 0.05$), we conducted Tukey's multiple comparison test (Steel et al., 1997).

To examine the relationship between the frequency of trees in crown dieback classes and environmental variables, we constructed contingency tables. For these contingency tables, we created two broad crown dieback classes by combining the ''none'' and ''slight'' crown dieback classes and the ''moderate'' and ''severe'' crown dieback classes. We used a Chi-square test (frequency procedure, SAS version 9.1, SAS Institute, Inc., Cary, NC, USA) to determine if the proportion of trees in these general crown dieback classes differed significantly ($\alpha = 0.05$) from the expected proportion among landforms, soil groups, or slope-aspect classes. As with the abundance and cumulative mortality analyses, the effects of soil

Table 2
Characteristics of the seven soil groups examined in the study

Soil group	Landform	Underlying bedrock formation[a]	Parent material[b,c]	Common soil classification (associated series)[b]
1	Upland waterways	Eminence	Alluvium	Loamy-skeletal, siliceous, superactive, nonacid, mesic Typic Udifluvents (Midco)
2	Upland waterways	Roubidoux, Gasconade	Alluvium	Sandy-skeletal, siliceous, mesic Mollic Udifluvents (Relfe)
3	Backlsopes, shoulders	Eminence	Pedisediments over residuum	Loamy-skeletal, mixed, superactive, mesic Lithic Hapludolls (Moko)
4	Backslopes, shoulders	Gasconade, Eminence	Pedisediments over residuum	Very-fine, mixed, active, mesic Mollic Hapludalfs (Arkana); loamy-skeletal over clayey, siliceous, semiactive, mesic Typic Paleudalfs (Alred)
5	Backslopes, benches, shoulders	Gasconade, Eminence	Pedisediments over residuum	Loamy-skeletal over clayey, siliceous, semiactive, mesic Typic Paleudalfs (Alred); loamy-skeletal, siliceous, active, mesic Typic Paleudalfs (Rueter)
6	Benches	Gasconade	Pedisediments	Loamy-skeletal, siliceous, active, mesic Typic Hapludults (Bendavis); fine-loamy, siliceous, active, mesic Oxyaquic Fragiudalfs (Viraton)
7	Backslopes, shoulders, summits	Roubidoux, Gasconade	Pedisediments	Loamy-skeletal, siliceous, semiactive, mesic Typic Paleudults (Clarksville); loamy-skeletal over clayey, siliceous, semiactive, mesic Typic Paleudults (Poynor)

Each group comprises distinct combinations of soils that developed on different landforms in parent materials derived from the underlying bedrock formations.
[a] Formations: Eminence (Cambrian-aged dolomite); Gasconade (Ordovician-aged dolomite with sandstone and chert beds); Roubidoux (Ordovician-aged dolomite and sandstone).
[b] Determined from soil borings made in the center of 0.2-ha vegetation plots.
[c] Here alluvium comprises sediments from the surrounding uplands deposited by water; residuum includes clayey sediments weathered from underlying dolomite; pedisediments comprise highly weathered colluvium and other sediments transported and deposited by water and gravity.

Table 3
Profile properties of the seven soil groups

Soil group	A-Horizon: Thickness (cm), mean ± standard deviation	A-Horizon: Model texture	Subsoil horizons: Thickness (cm), mean ± standard deviation	Subsoil horizons: Model texture[a]	Depth to bedrock[b] (cm), mean ± standard deviation	Percent rock outcrop[c]	Percent soil borings with fragipans[b]	Available water holding capacity[d] (cm), mean ± standard deviation	Percent base saturation at diagnostic depth[e], mean ± standard deviation
1	28 ± 10	Very gravelly silt loam	85 ± 16	Gravelly loamy sand	>120	None	None	8 ± 3	45 ± 19
2	18 ± 4	Very cobbly loam	104 ± 4	Very cobbly sandy loam	>120	None	None	7 ± 3	35 ± 22
3	15 ± 6	Very cobbly silt loam	15 ± 16	Clay	30 ± 15	>50	None	2 ± 2	No data collected
4	12 ± 4	Very gravelly silt loam	80 ± 36	Clay	98 ± 34	10–50	None	11 ± 6	60 ± 15
5	13 ± 4	Very gravelly silt loam	92 ± 32	Clay	>120	None	None	13 ± 4	43 ± 20
6	15 ± 2	Very gravelly silt loam	73 ± 33	Very gravelly silty clay loam	90 ± 30	None	33	12 ± 6	32 ± 15
7	13 ± 4	Very gravelly silt loam	83 ± 30	Very gravelly silt loam	106 ± 23	None	1	10 ± 4	25 ± 15

[a] Texture determine in the lower portion of the profile.
[b] Determined from soil borings made to a maximum depth of 120 cm in the center of 0.2-ha vegetation plots.
[c] Determined throughout 0.2-ha vegetation plots.
[d] Estimated in the center of 0.2-ha vegetation plots to a depth up to 120 cm by summing the available water holding capacity by horizon based on texture (subtracting gravel and cobbles) using the following water holding estimates (cm water per cm soil): silt loam, loam, silty clay loam, silty clay loam, silty clay, and clay = 0.16; sandy loam = 0.12; loamy sand = 0.05; sand = 0.02.
[e] Derived from soil horizon samples collected in four or more soil excavations in each group. Diagnostic depth is that used in Soil Taxonomy to distinguish Alfisols from Ultisols (Soil Survey Staff, 1999).

Table 4
Initial stand density and density of trees that died during the 10-year monitoring period

	Stems ha^{-1}		Basal area ($m^2\ ha^{-1}$)	
	Initial density	Mortality	Initial density	Mortality
Red oaks	105	14.9	8.2	1.4
White oaks	49.2	1.1	3.4	0.1

Data are for canopy dominant and co-dominant trees. The red oak group comprises scarlet oaks (*Quercus coccinea* Muenchh.) and black oaks (*Q. velutina* Lam.); the white oak group comprises white oaks (*Q. alba* L.) and post oaks (*Q. stellata* Wangenh.).

groups were examined separately within upland waterways, backslopes and shoulders, and benches.

3. Results

Red oaks were much more abundant at the study sites than were white oaks, having stem densities and basal areas more than two times greater than for white oaks (Table 4). We also found that mortality differed between species groups. Ten years after our study was initiated, red oak mortality was more than 10 times greater than for white oaks. Red oaks also exhibited more crown dieback than did white oaks (Fig. 1).

The distribution of oaks was related to many of the site factors that we investigated (Figs. 2 and 3). Red oak basal area differed significantly among landforms ($P < 0.01$) and was greater on summits and shoulders than on backslopes and upland waterways. Within backslope and shoulder positions, red oak basal area differed significantly ($P < 0.01$) among soil groups and was two to three times greater on soils that were gravelly and low in base cation saturation (Ultisols) than on other soils. Red oaks also were slightly more abundant ($P = 0.02$) on protected aspect classes. White oaks were more evenly distributed with respect to landforms and slope-aspects, although they were slightly more abundant ($P = 0.01$) on deep soils (>1.2 m) having moderate base saturation (Alfisols) and high water holding capacity (soil group 5) on backslopes and shoulders.

Cumulative oak mortality occurring during the 10-year duration of our study was related to the site factors we investigated, particularly for red oaks (Figs. 2 and 3). Red oak

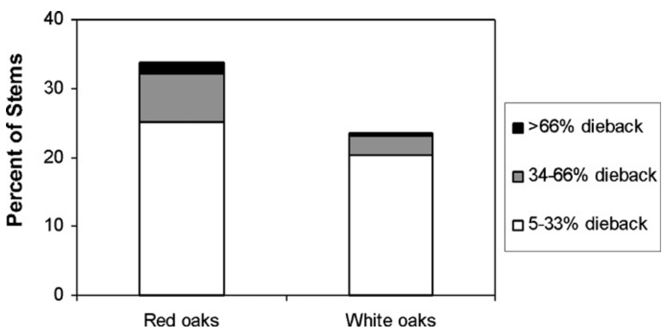

Fig. 1. Proportion of canopy dominant or co-dominant red oaks and white oaks by crown dieback classes. The red oak group comprises scarlet oaks (*Quercus coccinea* Muenchh.) and black oaks (*Q. velutina* Lam.); the white oak group comprises white oaks (*Q. alba* L.) and post oaks (*Q. stellata* Wangenh.).

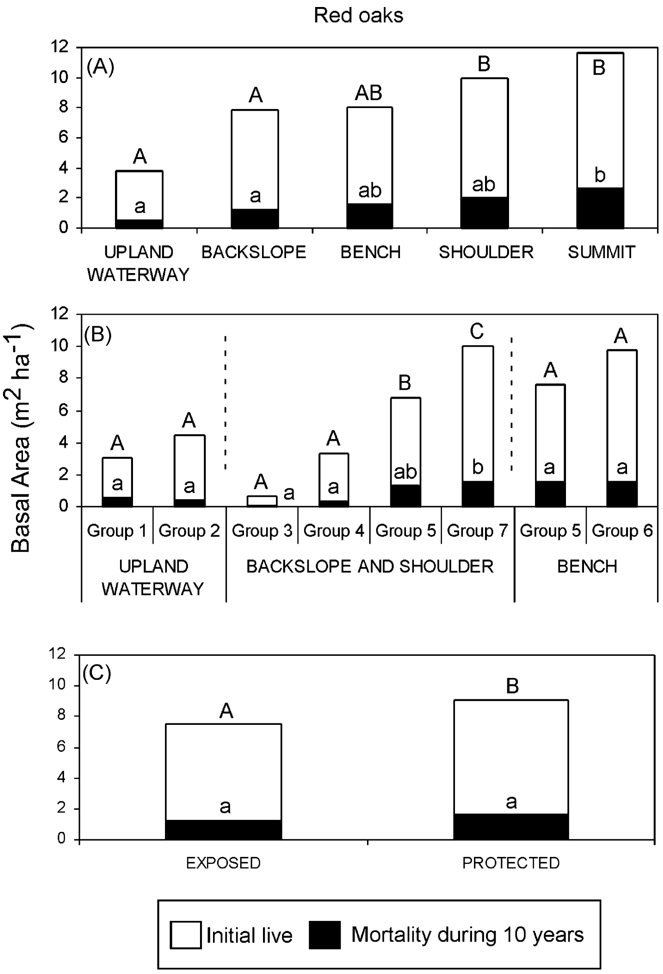

Fig. 2. Initial basal area and cumulative mortality during the subsequent 10-year period for red oaks by (A) landform, (B) soil group within landform, and (C) aspect class. The red oak group comprises scarlet oaks (*Quercus coccinea* Muenchh.) and black oaks (*Q. velutina* Lam.). Data include canopy dominant or co-dominant trees >11 cm dbh. Different uppercase letters indicate significant differences in initial basal area and different lowercase letters indicate significant differences in cumulative mortality. Soil groups within landforms were analyzed separately.

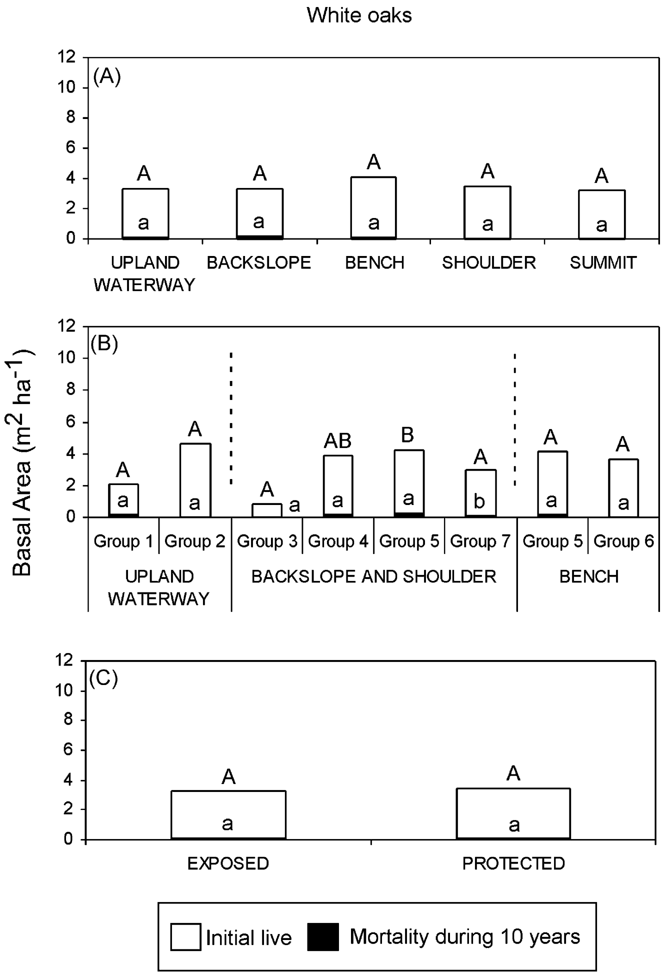

Fig. 3. Initial basal area and cumulative mortality during the subsequent 10-year period for the white oak group by (A) landform, (B) soil group within landform, and (C) aspect class. The white oak group comprises white oaks (*Q. alba* L.) and post oaks (*Q. stellata* Wangenh.). Data include canopy dominant or co-dominant trees >11 cm dbh. Different uppercase letters indicate significant differences in initial basal area and different lowercase letters indicate significant differences in cumulative mortality. Soil groups within landforms were analyzed separately.

mortality increased gradually from a minimum in upland waterways to a maximum on summits ($P < 0.01$). Within backslopes and shoulders, red oak mortality was greater ($P < 0.01$) on soils that were gravelly and low in base cation saturation (Ultisols) than on other soils. Much like with its abundance, white oak mortality was neither related to landform nor very closely correlated to soil groups within them. For both species groups, we found no significant mortality differences related to slope-aspect.

Because of the apparent correlation between mortality and initial live basal area for red oaks, we also examined the effects of site factors with and without the initial live basal area as a model covariate. We found initial live basal area to be a highly significant covariate that, when included in the analysis, caused none of the site factors to appear as significant effects (Table 5). We also examined mortality as a proportion of the initial live basal area (without covariates) and found similar results (data not shown).

The proportion of red oaks exhibiting crown dieback was related to site factors (Figs. 4 and 5) but our findings differed from our expectations. We observed that a greater proportion ($P = 0.04$) of dominant and co-dominant red oaks exhibited crown dieback in alluvial soils on upland waterways, particularly where the alluvium was cobbly and lower in base cations ($P = 0.03$; soil group 2). We expected proportionally more crown dieback on more stressful sites such as those with gravelly soils and low base cations (Ultisols) or on summits and shoulders. The frequency of white oak crown dieback was not particularly related to environmental variables except that within bench landforms, we did find a slightly greater frequency of moderate crown dieback on soils having fragipans ($P = 0.03$; soil group 6).

4. Discussion

Much has been written about the multiple factors contributing to physiologic stress of oaks that eventually leads

Table 5
Analysis of variance significance values for effects of site factors on red oak group mortality with and without the initial basal area included as a covariate

Effect	d.f.	*P*-value	
		Without basal area as covariate	With basal area as covariate
Initial basal area ($m^2\ ha^{-1}$)	1	–	**<0.01**
Landform	4	**<0.01**	0.17
Nested soil groups			
Groups 1 and 2 on upland waterways	1	0.79	0.16
Groups 3, 4, 5, and 7 on backslopes and shoulders	3	**<0.01**	0.52
Groups 5 and 6 on benches	1	0.99	0.40
Aspect class	1	0.25	0.85

The site factors of landform and soil groups with backslopes and shoulders are significant effects unless the initial basal area of live red oaks are is accounted for in the analysis. Red oaks include black oak (*Quercus velutina* Lam.) and scarlet oak (*Q. coccinea* Muenchh.). Soil groups are defined in Tables 2 and 3. Significant *P*-values are shown in bold.

to the disease complex described as oak decline (Kessler, 1989; Millers et al., 1989; Starkey et al., 1989). Throughout eastern and southern North America and particularly in the Ozark Highlands, drought principally has been identified as the most important inciting factors triggering episodes of decline (Law and Gott, 1987; Starkey et al., 1989; Stringer et al., 1989). Stressful site conditions, including shallow, rocky soils, particularly those of ridges or south-facing slopes, are often identified as the most important factors predisposing oaks to the onset of decline, particularly those of the red oak group

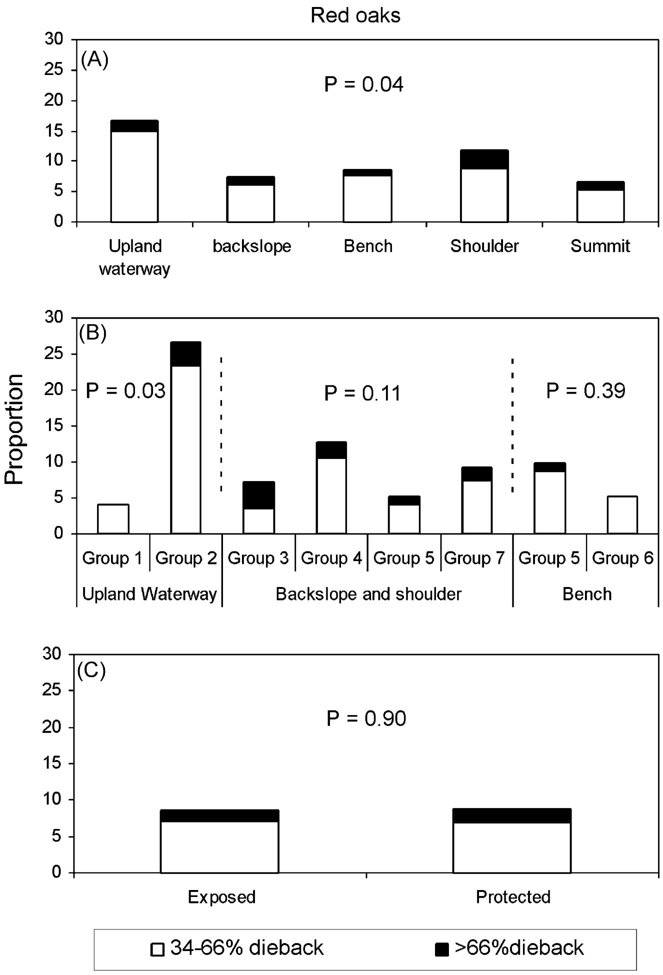

Fig. 4. Proportion of dominant or co-dominant red oaks by moderate (34–66% dieback) and severe (>66% dieback) crown dieback classes by (A) landform, (B) soil group within landform, and (C) aspect class. The red oak group comprises scarlet oaks (*Quercus coccinea* Muenchh.) and black oaks (*Q. velutina* Lam.). Values for soil groups within landforms were calculated separately. *P*-values are from Chi-square analyses examining whether crown dieback was related to landforms, soil groups within landforms, or slope-aspects classes.

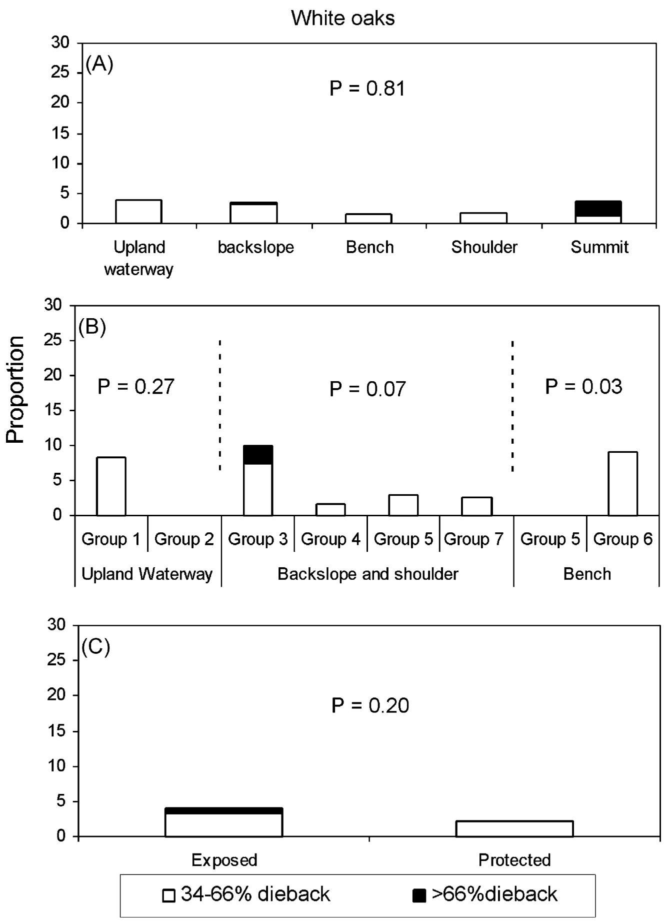

Fig. 5. Proportion of dominant or co-dominant white oaks by moderate (34–66% dieback) and severe (>66% dieback) crown dieback classes by (A) landform, (B) soil group within landform, and (C) aspect class. The white oak group comprises white oaks (*Q. alba* L.) and post oaks (*Q. stellata* Wangenh.). Values for soil groups within landforms were calculated separately. *P*-values are from Chi-square analyses examining whether crown dieback was related to landforms, soil groups within landforms, or slope-aspects classes.

(Starkey and Oak, 1989b). Throughout the Ozark Highlands, decline and widespread mortality are reportedly more prevalent and severe on ridges, south-facing slopes, particularly where soils are rocky (Law and Gott, 1987; Lawrence et al., 2002).

Much like other studies have reported (Starkey and Oak, 1989a,b; Heitzman and Guldin, 2004; Oak et al., 2004; Rosson, 2004), we found that red oaks were more likely to exhibit decline symptoms such as crown dieback than white oaks. Moreover, we also found that the cumulative mortality of red oaks during a 10-year period was significantly greater on a per hectare basis on upper slope positions or on soils that were droughty and deficient in base cations. However, our study also showed that red oaks were more abundant on drought-prone and nutrient-deficient sites. When we accounted for the abundance differences of the red oaks by including their initial basal areas as covariates in our analyses, or by examining the relative mortality rate, we found that the site factors were no longer significant effects, thus suggesting that the relative mortality rate of red oaks was approximately the same regardless of site conditions. Shifley et al. (2006) also found that the red oak mortality rate was not closely related to variables that are surrogates for site condition throughout the Missouri Ozarks. Stringer et al. (1989) found no relationship between site water availability classes and the proportion of red oak mortality in Eastern Kentucky. In fact, our data suggest that the proportion of oaks exhibiting moderate to severe crown dieback was greater on alluvial soils in upland waterways where the capacity to supply water and nutrient was greater. Although our findings demonstrate that cumulative oak decline and mortality is greater on droughty, nutrient-deficient sites, they also cast some doubt on the belief that poor site conditions predispose red oaks to decline or accelerate oak mortality in the Ozark Highlands.

Despite finding that poor site conditions do not appear to accelerate oak decline and mortality, we do think that environmental variables have played a prominent but indirect role in the oak decline episodes across the Ozark Highlands. Rather than simply predisposing oaks to decline, droughty and nutrient-deficient site conditions most likely favored the establishment and growth of scarlet oak and black oak (the two dominant red oak group species in our study) following the extensive logging, grazing and burning era in the early 1900s (Cunningham and Hauser, 1989). After logging, European-American settlers burned much of the cutover forest land, attempting to use the native grasses, forbs, and woody sprouts and regrowth as forage for free-ranging cattle, hogs, and other livestock (Cunningham and Hauser, 1989). Where the soil was infertile and too droughty for grazing or other agricultural practices, the land was eventually abandoned, allowing forests to naturally return.

Scarlet oak and black oak have an ecological advantage on the poorer sites because these two oak species are capable of maintaining rapid growth on dry or nutrient-deficient sites allowing them to outgrow competing species such as white oaks, post oaks, and other hardwoods native to the region (Burns and Honkala, 1990). Shortleaf pine was one of the few native tree species that originally was dominant on these dry and nutrient-deficient sites that likely could have competed with black oak and scarlet oak had adequate reproduction been present. However, the frequent fire regime of the post-logging era (Cunningham and Hauser, 1989) favored the accumulation of oak reproduction because oaks have a greater ability to re-sprout when repeatedly top killed than shortleaf pine reproduction (Guyette and Dey, 1997). Thus annual surface fires have the potential to eliminate shortleaf pine reproduction much more quickly than oak reproduction (Dey and Hartman, 2005). Even some of the early forest surveys indicated that frequent burning favored oaks and other hardwoods as Record (1910) reported that annual fires eliminated pine from the understory of mature pine stands and encouraged an undergrowth of oaks and other hardwoods in the Shortleaf Pine Region of Missouri.

Both black oaks and scarlet oaks are also short-lived compared to other oaks (Burns and Honkala, 1990; Hicks, 1998). As these even-aged stands of black oak and scarlet oak have matured, they have become increasingly vulnerable to environmental stress caused by drought. Reports of extensive decline generally occurred within a few years following occurrences of widespread drought which occur regularly in the Ozark Highlands (Law and Gott, 1987; Lawrence et al., 2002; Rosson, 2004). In this region, severe droughts were recorded during the mid 1950s, early 1980s, and late 1990s (Lawrence et al., 2002).

Armillaria root disease has undoubtedly hastened the mortality of red oak group species (Bruhn et al., 2000) and is largely considered to be a prominent contributing factor associated with oak decline in Missouri Ozark forests (Johnson and Law, 1989). Bruhn et al. (2000) reported that three species of Amillaria (*Armillaria mellea*, *A. gallica*, and *A. tebescens*) are widespread in the study region. The presence of *A. mellea*, a reportedly pathogenic species (Guillaumin et al., 1993) that is considered particularly virulent, was highly correlated to the abundance of black oaks and scarlet oaks regardless of soil and other site factors (Bruhn et al., 2000). The presence of *A. mellea* was also highly correlated to tree mortality in our study region (Bruhn et al., 2000). Because Armillaria root disease is so widespread in the study area, its presence may be masking any benefits of increased water and nutrient supply differences on some of the better sites that we have investigated.

The red oak borer (*Eenaphalodes rufulus* (Haldeman) Coleoptera: Cerambycidae) has often been associated with oak decline (Starkey and Oak, 1989a) particularly recently in the Ozark Highlands (Oak et al., 2004; Starkey et al., 2004). In our study sites, Jensen et al. (2004) reported that 77% of the red oak group species and 33% of the white oak group species had some evidence of borer activity on the 2.4-m butt log including the presence of exit holes, bark scars, and sap stains. However, most of the borer activity was found on oaks that were under stress associated with competition for growing space as 54% of oaks with suppressed or intermediate crowns exhibited more than 10 signs of borer activity on the butt log compared to only 9% of canopy dominants (Jensen et al., 2004). Despite the degradation in timber quality from the galleries that red oak borers excavate in the boles of oaks, rarely do they directly cause tree mortality (Solomon, 1995).

There may be physiological explanations for why site factors do not appear to accelerate the proportion of cumulative oak mortality. Moderate water deficits generally elicit a greater root:shoot ratio in woody plants (Kozlowski and Pallardy, 1997). The relatively large root systems that develop on poorer sites better enable nutrient and water absorption (Oliver and Larson, 1996). Jenkins and Pallardy (1995) suggested that this mechanism may enable oaks on the poorer sites to withstand the deleterious effects of extreme drought as well or better than those on higher quality sites. A similar mechanism has been suggested for explaining why oaks growing on low site index sites often better withstand gypsy moth defoliation events in the eastern U.S. (see review by Davidson et al., 1999). This same mechanism may partially explain why the mortality rate of red oaks in the Ozark Highlands is about the same regardless of local site conditions and why red oaks in upland waterways generally exhibited greater crown dieback than on other landforms.

Regardless of the causal mechanisms, our findings suggest that forest managers should not assume that individual red oaks growing on poor sites are more vulnerable to oak decline than those on high quality sites. Conversely, they should not assume that red oaks on high quality sites are at lower risk. Shifley et al. (2006) showed that risk factors most useful for predicting stand-level oak mortality throughout the Missouri Ozark Highlands were generally related to the species of oaks in the stand as well as to the crown class, and size (diameter) of individual oaks; dominant and co-dominant black oaks and scarlet oaks larger than 25 cm dbh have a 10-fold greater mortality rate than do their cohorts of the white oak group or shortleaf pine. Heitzman and Guldin (2004) also showed that red oak mortality was highly correlated to the red oak abundance elsewhere in the Ozark Highlands. Collectively, these and our findings suggest that high risk stands are those where mature red oaks are most abundant regardless of site conditions. This also suggests that inclusion of environmental or site variables in addition to composition and abundance variables may offer little improvement in models used for forecasting oak decline events. Nonetheless, environmental and site variables do appear useful for identifying where red oaks are likely to be more abundant across the present-day landscape and consequently where to anticipate higher stand-level mortality due to the abundances of mature black oaks and scarlet oaks.

5. Conclusion

Red oaks were more likely to exhibit decline symptoms such as crown dieback than white oaks and the cumulative mortality of red oaks during a 10-year period was significantly greater on a per hectare basis on upper slope positions or on soils that were droughty and deficient in base cations. However, red oaks were more abundant on drought-prone and nutrient-deficient sites and, when this was accounted for in the statistical models, we found that the site factors no longer significantly effected the mortality rate of red oaks, which was approximately the same regardless of site conditions.

Despite finding that poor site conditions do not appear to be accelerating decline and mortality, we do think that environmental variables have played a prominent but indirect role in the oak decline episodes across the Ozark Highlands. Rather than simply predisposing oaks to decline, droughty and nutrient-deficient site conditions most likely favored the establishment and growth of red oaks following the extensive logging and frequent burning during the early 1900s. Our findings suggest that high risk stands are those where mature red oaks are most abundant regardless site conditions.

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