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The effects of environment and life stage on *Quercus* abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients?

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Abstract

Most studies that describe tree species distributions across environmental gradients focus only on the abundance of adults. This approach may overlook the response of younger life stages (i.e., seedlings and saplings) and thus may fail to identify the life stage that is most sensitive to a particular environmental gradient (i.e., site characteristics that vary across landscapes such as elevation or aspect). Alternatively, seedling and sapling abundance may be unrelated to environmental gradients and may be entirely dependent on adult abundance. In order to effectively manage eastern hardwood forests to promote species compositions that maximize economic or ecological value, we need to understand the relative roles of site characteristics and adult abundance on all life stages. To address this need, we examined the relationships between five site characteristics (aspect, slope position, site index, stand age and elevation) and the abundance of seedlings, saplings and adults of three species of oak (*Quercus rubra*, *Quercus alba*, and *Quercus prinus*). We assessed these relationships by censusing seedlings, saplings, and adults in large plots (500 m^2) and quantifying local site characteristics in 21 forest stands in the Monongahela National Forest in North Central West Virginia.

Adult white oak densities peaked on southwestern slopes ($R^2 = 0.24$); adult chestnut oak densities peaked on ridge tops ($R^2 = 0.58$); and adult northern red oak densities were not correlated with any site characteristics ($R^2 = 0.00$). Densities of white oak and chestnut oak saplings were highly correlated with a combination of site characteristics and seedling densities ($R^2 = 0.75$, 0.81, respectively), and northern red oak densities were highly correlated with site characteristics solely ($R^2 = 0.70$). For seedlings, white oak and chestnut oak densities were correlated only with adult abundance ($R^2 = 0.53$, 0.56, respectively), and northern red oak densities were correlated solely with site characteristics ($R^2 = 0.45$).

These data suggest that in the absence of disturbance, site characteristics have the strongest effects on abundance patterns of these oaks during the sapling stage. For each of the three species, seedling, sapling and adult densities were correlated with a different subset of factors meaning that different biotic and abiotic conditions promoted peak densities for each life stage. Such a pattern indicates that important ‘‘demographic conflicts’’ exist (sensu [Battaglia, L.L., Fore, S.A., Sharitz, R.R., 2000. Seedling

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1. Introduction

Environmental gradients largely determine plant species distributions (e.g., elevation, edaphic factors; Whittaker, 1956). Traditional gradient studies that examine changes in tree abundance typically concentrate on adults and assume that either all life stages are responding similarly, or that the adult response to gradients is stronger than the juvenile response (Crawley, 1997; Clark et al., 1998; Sardinero, 2000). Therefore, we often assume that adult response to gradients determines the distribution of that species. That assumption has rarely been tested (but see Stohlgren et al., 1998), which is surprising considering the evidence that juvenile and adult tree abundances respond differently to gradients (e.g., Nowacki et al., 1990; Downs and Abrams, 1991; Goebel and Hix, 1996). Identifying the life stage that is most responsive to environmental gradients will likely identify the life stage that is setting future distribution patterns for the species. Such information is vital to managing species with declining populations because management efforts could be focused on the life stage, which is limiting the species abundance.

The abundance of juvenile trees, however, may not respond directly to environmental gradients, but may be dependent on the abundance of seed-producing adults (Clark et al., 1998). Ribbens et al. (1994) suggested through modeling that adult abundances were more important than environmental conditions in predicting patterns of juvenile abundances in temperate, deciduous trees. Therefore, understanding the combined effects of adult abundance and environmental gradients on patterns of juvenile abundance is critical to identifying the mechanisms that determine juvenile abundances. To that end, we address two questions. What are the strengths of the correlations between environmental gradients and different life stages of tree species? Are adult abundances or environmental conditions more strongly correlated with juvenile abundances for these species?

We address these two questions for three species of oak (*Quercus*) in the eastern USA: northern red oak, white oak and chestnut oak (*Quercus rubra*, *Quercus alba* and *Quercus prinus*, respectively). Although dominant in the overstory in many areas, oaks are failing to regenerate across much of their ranges (Pallardy et al., 1988; Abrams, 1992; Smith, 1992). Many studies, although not traditional gradient studies (sensu Whittaker, 1956), have illustrated that oak abundances change across environmental gradients (i.e., variation in local site characteristics; see reviews: Crow, 1988; Cook et al., 1998; Abrams, 1992; Loftis and McGee, 1992; McShea and Headly, 2002). These studies have identified six key site characteristics that affect oak abundance: site productivity (e.g., site index), slope position (e.g., ridge top, side slope, bottom land), soil moisture (mesic versus xeric), stand age, aspect, and elevation. We reviewed 15 studies that reported the response of northern red oak, white oak or chestnut oak to at least one of these six key site characteristics (Table 1).

Because the studies we reviewed (Table 1) were designed for other purposes, none of the authors tested the strength of the relationships between different life stages and variation in site characteristics (e.g., environmental gradients) or tested all the site characteristics together. Regardless, these studies suggest relationships that are testable. Generally, on sites where adults are abundant, seedlings and saplings are often rare (Lorimer, 1984; Nowacki et al., 1990). This pattern suggests that adult and juvenile oaks respond differently to environmental gradients. At the species level, northern red oak *adults* can be common on productive, mesic sites. *Juveniles*, however, are often rare on these sites and are more common on low productivity, xeric, and ridge tops sites (Lorimer, 1984; Lorimer, 1985; Nigh et al., 1985; Crow, 1988; Pallardy et al., 1988; Lorimer et al., 1994). White oak adults and juveniles are found in higher abundances on south facing, drier sites (Keever, 1953; McCarthy et al., 1984; Pallardy

Table 1
Literature review of the relationships between six key site characteristics and abundance of northern red oak, white oak and chestnut oak

Site characteristics species	Life stage	Correlation to site characteristic	Study location	Citation
Aspect				
N. red oak	Juvenile	Higher abundance on south and southeastern aspects	Pennsylvania	Steiner et al. (1993)
N. red oak	Juvenile	Only found on protected, south facing slopes	Missouri	Zimmerman and Wagner (1979)
N. red oak	Adult and juvenile	Density did not differ with aspect	North Carolina	Keever (1953)
N. red oak	Adult and juvenile	More abundant on north and west slopes	Pennsylvania	Keever (1973)
N. red oak	Adult	No significant correlation btwn IV[a] and aspect	Ohio	McCarthy et al. (1984)
White oak	Adult	Higher IV on southern aspects	Ohio	McCarthy et al. (1984)
White oak	Adult and juvenile	Higher density on south-facing slopes	North Carolina	Keever (1953)
White oak	Adult	Greater height growth on north-facing slopes	Indiana	Hannah (1968)
Chestnut oak	Adult	Higher IV on southern aspects	Ohio	McCarthy et al. (1984)
Chestnut oak	Adult and juvenile	Higher density on north-facing slopes	North Carolina	Keever (1953)
Slope position				
Oak[b]	Large juvenile	Highest abundance on ridge tops	New Jersey	Buell et al. (1966)
N. red oak	Adult	Highest abundance on upper and open slopes	North Carolina	Whittaker (1956)
N. red oak	Saplings	Higher densities on upper slopes and ridgetops	Missouri	Rochow (1972)
N. red oak	Adults	Higher densities on mid slopes	Missouri	Rochow (1972)
White oak	Saplings	Higher densities on upper slopes and ridgetops	Missouri	Rochow (1972)
White oak	Adults	Higher densities on upper slopes and ridgetops	Missouri	Rochow (1972)
White oak	Adult & juvenile	Higher abundance of "flats"[3] vs. slopes	New York	Greller et al. (1979)
White oak	Adult	Highest abundance on ridges and peaks	Tennessee	Whittaker (1956)
White oak	Adult	Higher height growth on lower slopes	Indiana	Hannah (1968)
Chestnut oak	Adult	Highest abundance on upper and open slopes	North Carolina	Whittaker (1956)
Chestnut oak	Adult	Dominated ridge tops	New Jersey	Buell et al. (1966)[c]
Chestnut oak	Adult	Higher density on upper slope positions	North Carolina	Lorimer (1980)
Site productivity (site index)				
N. red oak	Juvenile	Survival increased with site index	North Carolina	Bourdeau (1954)
N. red oak	Juvenile	Higher abundance on lower site index	Pennsylvania	Steiner et al. (1993)
Soil moisture (e.g. mesic to xeric)				
N. red oak	Adult	Higher abundance on more mesic sites	Wisconsin	Peet and Loucks (1977)
N. red oak	Adult	Highest abundance on mesic slopes	Missouri	Pallardy et al. (1988)
N. red oak	Juvenile	Highest abundance on xeric slopes	Missouri	Pallardy et al. (1988)
N. red oak	Seedling	Highest density on drier sites	Wisconsin	Nowacki et al. (1990)
N. red oak	Sapling	Highest densities on transitional dry mesic[d]	Wisconsin	Nowacki et al. (1990)
N. red oak	Adult	IV: no pattern across soil moisture	Wisconsin	Nowacki et al. (1990)
N. red oak	Saplings	Higher densities xeric sites	Missouri	Rochow (1972)
N. red oak	Adults	Higher densities on mesic slopes	Missouri	Rochow (1972)
White oak	Saplings	Higher densities on xeric sites	Missouri	Rochow (1972)
White oak	Adults	Higher densities on xeric sites	Missouri	Rochow (1972)
White oak	Seedling	Highest densities on transitional dry mesic	Wisconsin	Nowacki et al. (1990)
White oak	Sapling	Highest densities on transitional dry mesic	Wisconsin	Nowacki et al. (1990)
White oak	Adult	Highest IV on transitional dry mesic	Wisconsin	Nowacki et al. (1990)
White oak	Adult	Highest abundance on xeric slopes	Missouri	Pallardy et al. (1988)
White oak	Juvenile	Highest abundance on xeric slopes	Missouri	Pallardy et al. (1988)
White oak	Adult	Higher abundance on more xeric sites	Wisconsin	Peet and Loucks (1977)
Chestnut oak	Adult	Dominated xeric sites	New Jersey	Buell et al. (1966)
Chestnut oak	Adult	The most abundant species on wettest sites	Pennsylvania	Keever (1973)

Table 1 (*Continued*)

Site characteristics species	Life stage	Correlation to site characteristic	Study location	Citation
Stand age				
N. red oak	Seedling	Higher densities in old-growth vs. 2nd growth	Pennsylvania	Downs and Abrams (1991)
N. red oak	Juvenile	No apparent relationship between stand age and density	Pennsylvania	Steiner et al. (1993)
N. red oak	Juvenile	No significant correlation btwn density and stand age	Ohio	Goebel and Hix (1996)
N. red oak	Adults	Higher IV in old-growth vs. 2nd growth	Pennsylvania	Downs and Abrams (1991)
N. red oak	Adult	No significant correlation btwn IV and stand age	Ohio	Goebel and Hix (1996)
White oak	Saplings	Higher densities in young oak stands	Missouri	Rochow (1972)
White oak	Seedling	Higher densities in old-growth vs. 2nd growth	Pennsylvania	Downs and Abrams (1991)
White oak	Adults	Higher IV in 2nd growth vs. old-growth	Pennsylvania	Downs and Abrams (1991)
White oak	Seedling	Higher abundance in stands 130-149 y[e]	Ohio	Goebel and Hix (1996)
White oak	Sapling	No significant correlation btwn density and stand age	Ohio	Goebel and Hix (1996)
White oak	Adult	IV[b] increases with stand age	Ohio	Goebel and Hix (1996)
Chestnut oak	Juvenile	No significant correlation btwn density and stand age	Ohio	Goebel and Hix (1996)
Chestnut oak	Adult	No significant correlation btwn IV and stand age	Ohio	Goebel and Hix (1996)
Elevation				
N. red oak	Juvenile	Higher abundances on higher elevations (625–686 m)	Pennsylvania	Steiner et al. (1993)
N. red oak	Adult	Higher abundance on lower elevations	Pennsylvania	Keever (1973)
N. red oak	Adult	Highest abundances 1,300–1,800 m	North Carolina	Whittaker (1956)
White oak	Adult	Highest abundances at 1,300 to1,800 m	North Carolina	Whittaker (1956)
Chestnut oak	Adult	Higher abundance on higher elevations	Pennsylvania	Keever (1973)
Chestnut oak	Adult	Highest abundances from 600 to 1,000 m	North Carolina	Whittaker (1956)

Life stage includes seed producing adults, seedlings, saplings or the general term juveniles, which includes seedlings, or saplings, or both.

[a] Importance value = (relative dominance + relative density)/2.

[b] Buell et al. (1966) considered n. red oak, white oak and chestnut oak combined, sometimes and confounds (1) soil moisture with slope position; and (2) slope position with successional stage.

[c] Greller et al. (1979) does not describe whether these "flats" are ridge top, bottom lands, or not associated with slope position.

[d] Nowacki et al. (1990) described their sites as mesic, transitional mesic, transitional dry mesic and dry mesic.

[e] Goebel and Hix (1996) used age classes: 70–98, 90–109, 110–129, 130–149 and, ≥150 years.

et al., 1988, Nowacki et al., 1990). Chestnut oak, both adults and juveniles, occur in higher relative abundances on xeric, low productivity, ridge top sites (Keever, 1953; Whittaker, 1956; Lorimer, 1980; Abrams et al., 1997).

To date, much of the work on oak abundance has concentrated on stands with high abundances of adult oaks and thus did not explicitly examine the importance of adult abundances on seedling and sapling (i.e., juvenile) abundances. Considering all life stages is essential to understand recruitment (Duchesneau and Morin, 1999) because during ontogeny the relative importance of site characteristics can change (Parrish and Bazzaz, 1985). For example, in balsam fir (*Abies balsamea*), seedling abundance was dependent on seed abundance, but sapling abundance was dependent on environmental conditions (Duchesneau and Morin, 1999). In fact, Goebel and Hix (1996) found that both adult abundance and site characteristics were correlated with seedling abundance for oaks. Their analysis, however, did not allow them to statistically distinguish between the relative role of site characteristics versus adult abundance on seedling abundance (Goebel and Hix, 1996).

In this study, we investigated both the effects of site characteristics and the effects of demographic factors (i.e., the effects of adults on juveniles) over a wide range of juvenile and adult oak densities. Specifically, we evaluated five of the six site characteristics identified in our review: slope position, site productivity (measured by site index), elevation, aspect and stand age. Although we did not directly measure soil moisture, we did measure site characteristics that are correlated with soil moisture (e.g., slope position and aspect; Dai et al., 2002). Our goals were: (1) for adults, to identify site characteristics that are significantly correlated with adult densities; (2) for saplings, to identify site characteristics significantly correlated with sapling densities and to compare the relative importance of site characteristics, adult densities, and seedling densities on sapling densities; and (3) for seedlings, to identify site characteristics significantly correlated with seedling densities and to compare the relative importance of site characteristics versus adult densities on seedling densities. The three oak species we studied are common in eastern hardwood forests, have high economical or ecological value or both, and appear to be experiencing declining populations or dominance across much of the eastern United States (Abrams 1992, Smith 1992).

2. Methods

2.1. Study sites

We surveyed 21 stands in August and September 1996 in the Cheat District in the Monongahela National Forest, West Virginia, USA. Stands were units of forest area that were generally uniform in canopy tree composition and age, and were delimited on U.S. Forest Service compartment maps. The land type association is Allegheny Front Side slopes (Demeo et al., 1996). All of the stands were located on soils of the Berks-Weikert association. These are shallow to moderately deep, well-drained soils formed in residuum weathered from shale, siltstone and fine-grained sandstone and are classified as loamy-skeletal, mixed, active, mesic Typic Dystrudepts or loamy-skeletal, mixed, active, mesic Lithic Dystrudepts, depending on depth of the solum. Slopes range from 0 to 100%. Permeability is moderate to moderately rapid. Forest type is mixed mesophytic to oak hickory (Braun, 1967). Dominant non-oak species include *Acer sacharum*, *Acer rubrum*, *Carya tomentosa*, *Carya ovata*, *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Prunus serotina*, and *Tillia americana*. Common shrubs include *A. pensylvanicus*, *Hamamelis virginiana*, and *Kalmia latifolia*. Mean annual precipitation is 143 cm distributed evenly throughout the year (Adams et al., 1994). The growing season is from May through October. Stands ranged from 4 to 53 ha, had 3–91% oak in the overstory, and were 71–126 years old. We examined stands across such a wide gradient of adult abundance so that we could better clarify relationships between site characteristics and oak abundance than if we had concentrated solely on oak dominated stands. Elevations ranged from 600 to 860 m. Site index for northern red oak at 50 years of age varied from 50 to 80 indicating a range from moderately-low to high productivity.

Commonly, foresters use site index to evaluate and quantify stand productivity in terms of commercial yield. Site index is defined as the total height of a free-growing tree at a specific age (e.g., 60 ft for northern red oak at 50 years). Site index is determined from site index curves, which are based on soil and physiographic characteristics, primarily soil fertility and water availability (Carmean et al., 1989; Fralish, 1994). Thus, this measure is an integrated index of site characteristics that typifies site productivity. Site index is limited because it was designed for single species stands and it assumes that height growth had not been influenced by stand density, disturbance, or history (Iverson et al., 1997). Although others have developed new measures of stand productivity (Fralish 1994, Berguson et al., 1994; Iverson et al., 1997), they have not been widely adopted by the USDA Forest Service or other foresters, likely because site index provides a satisfactory measure of site productivity (Carmean et al., 1989).

2.2. Measurements

We distinguished between juvenile (pre reproductive) and adult (potentially reproductive) trees by crown position as described by Smith et al. (1997).

Generally, in closed canopies, oaks produce very few seeds until they reach the canopy including the crown positions of intermediate, codominant, or dominant. Over-topped oaks, however, very rarely produce any seeds under a closed canopy (Dale et al., 1995). These over-topped juveniles were divided into two size classes: seedlings ($\leq$50 cm tall) and saplings ($>$50 cm tall and less than the height of the canopy; i.e., ‘‘over topped’’).

In each stand, we randomly located two 10 m $\times$ 50 m plots per 60 m of elevation parallel with the slope. Two to eight plots were surveyed in each stand with an average of one plot every 3.9 ha ($\pm$2.6S.D.). Within plots, all oak individuals (northern red oak, white oak, and chestnut oak) were identified and tallied by size class: seedling, saplings, or adults. Our sample of juveniles was extremely thorough due to large plot size (500 m^2). We converted the tallies into densities (i.e., number of stems per ha). We use the term abundance in the general sense and the term density as a measure of abundance.

We obtained stand age and site index data from USDA Forest Service stand datasets. From topographic maps we determined elevation and aspect. Slope position for each plot was determined as the percentage of the distance from the ridge and the nearest permanent stream (Fralish, 1994) and then categorized as 1 = lower third, 2 = middle third, and 3 = upper third, which included ridge tops (Golden et al., 1999). For each stand, we averaged these values to give a slope position index. Most stands were comprised of only one or two slope positions (18 of 21 stands surveyed). In all, slope position, aspect and elevation were calculated from transect means, whereas, site index and stand age were stand level attributes.

2.3. Data analysis

Densities varied over four orders of magnitude, therefore we transformed ($\log_{10}(Y + 1)$) densities to linearize the data (Sokal and Rohlf, 1995). To account for the circular nature of aspect (i.e., 0° and 360° are the same direction, North), we sine transformed aspect, following Hannah (1968). We conducted nine separate stepwise multiple regressions, one for each life stage (seedling, sapling and adult) by species combination. We used stepwise regression because parameters can leave and enter repeatedly until the best model is found (Sokal and Rohlf 1995). We set levels of $P < 0.06$ and >0.05 for parameters to enter or leave the models, respectively. The transformed densities for each size class and species were the response variables. The independent variables included site index, aspect, slope position, stand age, and elevation. Additionally, for the seedling and sapling regressions, we added adult densities to the set of independent variables to examine the relative influence of adult densities versus site characteristics. Similarly, we added seedling densities to the set of independent variables in the sapling regressions because seedlings grow into saplings. Thus, we could distinguish between the effects of environmental factors and demographic factors on juvenile densities.

The multiple regression analyses allowed us to interpret the results as follows. First, we identified the life stage that was most responsive to environmental gradients by identifying which life stage had the highest correlation with all significant site characteristics combined (i.e., the largest R^2; Stohlgren et al., 1998). This is because R^2 (i.e., the coefficient of determination) measures the proportion of the variance that is explained by the significant site characteristics in the regression analyses (Sokal and Rohlf, 1995).

Second, we identified which individual site characteristics were significantly more important than others by simply enumerating the number of times each site characteristic was significantly correlated with oak densities across all nine regression analyses (i.e., $P < 0.05$). When a regression analysis revealed multiple significant site characteristics, we could rank the importance of each site characteristics using the partial correlations values. This is because partial correlations report the proportion of the variance that is explained by each significant parameter in the regression analyses (Sokal and Rohlf, 1995).

Third, we evaluated the relative importance of site characteristics versus demographic factors (e.g., adult densities) in predicting oak densities across life stage. Specifically, we examined the significant parameters in the models and their partial correlations to determine the relative importance of (1) site characteristics versus seedling densities and adult densities for sapling densities and (2) site characteristics versus adult densities for seedling densities.

Table 2
Summary of significant parameters and relationships between oak densities and significant parameters in nine stepwise multiple regressions

Species	Life stage	Significant parameters	Highest densities were found in stands with these attributes
Northern red oak (QURU)	Seedlings	Aspect	Southern and western aspects (150–275°)
		Elevation	Lower elevations
	Saplings	Elevation	Lower elevations
		Site index	Lower site indexes
		Slope position	Upper slopes and ridge tops
	Adults	No variables were statistically significant	
White oak (QUAL)	Seedlings	QUAL adult density	High adult densities
	Saplings	Aspect	Southern aspects (225–270°)
		QUAL seedling density	High seedling densities
		Site index	Lower site indexes
	Adults	Aspect	Southwestern and northwestern aspects (225–315°)
Chestnut oak (QUPR)	Seedlings	QUPR adult density	High adult densities
	Saplings	QUPR seedling density	High seedling densities
		Slope position	Upper slopes and ridgetops
		Stand age	Older stands
	Adults	Slope position	Upper slopes and ridge tops

Details of statistics are in Tables 3–5.

Table 3
Results of stepwise regression analyses on adult densities

(A) Northern red oak adults					
(i) Analysis of variance					
No variables met the significance level for entry into the model					
Source	d.f.	Sum of squares	F value	P	R^2
(B) White oak adults					
(i) Analysis of variance					
Model	1	2.37	5.84	0.0259	0.24
Error	19	7.74			
Total	20	10.11			
Variable	Parameter estimate	P	Partial correlation		
(ii) Regression parameters estimates					
Intercept	14.11	0.0001			
Aspect	0.58	0.0259	0.24		
Source	d.f.	Sum of squares	F value	P	R^2
(C) Chestnut oak adults					
(i) Analysis of variance					
Model	1	5.48	25.938	0.0001	0.58
Error	19	4.01			
Total	20	9.50			
Variable	Parameter estimate	P	Partial correlation		
(ii) Regression parameters estimates					
Intercept	3.12	0.0001			
Slope position	−0.98	0.0001	0.58		

Independent variables were stand age, slope position, site index, aspect, and elevation. P values to enter and exit the model were 0.06 and 0.05, respectively. N is 21 stands.

Table 4
Results of stepwise regression analyses on sapling densities

Source	d.f.	Sum of squares	F value	P	R^2
(A) Northern red oak saplings					
(i) Analysis of variance					
Model	3	13.26	13.45	0.0001	0.70
Error	17	5.59			
Total	20	18.84			
Variable	**Parameter estimate**	**P**	**Partial correlation**		
(ii) Regression parameters estimates					
Intercept	11.44	0.0001			
Slope position	1.261	0.0010	0.48		
Elevation	−0.002	0.0171	0.29		
Site index	−0.047	0.0345	0.24		
Source	**d.f.**	**Sum of squares**	**F value**	**P**	**R^2**
(B) White oak saplings					
(i) Analysis of variance					
Model	3	3.54	24.11	0.0001	0.81
Error	17	0.83			
Total	20	4.37			
Variable	**Parameter estimate**	**P**	**Partial correlation**		
(ii) Regression parameters estimates					
Intercept	2.52	0.0003			
Log [QUAL seedling density]	0.42	0.0001	0.69		
Site index	−0.04	0.0001	0.60		
Aspect	−0.26	0.0273	0.25		
Source	**d.f.**	**Sum of squares**	**F value**	**P**	**R^2**
(C) Chestnut oak saplings					
(i) Analysis of variance					
Model	3	11.42	17.36	0.0001	0.75
Error	17	3.73			
Total	20	15.15			
Variable	**Parameter estimate**	**P**	**Partial correlation**		
(ii) Regression parameters estimates					
Intercept	−1.23	0.1431			
Stand age	0.02	0.0024	0.43		
Log [QUPR seedling density]	0.48	0.0056	0.37		
Slope position	−0.52	0.0326	0.24		

Independent variables were stand age, slope position, site index, aspect, elevation, adult densities, seedling densities. P values to enter and exit the model were 0.06 and 0.05, respectively. Saplings are greater than 50 cm tall and less then the height of the main canopy (over-topped). N is 21 stands.

Fourth, we characterized the type of stand where oaks reached peak densities. The set of significant parameters in each analysis identified the set of conditions and also type of stand where each life stage of each species achieved its highest densities. If different life stages of the same species reached peak densities in different stand types then this would indicate that these life stages were responding either to different environmental conditions, or demographic factors, or both. Such patterns would indicate a ‘‘demographic conflict’’ where conditions that promote one life stage do not promote another (sensu Battaglia et al., 2000).

Table 5
Results of stepwise regression analyses on seedling densities

Source	d.f.	Sum of squares	*F* value	*P*	R^2
(A) Northern red oak seedlings					
(i) Analysis of variance					
Model	2	2.16	7.367	0.0046	0.45
Error	18	2.64			
Total	20	4.81			
Variable	**Parameter estimate**	***P***	**Partial correlation**		
(ii) Regression parameters estimates					
Intercept	5.01	0.0003			
Aspect	0.49	0.0036	0.38		
Elevation	−0.00	0.0370	0.22		
Source	**d.f.**	**Sum of squares**	***F* value**	***P***	**R^2**
(B) White oak seedlings					
(i) Analysis of variance					
Model	1	7.35	23.98	0.0001	0.56
Error	19	5.82			
Total	20	13.18			
Variable	**Parameter estimate**	***P***	**Partial correlation**		
(ii) Regression parameters estimates					
Intercept	0.77	0.0017			
Log [QUAL canopy tree density]	0.85	0.0001	0.56		
Source	**d.f.**	**Sum of squares**	***F* value**	***P***	**R^2**
(C) Chestnut oak seedlings					
(i) Analysis of variance					
Model	1	6.77	21.08	0.0002	0.53
Error	19	6.11			
Total	20	12.88			
Variable	**Parameter estimate**	***P***	**Partial correlation**		
(ii) Regression parameters estimates					
Intercept	0.83	0.0074			
Log [QUPR canopy tree density]	0.84	0.0002	0.53		

Independent variables were stand age, slope position, site index, aspect, elevation, and adult densities. *P* values to enter and exit the model were 0.06 and 0.05, respectively. Seedlings were 1–50 cm tall. *N* is 21 stands.

3. Results

In all analyses, all significant parameters entered once and no parameters were removed, meaning that the addition of parameters did not change the significance of parameters already in the models. Additionally, all non-significant parameters had *P* values >0.1, therefore, no parameters were "marginally significant". Consequently, the implications of the regression analyses are robust. For all nine analyses, we summarized the significant parameters (Table 2) then report each analysis in greater detail (Tables 3–5).

3.1. Adults

Across our study sites, mean densities of northern red oak and chestnut oak adults were greater than mean densities of white oak adults (Fig. 1). For northern red oak, no variables were significantly

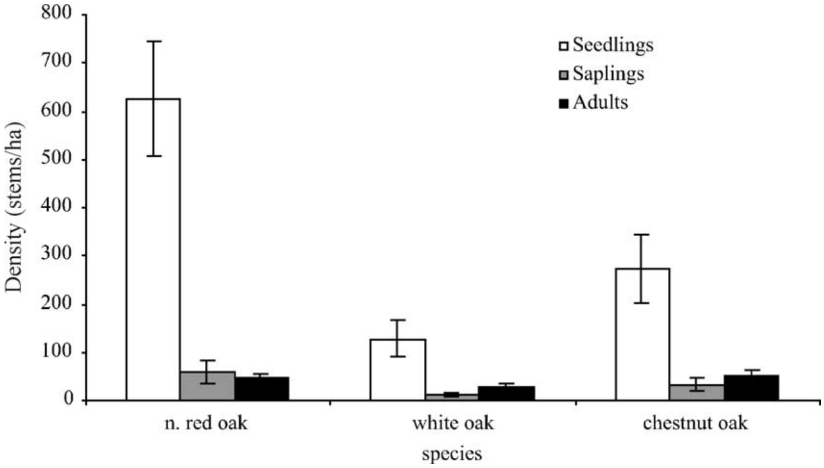

Fig. 1. Mean density (±1S.E.; $N = 21$ stands) per hectare of adults (intermediate, codominant and dominant crown classes; Smith et al., 1997), saplings (>50 cm tall to less than the height of the main canopy; i.e., overtopped; Smith et al., 1997) and seedlings (1–50 cm in height) for three species across 21 stands surveyed.

correlated with adult densities (Table 3A). White oak adult densities were significantly higher on south-western to northwestern aspects (225–315°; $R^2 = 0.24$, $P = 0.0259$; Table 3B; Fig. 2B). Chestnut oak densities were greater on upper slopes and ridge tops ($R^2 = 0.58$; $P < 0.0001$; Table 3C; Fig. 2C).

3.2. Saplings

Northern red oak was the most abundant species in the sapling life stage and white oak was the least abundant (Fig. 1). For all species, sapling densities were significantly correlated with at least one site characteristic (Tables 2 and 4). For both white oak and chestnut oak, sapling densities were also correlated with seedling densities. Specifically, northern red oak densities were significantly higher on upper slopes and ridge tops (slope position partial correlation (pc) = 0.48), on lower productivity sites (site index pc = 0.24) and at lower elevations (pc = 0.29; $R^2 = 0.70$; $P < 0.0001$; Table 4A). White oak sapling densities were significantly higher on lower productivity sites (site index pc = 0.60), on southwestern aspects (225–270°; pc = 0.22) and where seedling densities were high (pc = 0.69; $R^2 = 0.81$; $P < 0.0001$; Table 4B, Fig. 2B). Chestnut oak sapling densities were significantly higher where seedling densities were higher (pc = 0.37), in older stands (pc = 0.43) and on upper slopes and ridge tops (pc = 0.24; $R^2 = 0.75$; $P < 0.0001$; Table 4C).

3.3. Seedlings

Seedlings were the most abundant size class. Northern red oak seedlings were the most abundant of the seedling species while white oak seedlings were the least abundant species (Fig. 1). Northern red oak seedling densities were significantly higher on southern and western aspects (150–275°; pc = 0.38) and at lower elevations (pc = 0.22; $R^2 = 0.45$, $P = 0.0046$; Table 5A; Fig. 2A). White oak and chestnut oak seedling densities were significantly higher where adult densities were high ($R^2 = 0.56$, $P < 0.0001$; $R^2 = 0.53$, $P < 0.0002$; respectively; Table 5B and C).

3.4. Aspect

Because of the circular nature of aspect, the relationships between aspect and oak abundance are more complicated than the linear relationships between the other parameters and oak abundance. Therefore, we further explored the relationship between aspect and oak abundance by plotting the log of seedling, sapling and adult densities by aspect for each species (Fig. 2). For northern red oak, adults

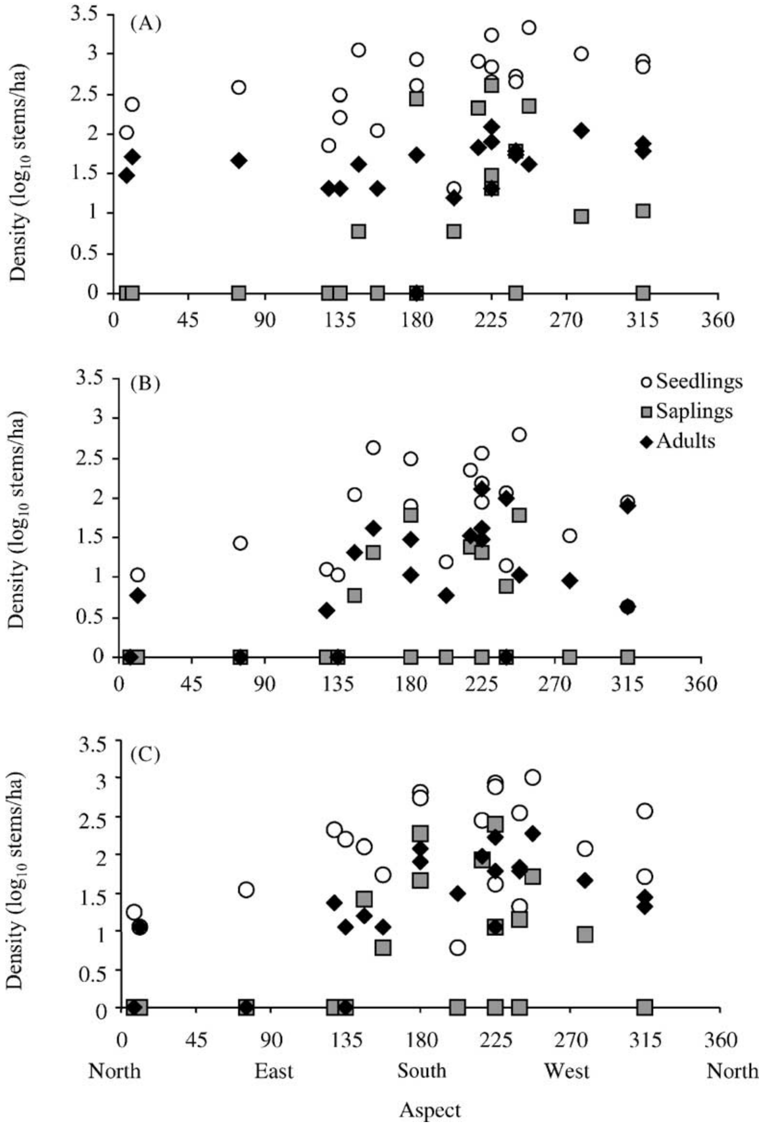

Fig. 2. Density (log_{10} stems/ha) across aspect for (A) northern red oak, (B) white oak and, (C) chestnut oak in 21 stands. White circles are seedlings (<50 cm tall); grey squares are saplings (>50 cm tall and less then the height of the main canopy of the stand); and black diamonds are adults (intermediate, codominant and dominant crown classes).

and seedlings were abundant across all aspects. In contrast, saplings were in higher abundance only on south and southwestern slopes compared to other aspects. For all species, generally, saplings peaked in abundance on southern and southwestern aspects and seedlings were nearly evenly distributed across all aspects. In other words, saplings densities peaked in stands that represented a narrower range of aspect than did other life stages.

4. Discussion

4.1. The strength of correlation between life stage and environmental gradients

4.1.1. Adult densities were least responsive to environmental gradients

For each species, adult densities had weaker correlations with environmental gradients than did densities of saplings, or seedlings, or both (Table 2). This pattern was particularly striking in northern red oak and white oak, possibly due to one or more of the following explanations. Factors that vary across temporal scales may be more influential than site characteristics in determining adult distributions (e.g., ice storms or insect outbreaks). Another possibility is that adult densities may be correlated with an unmeasured site characteristic (e.g., soil resource levels). Alternatively, adult oaks may have become established under a different set of site characteristics than those that occur today. For example, many mature oak forests in the eastern U.S. originated following logging and burning circa 1880–1920 (Abrams, 1992; Schuler and McClain, 2003). Therefore, adults that regenerated 100 years ago were subject to a different set of environmental conditions than saplings today, which are under mature canopies. Site characteristics that we measured (e.g., slope position and site index) may have played little role in determining patterns of oak establishment 100 years ago. Today, sapling densities, for all three species, are highly correlated with site characteristics and not adult density (see below) because these site characteristics are the environmental conditions under which these current saplings are surviving and growing.

4.1.2. Sapling densities were most responsive to environmental gradients

Stohlgren et al. (1998) suggested that either seedlings or adults would have the strongest correlations with environmental gradients depending on the dynamics of the system (i.e., ecotone type or frequency of disturbance). They did not consider the possibility that an intermediate life stage (i.e., saplings) might be more highly correlated with environmental gradients. Indeed, our results demonstrate that sapling densities had the strongest correlations with environmental gradients (Tables 3–5). Site characteristics, sometimes in combination with seedling density, were good predictors of sapling density, although the specific subset of significant site characteristics changed with species.

This finding that sapling densities had the strongest correlations with the variation in site characteristics means that saplings densities peaked across a narrower range of site characteristics than did other life stages. For example, sapling densities peaked over a narrow range of aspect, where as seedlings and adult densities were more uniformly distributed across all aspects (Fig. 2). Thus, saplings were abundant at a fewer number sites compared to adults or seedlings. If these species are currently declining, then the sites where saplings are most abundant today may represent refuges where adults may be restricted to in the future (Stohlgren et al., 1998). In fact, much of the oak regeneration literature suggests that adult abundances are declining across parts of some environmental gradients (e.g., on highly productive sites and at lower slope positions; Lorimer, 1984; Nowacki and Abrams, 1991).

4.1.3. Seedling densities demonstrated little responsiveness to environmental gradients

Regression analyses explained less variation in seedling densities than did analyses on sapling densities (Tables 3 and 4). Further, northern red oak was the only species with seedling densities that were correlated with site characteristics. Seedling densities may have been less sensitive to variation in the site characteristics than were sapling densities simply because seedlings are small. Therefore, seedling densities are more responsive to smaller scale variation in environmental heterogeneity than the stand level (e.g., site index) and the plot level (e.g., slope position) site characteristics that we measured. Indeed, seedlings are more sensitive than older life stages to conditions that change over small spatial scales (Sork, 1987). Seedling establishment and early survival are critically dependent on microsite conditions (Augspurger, 1983; Duchesneau and Morin, 1999; Battaglia et al., 2000). Additionally, seedling densities may be more sensitive than other life stages to temporal variation (e.g., masting cycles, erratic weather, fluctuations in seed predator populations; Crawley and Long, 1995; Meiners et al., 2000). Thus, seedling densities may be less likely to respond to site characteristics critical to other life stages of oak.

4.2. The relative role of site characteristics versus demographic factors across life stages.

4.2.1. White oak and chestnut oak

At our study sites, as life stage moved from seedling to adult, factors that were significantly correlated with density shifted from solely adult density, which is a demographic factor, to site characteristics, which are environmental factors (Table 2). Specifically, seedling densities were correlated solely with the densities of seed-producing adults, whereas sapling densities were significantly correlated with a combination site characteristics and seedling densities. In fact, the role of site characteristics was at least as important as seedling densities in predicting sapling densities (i.e., partial correlations of site characteristics were 0.25 and 0.60 for white oak and 0.43 and 0.24 for chestnut oak; partial correlation of seedling densities were 0.69 for white oak and 0.37 for chestnut oak; Table 4B and C). For these two species, our data suggest that adult densities govern seedling densities. Subsequently, site characteristics act as filters between the seedling and sapling stage significantly altering abundance patterns.

For many plant species, factors that are correlated with plant densities change across life stage because each life stage has a different set of habitat requirements (Parrish and Bazzaz, 1985; Bazzaz, 1991; Battaglia et al., 2000). For example, adult abundances have determined abundance patterns of newly germinating seedlings through seed-source effects, through seed dispersal dynamics, and by creating microsite environments conducive to germination (Ellner and Shmida, 1981; Schupp, 1995; Duchesneau and Morin, 1999). Then as juveniles aged, the environment acted as a filter and shifted the surviving-juvenile abundance patterns causing correlations between juvenile and adult densities to decrease or became negative (Augspurger, 1983; Schupp, 1995). We found a similar pattern. As life stage moved from seedlings to saplings, the correlation between juvenile densities and adult densities went from being positive to being uncorrelated (Table 2).

Further, our work exemplifies the nature of the relationship between life stage and habitat requirements in white oak and chestnut oak. We found that for each of these two species, adult and sapling densities (1) were uncorrelated, (2) were significantly correlated with a common site characteristic, but (3) did not share a complete set of significant site characteristics. We interpret these results to mean that peak densities of adults and saplings occurred in stands with different site conditions. Thus, the ‘‘realized niches’’ (sensu Patten and Auble, 1981) for saplings and adults were similar but not identical within these two species at our study sites.

4.2.2. Northern red oak

Unlike white oak and chestnut oak, densities of northern red oak seedlings and saplings were not correlated with demographic factors (e.g., adult or seedling densities; Table 2) but were significantly correlated with site characteristics. These results suggest that the effects of site characteristics were relatively more important than (1) the effects of adult densities on seedling densities and (2) the effects of adult or seedling densities on sapling densities. Thus, the relative role of adult abundance versus site characteristics on oak densities varies by species at our study sites.

Similar to white oak and chestnut oak, northern red oak also exhibited different ‘‘realized niches’’ across life stage. Specifically, the findings that seedling densities and sapling densities each were correlated with a different subset of site characteristics and that adult densities were not correlated with any factor we measured, provide evidence that life stages have distinctive environmental requirements (Table 2). When environmental conditions that are favorable for seedlings are not optimal for saplings (Grubb, 1977) or adults, then a ‘‘demographic conflict’’ may arise (Battaglia et al., 2000). For example, Buckley et al. (1998) found that northern red oak seedlings in openings had high mortality but surviving seedlings had high growth. Yet under intact canopies, oak seedlings had high survival but poor growth. Thus, under a single set of environmental conditions, seedlings may be abundant due to high survival but saplings may be rare due to poor seedling growth. A ‘‘demographic conflict’’ may explain the Buckley et al. (1998) results and why in this study, seedling and sapling peak densities were found in stands with different conditions for all three species of oak.

4.3. Identifying the relative importance of each site characteristics in oak abundance

Similar to the findings of many other studies, we found that each of the five site characteristics tested was significantly correlated with the oak densities for least one life stage and species combination (Tables 1 and 2). Our study, therefore, adds to a growing consensus that these site characteristics represent critical site characteristic for oaks (Table 1). Importantly, only a small number of site characteristics were significant for any one species and life stage combination. And, no single site characteristic emerged as being significantly correlated with oak densities across all life stages and species. Aspect and slope position were significant in three out of nine models. Site index and elevation were significant in two models each. Stand age was significant in only one model.

4.3.1. Aspect

Aspect was significantly correlated with the densities of northern red oak seedlings, and white oak saplings and adults. These results support other studies that reported oaks were more abundant on southern and western aspects (Keever, 1953; McCarthy et al., 1984; Steiner et al., 1993). Our work builds on these previous studies because we demonstrate that the correlation between aspect and oak abundance was significant even when other factors are also considered (Tables 1 and 2; but see Hannah, 1968). In our study, sapling densities generally peaked on a narrower range of south and western aspects, where as, adult and seedling densities were either nearly uniformed across aspect or peaked over a broader range of aspect (Fig. 2). Our data suggest that in the absence of disturbance, adult oaks may recruit in higher densities on south and southwestern slopes. Our data, however, cannot address how adults, currently on north and east aspects, recruited or the fate of the seedlings that are there now.

4.3.2. Stand age

Stand age was a significant correlate in only one of nine regressions (i.e., density of chestnut oak saplings), which lends little support for stand age as an important site characteristic related to oak abundance. Prior to 1900, seedling and sapling oaks were likely abundant in old-growth forests and readily recruited into adult stages (Abrams et al., 1995; Abrams and Copenheaver, 1999). Peet and Loucks (1977) described white oak as self-replacing in ‘‘climax’’ forests. Indeed, juveniles may have been abundant in old growth stands 100–300 years ago (Peet and Loucks, 1977; Dahir and Lorimer, 1996). We suggest that higher understory light levels in old-growth forests compared to younger forests promoted the regeneration of these intermediate shade-tolerant species. Historically, eastern deciduous forests likely had more light in the understory due to frequent, low intensity disturbances (Guyette and Dey, 1995; Dahir and Lorimer, 1996; Runkle, 1982). Nonetheless, recent studies are equivocal. Downs and Abrams (1991) reported that for some oak species, sapling densities or importance values were greater in older stands. Other studies, however, found no relationship between stand age and oak sapling density (Goebel and Hix, 1996; Steiner et al., 1993; Table 1). Perhaps in current forests, another factor (e.g., herbivory or past land use) is masking the relationship between stand age and oak density. Alternatively, stand age may have been relatively unimportant in our study because the range of stand ages we used (i.e., 70–126 years) was not great enough to show an effect of stand age on oak densities. That is, none of our stands were ‘‘old-growth’’.

4.3.3. Are site index, aspect and slope position similarly linked to the same resource?

We found that these three site characteristics had similar relationships with oak densities as those reported by others (i.e., highest sapling densities at low site indexes, southern aspects, and on upper slopes and ridgetops; Table 1). At least one of these three site characteristics was significant in six of nine regression models and specifically was significant in all sapling models. This leads us to suggest that these three site characteristics may be more important in predicting sapling densities than are elevation and stand age. One explanation to account for why oak densities are consistently correlated with these three site characteristics is that they are correlated with each other. For example, (1) southwestern aspects generally have lower site indices than northeastern aspects and (2) upper slopes and ridge tops generally have lower site indices than lower slope positions (Yawney, 1964). But more specifically, we suggest that site index, aspect, and slope position may have similar relationships to a limiting resource for oak. Thus, oak saplings are responding to changes in that resource and not to variation in a particular site characteristic, per se. Forest stands that have low site indices, south and southwestern aspects, and ridge top slope positions all represent areas that generally have the highest light levels, lowest soil moisture, and lowest fertility levels (Fralish, 1994; Condit et al., 1995; Bale et al., 1998; Coomes and Grubb, 2000; Small and McCarthy, 2002). Therefore, oak saplings may be at peak densities in these stand types due to light, nitrogen or water requirements. Regardless of the exact mechanisms, we suggest that oak saplings are responding to a common pattern of resource availability across these three site characteristics.

4.4. Management Implications

We found two patterns that were consistent with previous studies and particularly relevant for management. White oak adult and sapling densities were highest on southern and southwestern slopes, as also reported by Keever (1953) and McCarthy et al. (1984). Likewise, chestnut oak adult and sapling densities were greater on upper slopes and ridge tops, which is in agreement with the findings of Whittaker (1956), Buell et al. (1966) and Lorimer (1980). Management strategies that consider aspect for white oak and slope position for chestnut oak will likely be more fruitful than strategies that focus on other site characteristics.

Management prescriptions for oak often emphasize managing for high sapling density prior to harvest through removal of competing vegetation either through prescribed fire, herbicide, mechanical removal, or a combination of these tools (Loftis, 1983; Johnson et al., 1986; Johnson and Law, 1989; Brose and Lear, 1999; Larsen et al., 1999). Such techniques, however, have yielded mixed results (Wendel and Smith, 1986; Merritt and Pope, 1991; Gordon et al., 1995; Schuler and Miller, 1995; Buckley et al., 1998), perhaps because the competing vegetation, per se, is not directly suppressing oak abundance. Rather, site characteristics may be unfavorable for oak saplings even when seedlings are abundant. This is because seedling densities are highly correlated with adult densities and sapling densities are highly correlated with site characteristics. Stands that are dominated by adult oaks today may represent stands that were good sites for saplings 100 years ago, but today are poor sites for saplings. For example, adult oaks may be abundant in some areas due to logging and burning when these stands were initiated and not because of ‘‘favorable’’ site characteristics (e.g., slope position or aspect; Whitney, 1987; Abrams, 1992; Schuler and McClain, 2003, and reviewed by Dey, 2002). Thus, management prescriptions that focus on enhancing sapling densities in stands where saplings are at peak densities, yet lower than recommended for regeneration, may yield more promising results than attempting to enhance sapling densities in stands with either high seedling or adult densities but low sapling densities.

5. Conclusions

For the three species of oak we evaluated, seedling and sapling densities each were correlated to a unique combination of site characteristics and demographic factors (e.g. adult densities). This means that peak densities of seedlings and saplings did not coincide within the same forest stands or conditions. Thus, oaks are experiencing ‘‘demographic conflicts’’ (sensu, Battaglia et al., 2000) at our study sites. Additionally, an assumption implicit in traditional work on environmental gradients is that adult trees respond to environmental gradients and determine distribution patterns for species. Alternatively, Stohlgren et al. (1998) suggested that either adults or seedlings can determine distribution patterns for a species depending on which life stage has the strongest correlation with environmental gradients. Our results demonstrate that a third pattern is possible. Sapling densities were more strongly correlated with environmental gradients than are either adult or seedling densities. Taken together, these findings lead us to hypothesize that under current conditions, saplings are determining the future distribution patterns for three species of oak at our study sites. Further work that explores successional trajectories for eastern deciduous oak forests is needed to test this hypothesis.

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