

Growth, survival and sunfleck response of underplanted red oaks (*Quercus* spp., section *Erythrobalanus*) along a topographic gradient in southern New England

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ABSTRACT

An understanding of the regeneration niche is critical to our ability to refine silvicultural approaches aimed at regenerating and maintaining diverse, mixed species stands. However, few studies have directly tested differences in habitat associations among closely related trees of the same genus, particularly to assess habitat partitioning at the regeneration stage. To evaluate differences in regeneration niche, we established a common garden experiment with five red oak species (*Quercus* spp., section *Erythrobalanus*) under-planted across a topographic gradient (valley, midslope and ridge positions) in mixed hardwood forests of Southern New England. Represented were three red oak species common to intermediate site conditions of southern New England (*Q. rubra* L., *Q. velutina* Lam., and *Q. coccinea* Münchh.), and two species commonly associated with more extreme site conditions - *Q. ilicifolia* Wangerh. (xeric, skeletal ridge tops) and *Q. palustris* Münchh. (river floodplains). Seedlings were caged to prevent deer browse, and seedling height and survival were measured annually for nine growing seasons. Response to sunflecks, a primary source of light for advance regeneration-dependent species that establish in the forest understory, was measured using a LiCor 6400 photosynthesis system. Overall, survival was highest for *Q. rubra*, followed by *Q. velutina*, *Q. coccinea*, *Q. ilicifolia* and finally *Q. palustris*. The pattern among species held for all topographic positions, with higher survival rates on the ridgetops, and lower survival in valley positions. Height development was highest in the valley, intermediate in the ridge, and lowest in the midslope positions. Survival patterns were positively correlated with light availability, and negatively correlated with site fertility. Based on net photosynthetic rates, *Q. rubra*, *Q. velutina*, and *Q. coccinea* were more responsive to sunflecks than *Q. ilicifolia* and *Q. palustris*, and maintained higher photosynthetic rates over the measurement period. Greater survival of all species in upper topographic position reflects in part adaptations of the red oak group in this region to higher light and lower soil fertility conditions. But sunflecks likely play a critical role as well, judging from the positive correlation of survival with understory light (43–80% of which occurs as sunflecks), the strong height development in the light-limited valleys (where sunflecks should be most critical), and the clear alignment of species sunfleck response with species survival patterns. Differences among the oaks in photosynthetic response to sunflecks may thus help explain their habitat associations and contribute to niche partitioning among these related species. These findings have important silvicultural implications, particularly for enrichment planting of different red oaks and the timing of overstory removal treatments to facilitate establishment of regeneration for growth into the canopy.

1. Introduction

The fundamental and realized niche concept (Hutchinson, 1957) has received renewed attention in recent years, particularly given concerns of global climate change impacts on ecosystems and the responses of individual species that comprise them (e.g. Gómez-Aparicio et al., 2008; Canham and Murphy, 2016; Máliš et al., 2016). Disentangling the

environmental limits of where a species can potentially grow and reproduce (its fundamental niche) from its realized limits due to biological constraints (competition, pathogens, etc. – i.e. the realized niche) is vital to understanding the ability of species to colonize new sites or persist under environmental change. The regeneration phase is a particularly important element of niche differentiation among species, and differences among species in their regeneration niche contribute to the

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maintenance of species diverse communities (Grubb, 1977). Recruitment and survival represent critical bottlenecks in the distribution and dynamics of tree populations (Canham and Murphy, 2016; Máliš et al., 2016). Consequently, understanding the regeneration niche is essential for accurately predicting forest dynamics and for developing adaptive silvicultural responses under global climate change (Gómez-Aparicio et al., 2008).

Despite the importance of the regeneration niche, few studies directly test plant-habitat associations using transplantation experiments in the field, and primarily only in open-light conditions. Rather, most studies of habitat association are inferred from observational or ecophysiological studies of natural establishment patterns (e.g. Webb and Peart, 2000) or in controlled environments (growth chambers, greenhouses), rather than direct assessments of fundamental versus realized niche using field experiments (Vetaas, 2002; Kellman, 2004; Baltzer et al., 2005). While many studies suggest that distribution typically reflects ecophysiological adaptation, studies have also shown that recruitment limitation can constrain abundance (Dalling et al., 2002; Svenning and Wright, 2005), such that absence does not necessarily reflect an inability to grow or be competitive on a site. Furthermore, high levels of human disturbance such as evidenced in the past several hundred years in New England, can complicate our understanding of vegetation patterns by altering historical species distributions (e.g. Whitney, 1990; Foster et al., 1992). As a consequence we cannot necessarily assume that current distributional patterns reflect the optimal niche of a species, as species can potentially grow over a wider range of conditions than currently distributed (i.e. have the potential for wider realized niches). For this reason it is important that studies directly test the bounds of a species' potential niche by evaluating growth and survival in neighboring marginal habitats where a species is not typically found.

Advance regeneration-dependent species, i.e. species that rely upon establishment in the understory prior to a canopy disturbance event (Smith and Ashton, 1993), represent an interesting functional group for assessing niche differentiation. The ability to colonize a forest gap and reach maturity depends upon presence in the understory, which requires persistence under shaded conditions, particularly for species that show infrequent seedling recruitment and cannot form persistent seed banks (Smith et al., 1997). Dense overstory, midstory, or understory layers can limit understory light transmission, reducing seedling growth and persistence and thus establishment of advance regeneration-dependent species (e.g. Fladeland et al., 2003; Leakey et al., 2003; Lhotka and Loewenstein, 2008; Nilsen et al., 2009; Way and Pearcy, 2012). Many species that rely upon an advance regeneration mode of establishment exhibit episodic seed production (masting), and asynchrony in masting among species could contribute to temporal niche partitioning (Grubb, 1977). Demographic studies indicate that seedling bank composition and abundance within a forest can vary significantly over time and in space attributed to environmental gradients and differences in microsite conditions, among other factors (see Frey et al., 2007). Species and community composition are understood to show site associations related to such gradients as light (e.g. Ashton and Berlyn, 1994), moisture (Daws et al., 2002), and soil fertility (e.g. Bigelow and Canham, 2002; Hall et al., 2004). Species co-occurrence along similar environmental conditions is thought to reflect differences (sometimes subtle) among species in their resource requirements (Beckage and Clark, 2003), and available light, soil water, and nutrients have been implicated in niche partitioning among closely associated species across a range of forest types (Latham, 1992; Sack, 2004; Gómez-Aparicio et al., 2008).

Differences in adaptation to understory light conditions likely represent an important determinant on the niche of advance regeneration-dependent species. Light is recognized as a key factor mediating niche differentiation among closely associated species through its effects on growth and survival during the regeneration phase (Kobe, 1999), such as evidenced by seedling gap-partitioning following canopy

disturbance (e.g. Van Couwenberghe et al., 2010). Understory light levels are typically a small percentage of open light conditions, often less than 5% of full light in many mesic forest types (Chazdon, 1988; Canham et al., 1990; Fladeland et al., 2003), values that may be at or below the light compensation point for survival (e.g. Lei et al., 2006 in Nilsen et al., 2009). Light at the groundstory is both qualitatively different, and quantitatively variable, and is mediated by overstory composition (Canham et al., 1994). Below a forest canopy, much of the daily available photosynthetically active radiation (PAR) occurs as sunflecks, short pulses of direct light, that can represent as much as 50–80% of photosynthetic light (Chazdon, 1988; Canham et al., 1990; Fladeland et al., 2003). Longer duration sunflecks result in higher maximum photosynthetic rates (Leakey et al., 2003; Nilsen et al., 2009), and can be critical for carbon gain and survival of seedlings in understory environments (Way and Pearcy, 2012; Zhang et al., 2012). As a result of topographically mediated stand structural differences, sunfleck frequency and duration has been shown to be higher in more open ridge top sites than in valleys (Fladeland et al., 2003). Variation among species in response and utilization of sunflecks may be a critical determinant of growth and survival in the forest understory (Leakey et al., 2005).

Understory light conditions vary in the topographically complex forests of southern New England, where a diversity of advance regeneration-dependent oak species occur. In general, oaks are considered more drought resistant than most of the temperate moist hardwoods of the region due to greater carbon allocation belowground (Ashton and Larson, 1996), tend to be better adapted to acid soils among associated species (Finzi et al., 1998), but only moderately shade tolerant. As a consequence, they are predominantly associated with upland sites. However there are notable exceptions, such as *Quercus palustris* Münchh. (pin oak) that is common to flood plain forests. Nonetheless, they occupy a diversity of sites and form important components of floodplain, mesic valleys, upland slopes, and ridge tops. There is evidence from observational studies of naturally recruited seedlings (Frey et al., 2007) and manipulative growth studies (e.g. Ashton and Berlyn, 1994) that there are different environmental affinities among associated oak species, suggesting niche differentiation among species in the group. Indeed, niche differentiation has been identified among oaks in other regions, and differences in functional traits are thought to contribute to a diversity of co-occurring oak species (Cavender-Bares et al., 2004; Valdés-Rodríguez et al., 2017).

While the role of environmental gradients in niche differentiation and species coexistence has been highlighted (Tilman, 1994), specific studies directly testing niche differentiation and trade-offs are sparse and more studies on component species are needed (Nakashizuka, 2001; Silvertown, 2004). We expect that variation in environmental conditions associated with topography will mediate species associations across the landscape. In southern New England mixed hardwood forests, species of the red oak group (*Quercus* spp. Section *Erythrobalanus*) are a dominant component of most stands, with *Q. rubra* L. (northern red oak) most common, followed by *Q. velutina* Lam. (black oak) and *Q. coccinea* Münchh. (scarlet oak). To a lesser extent, *Q. palustris* and *Q. ilicifolia* Wangenh. (bear oak) are found, primarily in association with river floodplains (*Q. palustris*) or xeric, skeletal ridge tops (*Q. ilicifolia*). Thus the latter species inhabit the more extreme end of gradients found in southern New England. While numerous studies have recognized that the genus *Quercus* is drought tolerant and that individual members have, to differing extents, traits which confer competitive advantage on drier sites (e.g. Abrams, 1990; Kubiske and Abrams, 1991; Ashton and Berlyn, 1994; Ashton and Larson, 1996; Dey and Parker, 1996; Orwig and Abrams, 1997; Tschaplinski et al., 1998), fewer studies have focused on light and shade tolerance, which are likely a more important determinant in these humid, moist forest types (Ashton and Berlyn, 1994; Ashton and Larson, 1996). Our hypotheses were as follows: (i) oak species should show an overall higher level of survival in upper slope positions, reflecting the relative shade intolerance of the genus;

(ii) species will differ in their overall survival, with species that are most locally abundant (*Q. rubra*, *Q. velutina*, *Q. coccinea*) showing greater survival than species that are relatively uncommon and effectively outside their common habitat (*Q. palustris*, *Q. ilicifolia*); and, (iii) species will differ in their photosynthetic responses to sudden increases in light availability. We expect that an improved understanding of niche differences among related oak species will aid in the refinement of silvicultural approaches aimed at maintaining the full diversity of oak species in managed stands.

2. Methods

2.1. Site description

The study was conducted within the 3160 ha Yale-Myers Forest, located in northeastern Connecticut (41°57'N, 72°07'W). The region is characterized by undulating topography, with parallel ridges and valleys ranging from 200 to 350 m above mean sea level. This region is characterized by a humid continental climate, with average highs near 29 °C in July, average lows near –8 °C in January, and relative humidity levels generally between 60 and 70% (NOAA). Mean annual precipitation is approximately 1100 mm, and is evenly distributed throughout the year. Study sites were located in 70 to 90-year old mixed deciduous stands that had arisen from advance reproduction following removal of old-field pine (*Pinus strobus* L.). The pine had colonized abandoned pastures after 1850. Sites have been described in detail by Ashton et al. (1998), Fladeland et al. (2003), and Frey et al. (2007). Briefly, nine sites were selected for the study, three from each topographic position (ridge, midslope and valley). These sites were selected randomly from the available ridge, midslope and valley sites that supported the desired mature, closed-canopy stand conditions. All sites were stony silty loam soils derived from thin glacial till that were classified as Typic and Lithic Dystrochrepts (USDA Soil Conserv. Serv., 1981). Soil depth decreased from the valley to ridgetop, with upper slope positions characterized by thin soils with exposed bedrock. Paralleling soil depth, nutrient availability was higher in the valley and decreased towards the upper slope positions (Ashton et al., 1998). Canopy structure and composition, based on measures of mean height of the canopy trees (one 10 × 30 m belt-transect at each site) and basal area (average of two 8 m radius plots/site), also varied among the topographic positions (Fladeland et al., 2003) (Table 1). Valley sites were composed primarily of equal amounts of *Acer saccharum* Marsh. (sugar maple), *Liriodendron tulipifera* L. (tulip poplar), *Fraxinus americana* L. (white ash), *Quercus* spp. (red oaks), and *Betula* spp. (tolerant birches), midslope sites were dominated by *Quercus* spp. (red oaks), and ridge sites were comprised largely of *Quercus* spp. (red and white oaks), and *Carya* spp. (upland hickories). Understory light availability (% PPF – photosynthetically-active photon flux density) assessed using 6 quantum sensors (LiCor LI-190SA) at each site, declined from approximately 9% of full light in the upper slope positions (midslope and ridge) to 3% in the valley position, in line with leaf area index (LAI) estimates (Fladeland et al., 2003) (Table 1).

2.2. Experimental design

A total of nine sites were selected, with three replicates of each topographic position (ridge, midslope and valley). Within each site, two 2 m × 2 m plots were randomly established for planting. Five seedlings of each of the five species were planted in each plot, with a random arrangement and approximate spacing of 50 cm between each seedling to limit competition among individuals. Seedlings of the five species had been propagated in pots in February using acorns acquired from a local seed supplier, and subsequently out-planted in early June. Plots were caged to exclude deer browse, and cages were subsequently maintained and weeded each summer to limit competition from understory plants. Plots were measured annually in mid-July for nine

Table 1

Overstory basal area (m²/ha) of all woody plants greater than 2.5 cm at diameter breast height (dbh). Values represent averages of 3 sites for each position, based on the average of two 8 m radius fixed area sample plots per site. Stand characteristics include average height of canopy trees (m), leaf area index (LAI), and growing season understory light availability (PPFD, photosynthetically-active photon flux density).

Species composition	Topographic position		
	Valley	Midslope	Ridge
<i>Acer saccharum</i> Marsh. ^a	6.06	1.16	0
<i>Quercus rubra</i> L. and <i>Q. velutina</i> Lam. ^b	5.95	14.93	8.99
<i>Liriodendron tulipifera</i> L. ^c	5.87	0	0
<i>Betula lenta</i> L. and <i>B. alleghaniensis</i> Britt. ^d	5.64	1.51	0
<i>Fraxinus americana</i> L. ^e	5.34	0.1	0.20
<i>Carya ovata</i> (Mill) K. Koch ^f	3.62	1.78	1.72
<i>Acer rubrum</i> L. ^g	2.04	2.3	0.04
<i>Tsuga canadensis</i> L. ^h	1.08	0	1.51
<i>Q. montana</i> Willd. and <i>Q. alba</i> L. ⁱ	0	1.75	3.29
<i>Carya</i> spp. ^j	0	0.53	9.95
Other canopy species ^k	0.07	0.88	0.15
Midstory species ^l	0.29	0.04	0.02
Total Basal Area (m²/ha)	35.96	24.98	25.87
Stand Structure and Understory Light			
Canopy height (m)	29.72	26.00	19.72
Leaf area index (LAI)	6.00	5.33	4.66
PPFD – cloudy days (mol/m ² /day)	0.37	0.53	1.00
PPFD – sunny days (mol/m ² /day)	1.01	1.66	2.91
% PPF vs. open – cloudy days	3.0	9.3	8.7
% PPF vs. open – sunny days	1.6	3.2	5.2

^a Sugar maple.

^b Red oaks - Northern red oak and black oak.

^c Tulip poplar.

^d Tolerant birches - Black birch and yellow birch.

^e White ash.

^f Shagbark hickory.

^g Red maple.

^h Eastern hemlock.

ⁱ White oaks - Chestnut oak and white oak.

^j Upland hickories - Pignut hickory (*C. glabra* ([Mill] Sweet.) and mockernut hickory (*C. tomentosa* (Poir.) Nutt.).

^k American elm (*Ulmus americana* L.), paper birch (*B. papyrifera* Marsh.), and eastern white pine (*Pinus strobus* L.).

^l American hornbeam (*Carpinus caroliniana* Walt.), flowering dogwood (*Cornus florida* L.), and American hophornbeam (*Ostrya virginiana* (P. Mill.) K. Koch).

growing seasons. Individual seedlings were assessed for survival, and measured for height and evidence of dieback.

In the fourth growing season, net photosynthetic assimilation response to sunflecks was evaluated using a LiCor LI-6400 portable photosynthesis system (LiCor Inc. Lincoln, Nebraska, USA). In each of the two plots, one healthy seedling of each species was randomly selected for measurements of sunfleck response, using healthy mature leaves for analyses (i.e. one leaf/seedling × 2 seedlings/site for each species). Leaves were placed in the LiCor chamber, and subjected to 2 min of low light (50 μmol/m²/s of PAR, photosynthetically active radiation) followed by 6 min of high light (1000 μmol/m²/s PAR) to simulate a sunfleck. LiCor leaf chamber and leaf surface temperatures were maintained at 27 °C, humidity was maintained at 55–60%, and vapor pressure deficit was maintained at approximately 1.35 kPa; these conditions are representative of conditions in the understory during the growing season. Photosynthetic response variables were recorded continuously during the measurement period.

2.3. Data analysis

All analyses were performed using SAS (2006). For seedling height

Table 2

Environmental conditions in surface mineral soils (0–5 cm depth) by topographic position pH, %C, %N, and nutrient availability in parts per million.

	pH	%C	%N	Ca	Mg	K	P	Al
Valley	4.87	16.07	1.07	193.02	47.43	35.43	0.03	17.14
Midslope	4.53	9.16	0.51	31.26	5.92	16.62	0.06	40.27
Ridge	4.57	9.33	0.58	10.61	3.24	15.51	0.09	44.47

and survival analyses, data from the seedlings of each species within the 2 plots/site were pooled (i.e. treated as subsamples). Analysis of survival and seedling height were performed using a repeated measures analysis of variance within the GLM procedure using both univariate and multivariate approaches. Results were evaluated based on both methods, with univariate tests providing comparisons averaged over all time intervals and multivariate tests providing evaluation of temporal trends. For the multivariate approach, where assumptions of sphericity (equal variance within-subject pairs) were violated (based on Mauchly's sphericity test), the Huynh-Feldt (H-F) adjusted p-values were used. Analysis of net photosynthetic response to simulated sunflecks was also performed using the same procedures.

We used environmental data from Ashton et al. (1998) and Fladeland et al. (2003) to correlate seedling height and survival with environmental data (light, soil nutrients) (Tables 1 and 2). These analyses were performed using the PROC CORR procedure in SAS.

Finally, we presented an index of site association (SAI) to graphically present topographic association of the different species over time (Frey et al., 2007). The SAI was calculated for each species as:

$$\frac{(\text{abundance}_R - \text{abundance}_V)}{\text{abundance}_{R+M+V}}$$

where R = ridge position, M = midslope position, and V = valley position. Plotted over time for each sampling interval, the SAI graphically presents species demographic trends in relation to topography. The index yields values between 1 and -1, where a value of 1 indicates exclusive association with the ridge position, a value of -1 indicates exclusive association with the valley position, and values near 0 represents an intermediate association (i.e. a lack of association with either the ridge or valley positions). We calculated the SAI for each year of the study to assess trends in topographic association.

3. Results

3.1. Survival

Survival varied significantly by topographic position ($p = 0.0013$, H-F adjusted $p < 0.0001$) and between species ($p = 0.0008$, H-F adjusted $p < 0.0001$), and no interactions were evident between topographic position and species (Table 3). Overall, survival was highest for seedlings on the ridge sites (~53%), intermediate in the midslope position (~25%), and lowest in the valley (~19%) (Fig. 1). Survival patterns were remarkably consistent among the species, with survival in each position highest for *Q. rubra*, intermediate for *Q. velutina*, *Q. coccinea*, and significantly lower for *Q. ilicifolia* and *Q. palustris*. The pattern among species held for all topographic positions.

3.2. Seedling height

Overall, average seedling heights differed between species ($p = 0.0046$), among topographic positions ($p = 0.0199$), and changed over time ($p < 0.0006$) (Fig. 2, Table 3). Seedling height, averaged over time, was highest in *Q. rubra*, intermediate for *Q. velutina* and *Q. coccinea*, and lowest for *Q. palustris* and *Q. ilicifolia* (Fig. 2). Seedling height development was highest in the valleys, intermediate in ridge-tops, and lowest in midslope positions (H-F adjusted $p = 0.0051$).

Table 3

Results of repeated measures analysis of variance for survival, seedling height, and sunfleck response over time (S = species, P = topographic position, T = time, df = degrees of freedom, SS = sum of squares, Pr = probability, H-F = Huynh-Feldt correction).

Source	df	Type III SS	Mean SS	F	Pr > F	H-F Adj. Pr > F
<i>Survival</i>						
S	4	13.01	3.25	6.37	0.0008	
P	2	8.56	4.28	8.38	0.0013	
S * P	8	1.26	0.16	0.31	0.9566	
T	7	52.55	6.57	261.38	< 0.0001	< 0.0001
T * S	28	2.67	0.08	3.32	< 0.0001	< 0.0001
T * P	14	2.79	0.17	6.95	< 0.0001	< 0.0001
T * S * P	56	6.03	0.03	0.88	0.7308	0.6762
<i>Height</i>						
S	4	2456.25	614.06	5.61	0.0046	
P	2	1089.88	544.94	4.98	0.0199	
S * P	8	90.94	18.19	0.17	0.9717	
T	7	585.54	83.65	9.55	< 0.0001	0.0006
T * S	28	386.21	13.79	1.57	0.0492	0.1722
T * P	14	560.03	40.00	4.57	< 0.0001	0.0051
T * S * P	56	310.36	8.87	1.01	0.4627	0.4531
<i>Sunfleck</i>						
S	4	62.41	15.60	5.38	0.0172	
P	2	0.018	0.01	0.00	0.9969	
S * P	8	63.84	7.98	2.75	0.0766	
T	8	264.91	37.84	359.02	< 0.0001	< 0.0001
T * S	28	11.38	0.41	3.85	< 0.0001	0.0056
T * P	14	1.63	0.12	1.10	0.3729	0.3861
T * S * P	56	12.04	0.22	2.04	0.0032	0.0618

Height development among species was not significantly different (H-F adjusted $p = 0.1772$), however height trends for *Q. rubra*, *Q. velutina* and *Q. coccinea* suggested positive height growth as compared to *Q. palustris* and *Q. ilicifolia* which did not appear to gain in height.

3.3. Site association

Visual comparisons of site association using the SAI showed divergence over time reflecting differential survival among species in the different topographic positions. All species exhibited a greater association to the ridge position over time (Fig. 3). *Q. ilicifolia* and *Q. palustris* were the most strongly associated with the ridge position, with *Q. coccinea* and *Q. velutina* intermediate between ridge and midslope, and *Q. rubra* the least associated to the ridge.

3.4. Sunfleck response

No differences were evident across topographic positions ($p = 0.9969$, H-F adjusted $p = 0.3861$), but species differed in their response to the sunfleck treatment ($p = 0.01722$, H-F adjusted $p = 0.0056$) (Fig. 4, Table 3). There were no differences among species at the lower light level (50 $\mu\text{mol}/\text{m}^2/\text{s}$), with net photosynthetic rates averaging 2 $\mu\text{mol}/\text{m}^2/\text{s}$. When light was increased from 50 to 1000 $\mu\text{mol}/\text{m}^2/\text{s}$, rates of net photosynthesis increased, and this response differed among species. Net photosynthetic rates increased more rapidly for *Q. rubra*, *Q. velutina*, and *Q. coccinea* than for *Q. ilicifolia* and *Q. palustris* (Fig. 4). The same species also maintained higher photosynthetic rates over the entire measurement period.

3.5. Relationships between survival, seedling height, and environmental conditions

A number of strong correlations were evident between survival and environmental variables (Table 4). Interestingly, survival was positively correlated with Al concentration in addition to light availability, and negatively correlated with Ca, Mg, and pH; the last three soil variables

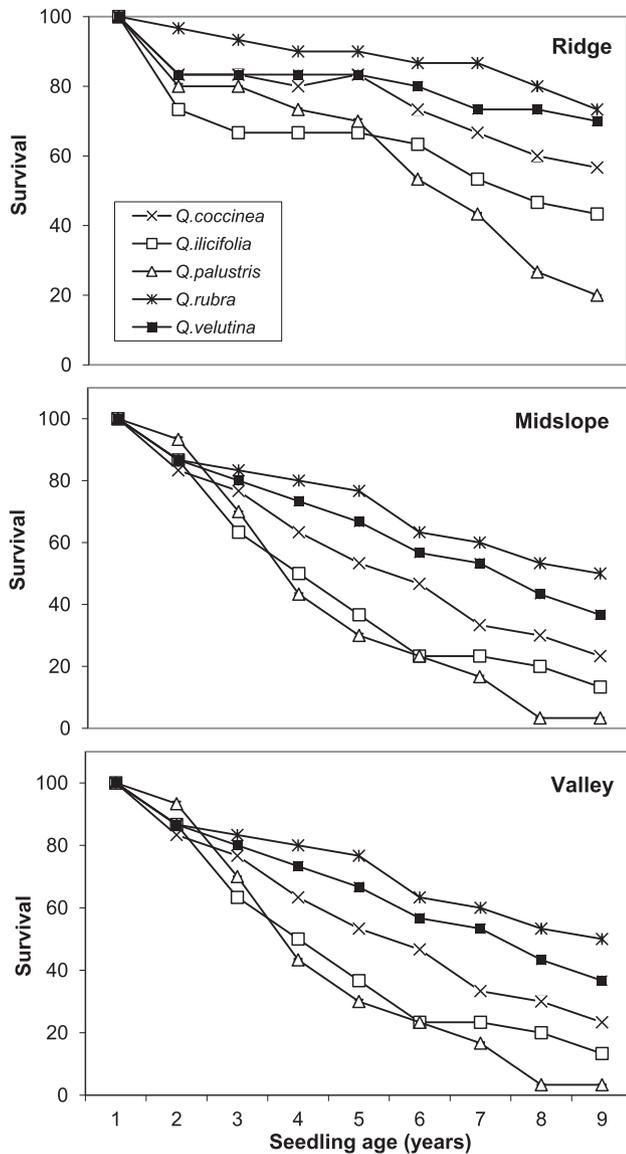


Fig. 1. Percent survival by topographic position for the five oak species.

were highly correlated (Table 2).

4. Discussion

While overall survival patterns varied topographically, relative survival patterns were remarkably consistent between species, providing limited evidence for habitat partitioning among these species during understory establishment. There was clear support for our main hypotheses: (1) that all species would have higher survival in upper slope positions; (2) that survival would differ among species, corresponding with their relative abundance in these forest types; and (3) that sunfleck response would also differ among species.

For all five species, survival increased moving from the valley position, through midslope, to the ridgetop. This confirmed our hypothesis of higher survival in upper slope positions. Oaks as a group are considered relatively shade intolerant, but with individual species of the red oak section (*Erythrobalanus*) differing in their photosynthetic capacity and shade-tolerance traits (Ashton and Berlyn, 1994). The higher understory light availability in the ridgetop positions and lower understory light availability in the valley positions would be expected to drive survival differences. The low understory light conditions (3% of full PPFD) would be expected to limit persistence of seedlings of less

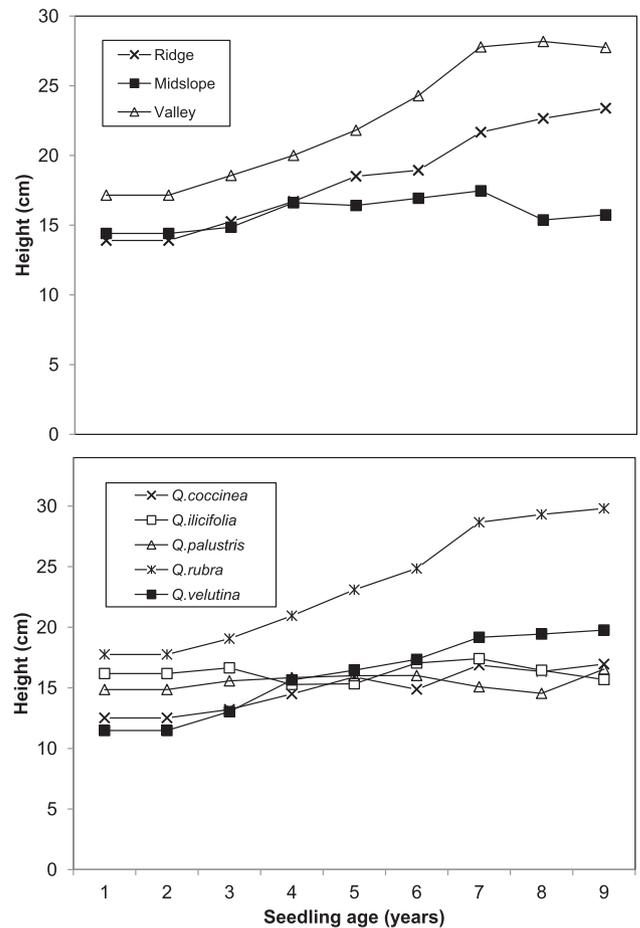


Fig. 2. Mean seedling height by topographic position and by species for individuals that survived until the end of the study.

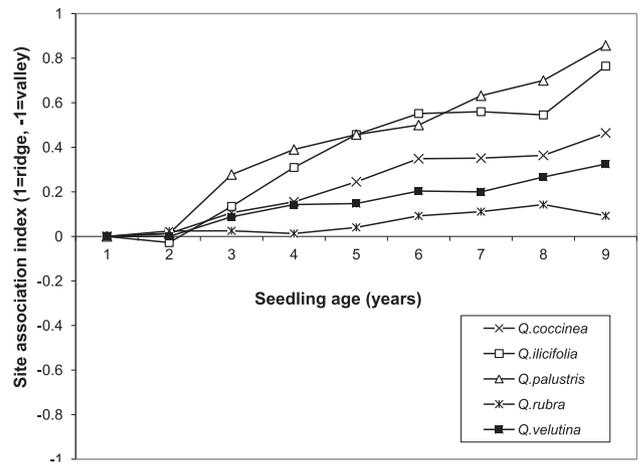


Fig. 3. Site association index (SAI) based on survival patterns among the species. SAI of 1 infers complete ridge association (lack of survival in valley or midslope), SAI of -1 infers complete valley association (lack of survival in midslope or ridge position).

shade tolerant species of the genus *Quercus* by constraining carbon gain (Kaelke et al., 2001). The more moderate light levels in the midslope and ridgetop positions (~3–5% of full PPFD on sunny days, and ~9% of full PPFD on cloudy days) would contribute to higher survival in upper slope positions.

Overall, as hypothesized, survival among species paralleled their relative abundances in forests within the region (*Q. rubra* dominates; *Q.*

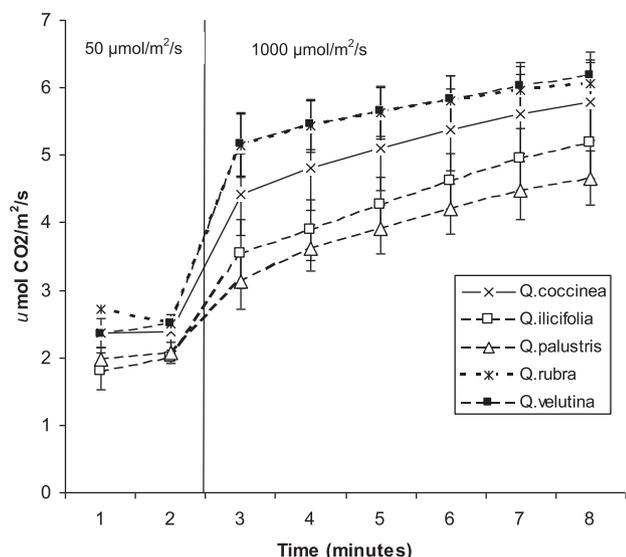


Fig. 4. Average photosynthetic rates (with SE) to simulated sunflecks (2 min at 50 $\mu\text{mol}/\text{m}^2/\text{s}$ followed by 6 min at 1000 $\mu\text{mol}/\text{m}^2/\text{s}$).

ilicifolia and *Q. palustris* are rare within the study area). This concurs with studies in other regions that suggest seedling abundance shows a strong positive correlation at landscape scales with overstory abundance (Comita et al., 2007; Canham and Murphy, 2016; Máliš et al., 2016). It also suggests that *Q. rubra*, and to a lesser extent *Q. velutina* and *Q. coccinea*, has a much wider regeneration niche, which allows it to establish across the wide range of site conditions that characterize the region.

In addition to the patterns above, we had expected that species would potentially show relative differences in survival across topographic positions (i.e. interaction of species x position), reflecting specialization to different habitat conditions. *Q. palustris* is a floodplain-associated species, yet it showed extremely low survival in the valleys. This suggests a higher degree of shade-intolerance, which is a characteristic of disturbance prone floodplain red oaks which are recognized to be among the most shade-intolerant canopy species in bottomland forest types (Oliver et al., 2005). Unfortunately, there is little physiological data on *Q. palustris*. Less surprising was the low survival of *Q. ilicifolia* in the midslope and valley, as it is commonly associated with xeric, open canopied communities on thin-soiled ridgetops where light is presumably not limiting. *Q. rubra*, on the other hand, is recognized as having a relatively higher degree of shade tolerance among the oaks (Kaelke et al., 2001; Kuehne et al., 2014), but lower maximum photosynthetic rates than other co-occurring red oaks (*Q. velutina* and *Q. coccinea*) in high light (Ashton and Berlyn, 1994). Even so, *Q. rubra* had superior survival rates in all positions.

As a consequence of survival patterns, site associations suggest that *Q. rubra* is the most site generalist of the group followed by *Q. velutina* and *Q. coccinea*, which again confirms their relative abundance patterns in the southern New England region (Westveld, 1956; Wharton et al., 2004) and in temperate hardwood forests of the eastern United States (Fei et al., 2011). Regeneration success should help support their wider distribution and importance in eastern hardwood forests, as greater persistence across all sites should confer greater probability of gap

colonization following canopy disturbance (Canham, 1989). Seedling height generally mirrored these trends as well, with *Q. rubra* showing greatest height development, and with *Q. ilicifolia* and *Q. palustris* showing almost no height gain. The latter two are planted off-site and near their range margins in this region (Burns and Honkala, 1990).

Light and soil characteristics correlated with, and likely contributed to, overall survival patterns. However, disentangling these effects is difficult given the high degree of correlation between the different environmental variables. Low light conditions are considered an important constraint on long-term survival of oak advance reproduction in the understory (Carvell and Tryon, 1961; Frey et al., 2007), and thus higher survival should be favored in more open light conditions characteristic of upslope positions (Fladeland et al., 2003). Even so, soil variables, particularly those related to soil acidity (pH, Ca, Mg, Al) tended to show an equal or greater degree of correlation with survival. Indeed, Al exhibited the highest correlation, which aligns with evidence from other studies that oaks show an association with more acidic, low fertility soils (Finzi et al., 1998) and that tolerance of Al may be an important determinant of seedling success, and thus control future distribution of canopy trees in temperate forests (Bigelow and Canham, 2010). Given the strong negative correlation between light and soil fertility, it is unclear which is the proximate driver of survival, but light seems more obvious as higher Al concentrations would not be expected to directly enhance survival. However, Al tolerance may have contributed to the enhanced survival of *Q. ilicifolia* over *Q. palustris* on the ridge sites, but other factors particularly greater drought-tolerance cannot be discounted. Nonetheless, the fact that *Q. palustris*, a floodplain species associated with higher pH and fertility sites, had higher survival on the more acidic upslope positions suggests a degree of Al tolerance across the red oak group. In the future, installation of fertilization studies such as that conducted by Bigelow and Canham (2010) may help refine these relationships.

Sunfleck response differed between the species, with photosynthetic response highest in *Q. rubra*, *Q. velutina*, and *Q. coccinea*, intermediate in *Q. ilicifolia* and lowest in *Q. palustris*. This differentiation among species, particularly evident between the abundant and marginal species, supported our hypothesis of species-specific differences in sunfleck response. Sunflecks contribute the majority of photosynthetic light for seedlings in eastern mixed-hardwood forest understories (Fladeland et al., 2003; Nilsen et al., 2009), particularly in mesic forest types. A study by Naumburg et al. (2001) on several temperate hardwoods of the eastern United States found that sunfleck response plays a critical role in carbon gain (and likely survival) at light levels below 3% of full sun (1.62 $\mu\text{mol}/\text{m}^2/\text{day}$). On our sites, average light levels on sunny days were somewhat higher than this threshold on the ridge (5.2%, 2.91 $\mu\text{mol}/\text{m}^2/\text{day}$), near this threshold in the midslope (3.2%, 1.66 $\mu\text{mol}/\text{m}^2/\text{day}$) and much lower in the valleys (1.6%, 1.01 $\mu\text{mol}/\text{m}^2/\text{day}$) (Fladeland et al., 2003). Low light conditions in the valleys, where canopy leaf area is higher than on ridge and midslope positions, would thus be expected to limit net carbon gain without the contribution of sunfleck photosynthesis (Naumburg et al., 2001; Fladeland et al., 2003). A more rapid sunfleck response, as evidenced in *Q. rubra*, and *Q. velutina*, would contribute to greater growth and survival (Zhang et al., 2012), making them better adapted for establishment as advance reproduction and thereby widening their regeneration niche. Supporting evidence for this mechanism is found in the greater height development in the valley. In contrast, photosynthetic adaptation to high light

Table 4

Pearson correlation coefficient (r) for correlations between seedling survival and environmental variables (r-values listed first with p-values directly below). Significant relationships indicated in bold text.

	Light	pH	C	N	Ca	Mg	K	P	Al
Survival	0.36	-0.32	-0.11	-0.12	-0.37	-0.40	-0.23	0.30	0.47
	0.01	0.03	0.48	0.44	0.01	0.01	0.12	0.05	0.00

environments is known to limit photosynthetic efficiency during sunflecks (Chazdon, 1988), which may explain the weaker sunfleck response evident among *Q. ilicifolia* and *Q. palustris* which predominate (and likely regenerate) in more disturbed or exposed conditions where sunflecks are less important. As a consequence, their regeneration niche appears constrained.

Given the importance of sunflecks in these light-limited forest understories (providing 43–80% of daily light in the understory) (Fladeland et al., 2003), we cautiously suggest that sunfleck response played a contributing role in the observed survival patterns. One major challenge is that light regimes are dynamic and the integrated responses of plants to variable light conditions can make it difficult to isolate the significance of sunflecks on growth and survivorship of understory plants (Chazdon, 1988). While studies such as Naumburg et al. (2001) have highlighted the importance of sunflecks at low light (< 3% of full), tying sunflecks to survival still requires integration of daily and seasonal contributions. We correlated average daily PPFD, which integrates diffuse and direct light, with survival and thus can only indirectly tie sunfleck response to survival outcomes. A modest correlation was found between light and survival ($r = 0.36$), which is fairly reasonable considering the high degree of microsite variation in moisture and soil fertility of the rocky, glacial till soils on these sites (McKenna, 2007). Assuming the 3% light threshold at which sunflecks become a determinant of carbon gain (Naumburg et al., 2001), their importance would begin to diminish from the midslope to the ridge position. Greater height development in the valley, where sunflecks should be critical, provides further support for the importance of sunflecks in carbon balance. At the same time, we cannot discount other factors that might have contributed to species-specific survival differences, e.g. leaf dark respiration (Ashton and Berlyn, 1994; Kuehne et al., 2014). Future studies that evaluate seedling performance and survival under controlled sunfleck regimes that can be integrated over extended time scales are needed to directly link sunfleck response, carbon balance, and survival. Even so, species-specific sunfleck responses showed strong alignment with observed survival patterns in this study, in line with the view that photosynthetic response to sunflecks can contribute to growth and survival differentiation among related species (Leakey et al., 2005; Zhang et al., 2012) and can thus shape a species regeneration niche.

5. Management implications

The results of this study suggest several management implications with regards to the regeneration of red oak species across diverse environmental gradients in southern New England. With respect to natural regeneration methods, results indicate that *Q. rubra* is much more persistent and exhibits better growth than the other oaks across a range of site conditions. As such, it has a general establishment advantage relative to associated oaks, a point of consideration when applying silvicultural treatments; targeted interventions such as timely overstory removal may be needed to promote and maintain the less abundant species when regenerating stands. In addition, natural regeneration treatments likely need to be applied earlier in lower slope positions to capture regeneration following oak masting events, as mortality rates are much higher and there is greater likelihood of losing advance reproduction. This is particularly true if a diverse assemblage of red oaks (*Q. rubra*, *Q. velutina*, *Q. coccinea*, and possibly *Q. palustris*) is to be maintained in lower slope positions. Another set of implications of these results is for enrichment planting in instances where restoration or supplementation of red oaks is desired. Overall, greater survival in midslope and ridgetops suggests that enrichment planting will be more successful in upper slope positions, where oaks are best adapted for longer-term growth and survival. Nonetheless, *Q. rubra* has the greatest potential for persistence and growth in the valley position (nearly 60% at 8 years), suggesting it is the most suitable of the red oak group for enrichment planting in lower slope positions. Finally, successful

recruitment to the canopy will depend upon overstory disturbance, and future studies should evaluate the potential for releasing under-planted red oak and promoting them into the canopy.

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