Forest Ecology and Management 419–420 (2018) 179–186

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# 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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ARTICLE INFO

*Keywords:*
Fundamental niche
Realized niche
Seedling survival
Niche partitioning
Sunfleck
Topography
Gradients
Congeneric

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* Wangenh. (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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https://doi.org/10.1016/j.foreco.2018.03.030
Received 31 July 2017; Received in revised form 14 February 2018; Accepted 16 March 2018
Available online 30 March 2018

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-Rodriguez 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;