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Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests

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Abstract

In many forests, advance regeneration represents an important 'seedling bank' for replacing overstory trees after canopy disturbance. However, long-term spatial and temporal dynamics of understory tree seedlings are poorly understood, particularly in topographically complex southern New England mixed-deciduous forests. From 1996 to 2005 we tracked the recruitment, growth and survival of seedlings of masting tree species across different topographic positions. Species included the largely valley associated sugar maple (*Acer saccharum*) and white ash (*Fraxinus americana*), the primarily ridge associated white oaks (*Quercus alba* and *Q. prinus*), and the site generalist red oaks (*Q. rubra and Q. velutina*) and red maple (*A. rubrum*). Four 1 m^2 circular plots were randomly established in nine different sites, which included three replicates of each topographic position (ridge, midslope and valley). Seedling recruits were tagged and measured annually. Densities varied largely between species, both over time and by topographic position. Ridge and midslope positions had similar patterns, with high densities of red oak (>200,000 seedlings/ha) declining over time, and other species generally fluctuating at much lower densities (<10,000 seedlings/ha). Trends differed in the valley, where higher white ash and sugar maple densities resulted in overlap with red oak. Overall declines in density were largely driven by a lack of significant recruitment events of red oak during the study, suggesting that seedling dynamics are driven by longer (decadal) cycles, likely reflecting the interaction of temporal variation in masting and conditions for establishment. Total recruitment for all species was positively related to overstory composition, as expected given topographic associations between species. Survival varied between species, but differed among topographic positions. White ash and sugar maple had relatively low survival in midslope and ridge positions relative to the red and white oaks, but higher survival than red oaks in valleys. Red maple had low overall survival, and only persisted beyond age 10 in the midslope position. Seedling heights generally increased with age for all species, but growth was slow, and many seedlings exhibited dieback. These survival patterns likely reflect effects of light limitation (in the valley) and moisture limitation (in the ridge) associated with topographic position. Overall, while seed inputs likely vary topographically related to differences in overstory abundance, differences in survival clearly reinforce these distributional patterns. In management terms, these survival patterns have significant site-specific implications for the type and timing of silvicultural interventions aimed at stand regeneration, particularly given infrequent events of seedling recruitment.

Keywords: *Quercus rubra*; *Acer saccharum*; Regeneration; Soil moisture; PPFD; Shade tolerance

1. Introduction

Advance regeneration, tree seedlings that establish and persist in the forest understory, represents an important 'seedling bank' (*sensu* Grime, 1979) for replacing canopy trees after canopy disturbance. Indeed, for many tree species, advance regeneration is the primary means by which they are recruited into the forest canopy after disturbance (Smith and Ashton, 1993). The dynamics of understory seedlings can be complex, as recruitment, growth, and survival fluctuate with annual seed production (Boerner and Brinkman, 1996; Marks and Gardescu, 1998), site conditions (Jones and Sharitz, 1998), annual variation in climate (Houle, 1994), animal damage (Kittredge and Ashton, 1995; Boerner and Brinkman, 1996; Marks and Gardescu, 1998) and between species and seedlings of different ages (e.g. Glitzenstein et al., 1986). Understanding

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the complexity of understory seedling dynamics requires longer-term studies that track the establishment, growth, and survival of individual seedlings. However, relatively few studies have tracked long-term (>5 years) dynamics of advance regeneration (Jones and Sharitz, 1998) and little information is available for understory seedling dynamics in southern New England forests (but see Ward et al., 1999). Longer-term studies are necessary to enhance our knowledge of understory seedling dynamics and improve management activities aimed at stand regeneration (Larsen and Johnson, 1998).

Recruitment patterns of seedlings depend on a number of factors, particularly the availability of seed producers, temporal patterns of seed production, and germination conditions. Many of the dominant hardwood species in southern New England forests produce large seed crops only intermittently, a phenomenon known as masting. These species include red oak (*Quercus rubra* L.) (Healy et al., 1999), white ash (*Fraxinus americana* L.) (Boerner and Brinkman, 1996), sugar maple (*Acer saccharum* Marsh.) (Boerner and Brinkman, 1996; Marks and Gardescu, 1998) and red maple (*Acer rubrum* L.) (Burns and Honkala, 1990). Pulses of seed production at irregular intervals, the 'storage effect' (Warren and Chesson, 1985), should produce large fluctuations in seedling establishment and population densities over time. Recruitment will also vary with the availability of seed sources and germination conditions. As many of these species show topographic associations, seed inputs (Ashton et al., 1998) and seedling recruitment will likely reflect topographic differences in overstory composition (Boerner and Brinkman, 1996; Collins and Carson, 2004). Furthermore, seedbed conditions (e.g. moisture) and seed size (reserves for initial growth) may also determine establishment patterns by affecting germination and early growth (Ashton and Larson, 1996; Battaglia et al., 2000; Garcia et al., 2002). Spatial and temporal variations in seed production and establishment will thereby contribute to complex dynamics in populations of understory seedlings.

Growth and survival of established seedlings in the understory will likely vary, to a large degree, by topography, which is a strong proxy for environmental conditions (e.g. Ashton et al., 1995; Ashton et al., 1998; Daws et al., 2002). In southern New England forests, topography creates broad gradients in resource availability, particularly light and moisture, which likely influence growth and survival of different species. Ridge positions are more subject to drying (Ashton and Larson, 1996), and thus should generally favour more drought-tolerant species such as oaks (Burns and Honkala, 1990). Higher leaf area development in valleys, driven by high moisture and nutrient conditions (Ashton et al., 1998), causes light availability to decline in lower slope positions (Fladeland et al., 2003). Observed declines in understory light availability from 9% (of full light) in ridge and midslope positions to 3% in valleys (Fladeland et al., 2003) should favour more shade tolerant species. Survival is clearly a function of a species shade tolerance, and large differences in survivorship amongst northern hardwood species emerge at low light levels (<5%) (Kobe et al., 1995). Height growth also tends to be lower under denser overstory conditions, as seen in red oak (Dey and Parker, 1997; Crow, 1992) and sugar maple (Marks and Gardescu, 1998). Nonetheless, despite low rates of growth in the understory, shade tolerant species such as sugar maple can form persistent long-lived seedling banks under a closed canopy (Marks and Gardescu, 1998). Other factors such as competition from herbaceous understory species (George and Bazzaz, 1999) or deer browse can severely reduce survival of understory seedlings, and may in some cases override the importance of environmental/climatic factors in determining survival (Kittredge and Ashton, 1995; Boerner and Brinkman, 1996).

Studies have documented distinct differences in patterns of germination and early growth of different oak species related to different canopy and site conditions in southern New England forests (Ashton and Larson, 1996). The purpose of this study is to examine long-term patterns of seedling recruitment, growth, and mortality, particularly in relation to topographic position. Specifically, this study examines the understory dynamics of advance regeneration of masting species of ash, maple, and oak. Based on commonly observed distributions of adult trees, these species show different site affinities (Burns and Honkala, 1990). In southern New England forests, white ash and sugar maple are strongly associated with the high moisture conditions of valley sites, as is red maple, although it is common in upper slope positions as well. In contrast, xerophytic oaks with greater drought tolerance such as white oak (*Q. alba*) and chestnut oak (*Q. prinus* L.) are more strongly associated with upper slope positions (midslope and ridge). Red oaks (red and black oak, *Q. velutina* L.) are more widely distributed across topographic positions. Based on differences in site affinity among species, and large topographic changes in light and moisture availability, we hypothesize the following:

1. Seedling recruitment and densities will show large year-to-year variation.
2. Recruitment will be positively correlated with a species overstory composition (basal area).
3. For a given species, growth and survival will be positively correlated with its overstory composition, i.e. survival patterns will reinforce existing vegetation patterns.
4. Among species within the same site, we expect differences in growth and survival related to environmental tolerances (particularly shade and drought) such that survival will be highest for the species most specialized to that site, i.e. species with higher shade tolerance favoured in the valley, and higher drought tolerance favoured on the ridge.

2. Methods

2.1. Site description

The experiment was conducted at the 3160 ha Yale Myers Forest in northeastern Connecticut (41°57′N, 72°07′W). The topography is undulating, with parallel ridges and valleys ranging from 200 to 350 m above mean sea level. Study sites were located in 70- to 90-year old mixed-deciduous stands that