

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 m² 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.

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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

had arisen from advance regeneration following removal of old-field pine. The pine had colonized abandoned pastures after 1850. Sites have been described in detail by Ashton et al. (1998) and Fladeland et al. (2003). Sites were selected for the study to include representation of the common range of topographic positions (valley, midslope, and ridge). 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 in the upper slope positions (Ashton et al., 1998). Canopy composition also differed among the topographic positions (Table 1). Valley sites were composed primarily of equal amounts of sugar maple, tulip poplar (*Liriodendron tulipifera* L.), white ash, red oak, and birch (*Betula* spp.), while midslope sites were dominated by red oak, and the overstory of ridge sites were comprised largely of red oak and hickory (*Carya* spp.) species. Light availability in the understory declined from approximately 9% of full light in the

upper slope positions (mid and ridge) to 3% in the valley position (Fladeland et al., 2003).

2.2. Experimental design

In 1996, a total of nine sites were selected, with three replicates of each topographic position (ridge, midslope and valley). Within each site, four 1 m² circular plots were randomly established. Plots were marked with a central stake and all seedlings of the species of interest (oak, maple and ash) were identified and aged by counting the number of flushes. Seedlings that were in their 2nd year or older were tagged and heights and flushes were recorded. Year of recruitment of seedlings present at the initiation of the study were estimated based on counts of flushes. Plots were revisited annually during the growing season to record seedling survival, height, number of flushes, and evidence of dieback over a 10-year period (1996–2005). In addition, any new recruits (greater than one year old) were tagged and measured. Because first-year mortality is typically high for ash, maple, and oak species (e.g. Hett and Loucks, 1971; Collins, 1990; Boerner and Brinkman, 1996; Jones and Sharitz, 1998; Küßner, 2003), most germinants fail to establish and thus are not considered to be advance regeneration (Marquis, 1982). Consequently, for the purposes of this study, we considered established seedlings to be those seedlings >1 year in age. Over the course of the study period, a total of 1212 established seedlings were identified, tagged, and monitored. These included 132 red maple, 759 red oak, 79 sugar maple, 225 white ash, and 17 white oak seedlings.

2.3. Data analysis

All analyses were performed using SAS (2006). Data from the four circular plots in each site were pooled (i.e. treated as subsamples) for purposes of analysis. Density and recruitment patterns were analysed in SAS using repeated measures analysis of variance within the GLM procedure using both univariate and multivariate approaches. Results were evaluated based on both methods, and where sphericity assumptions were violated the Huynh–Feldt adjusted *p*-values were used.

Regression analysis of total recruitment (including the initial population in 1996) by overstory basal area was performed using the REG procedure in SAS.

Analysis of survival was performed in SAS using a Cox proportional hazard model (PHREG procedure), a regression approach that evaluates time until failure (death) (Cox and Oakes, 1984). This analysis has been employed in previous studies of tree seedling survival (e.g. Clark, 2002), and is a suitable approach to evaluate survival patterns between treatments where the cumulative hazards over time (hazard functions) are generally proportional. Furthermore, proportional hazards regression models can accommodate censored data (i.e. unknown data) that result from experimental units not having yet failed (i.e. seedlings that are still alive at the time of analysis) and or seedling cohorts that have entered the study at different stages (i.e. seedlings more than 2 years of age at the start of the study). For purposes of this analysis, all seedlings

Table 1
Overstory basal area (m²/ha) of all woody plants greater than 2.5 cm at diameter breast height (dbh)

Species	Topographic position		
	Valley	Midslope	Ridge
Sugar maple ^a	6.06	1.16	0
Red oak ^b	5.95	14.93	8.99
Tulip poplar ^c	5.87	0	0
Tolerant birches ^d	5.64	1.51	0
White ash ^e	5.34	0.1	0.20
Shagbark hickory ^f	3.62	1.78	1.72
Red maple ^g	2.04	2.3	0.04
Eastern hemlock ^h	1.08	0	1.51
Other ⁱ	0.07	0.88	0.15
White oaks ^j	0	1.75	3.29
Upland hickories ^k	0	0.53	9.95
Understory treelets ^l	0.29	0.04	0.02
Total overstory basal area (m ² /ha)	35.96	24.98	25.87
Stand characteristics			
Canopy height (m)	29.72	26.00	19.72
LAI	6.00	5.33	4.66
% PPF to open	3.00	9.3	8.7

Values represent averages of three sites for each position, based on 2–8 m radius fixed area sample plots per site.

^a *Acer saccharum* Marsh.

^b *Q. rubra* L., and *Q. velutina* Lam.

^c *Liriodendron tulipifera* L.

^d *Betula lenta* L. (black birch) and *B. alleghaniensis* (yellow birch).

^e *Fraxinus americana* L.

^f *Carya ovata* (Mill) K. Koch.

^g *A. rubrum* L.

^h *Tsuga canadensis* L.

ⁱ *Ulmus americana* (American elm), *B. papyrifera* (white birch), *Pinus strobus* (white pine).

^j *Quercus prinus* L. (chestnut oak) and *Q. alba* L. (white oak).

^k *C. glabra* ([Mill] Sweet.) (pignut hickory) and *C. tormentosa* (Poir.) Nutt. (mockernut hickory).

^l *Carpinus caroliniana* Walt., *Cornus florida* L., *Ostrya virginiana* (P. Mill.) K. Koch.

present during the study period were normalized by age, and included in the analysis, subject to the censoring rules above. Plots of log cumulative hazard over time for different treatments were generally parallel indicating proportionality (Clark, 2002). Likelihood ratio tests were then used to determine significant differences between species and topographic positions.

Analysis of growth was limited by the large differences in survival times among the species. For this reason, growth data was summarized by age and fitted with exponential growth curves for qualitative comparison only.

Finally, we developed an index of site association (SAI) to predict the population dynamics of cohorts over time with respect to topographic position. The SAI was calculated for each species as:

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

where R is the ridge position, M the midslope position, and V is the valley position. Plotted over time for a given cohort, 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).

For purposes of this simulation, we allocated 100 seedlings of each species to each position in which it established during the study period. All species occurred in all positions, except for white oak; it did not establish in the valley and thus no seedlings were allocated to white oak in the valley position. The number of seedlings surviving at each age was predicted based on the survival data. The SAI was then calculated on these cohorts over time, based on the SAI equation above.

3. Results

3.1. Density

Overall, seedling densities declined during the course of the study, reflecting the downward trend of the numerically dominant red oaks (Fig. 1). Densities differed substantially among species, but trends differed both over time and depending upon position (Table 2). 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 lower densities (<10,000 seedlings/ha). Notable fluctuations included sharp increases in red maple densities in 2004 and increases in sugar maple in 2002 and 2004 (midslope). Trends differed in the valley over the study period, where higher white ash and sugar maple densities and a lower density of red oak resulted in overlap among these species. Density declines in red oak were greater than in white ash in the valley, decreasing from approximately 100,000 seedlings/ha to

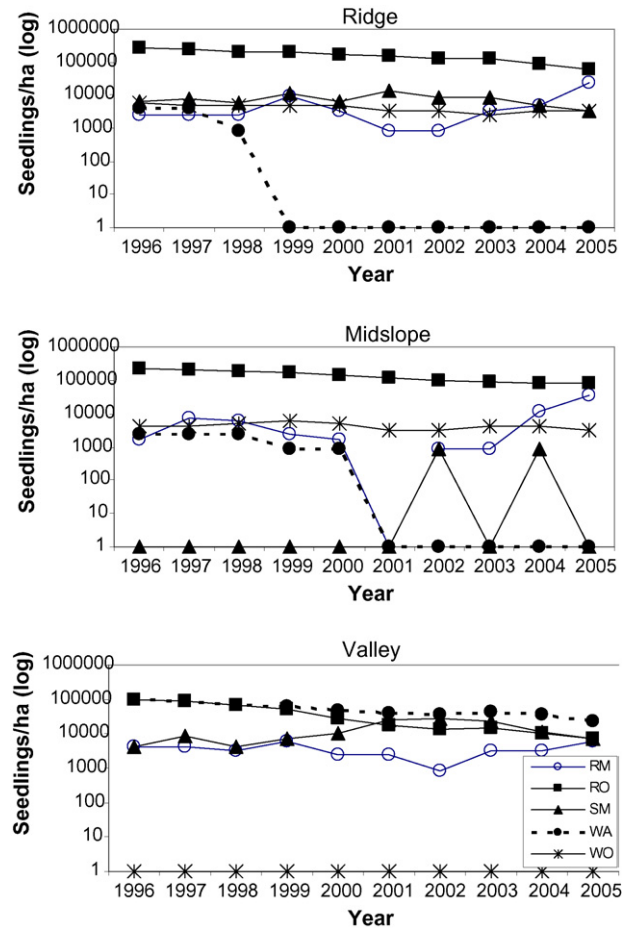


Fig. 1. Annual density by species for ridge, midslope and valley positions.

40,000 seedling/ha for white ash and 10,000 seedlings/ha for red oak. Sugar maple density fluctuated upwards above 25,000 seedlings/ha.

3.2. Recruitment

There were large variations in establishment among the different species (Fig. 2). The effect was again dependent upon position and differed temporally among the species (Table 2). Red oak establishment was extremely high during the 1993–1995 period, reflecting the particularly heavy mast year in the region in 1993 (Healy et al., 1999). Subsequent red oak recruitment was low, except for a small increase in 2002–2003, likely related to a heavier mast in 2002 (Ashton, personal observation). White ash recruitment showed a similar but less dramatic increase as red oak during 1993–1995 period, although at lower densities and with no increase in 2002–2003. In contrast to red oak and white ash, sugar maple recruitment was relatively low, but increased in 1998, 2000, and 2002. Red maple recruitment was also low in most years, except for increased recruitment in 1996, 1998 and large recruitment in 2003 and 2004. White oak recruitment was also low in most years, except for elevated recruitment in 1994. Finally, recruitment trends varied by position; red maple, and red and white oaks were higher

Table 2
Results of repeated measures analysis of variance for density and recruitment over time

Variable	Source	d.f.	Type III SS	Mean SS	F	Pr > F	H–F Adj Pr > F	Wilks–Lambda probability
Density	sp	4	134348.4	33587.1	22.22	<0.0001		
	pos	2	2725.1	1362.5	0.9	0.4167		
	sp × pos	8	50512.5	6314.1	4.18	0.0019		
	time	9	8439.1	937.7	21	<0.0001	<0.0001	0.0112
	time × sp	36	27810.8	772.5	17.3	<0.0001	<0.0001	<0.0001
	time × pos	18	466.2	25.9	0.58	0.9127	0.6946	0.0097
	time × sp × pos	72	5021.1	69.7	1.56	0.0061	0.0985	0.0327
Recruitment	sp	4	2377.7	594.4	18.63	<0.0001		
	pos	2	17.5	8.8	0.27	0.7617		
	sp × pos	8	864.2	108	3.39	0.0069		
	time	16	7464.9	466.6	28.1	<0.0001	<0.0001	<0.0001
	time × sp	64	23714.8	370.5	22.32	<0.0001	<0.0001	<0.0001
	time × pos	32	527.8	16.5	0.99	0.4798	0.4256	<0.0001
	time × sp × pos	128	4662.9	36.4	2.19	<0.0001	0.009	<0.0001

sp, species; pos, topographic position; d.f., degrees of freedom; SS, sum of squares; Pr, probability; H–F, Huynh–Feldt correction.

in ridge and midslope positions, and sugar maple and white ash were highest in valley and midslope positions.

As expected, total recruitment for all species was positively related to overstorey composition ($r = 0.57$, $n = 45$, $p < 0.01$), although with considerable variability (Fig. 3).

3.3. Survival

Overall, survival varied between species ($p = 0.0002$, maximum likelihood test), but responses differed among the topographic positions (Fig. 4). Red oak had significantly lower survival in valley positions and highest survival in the ridge positions and midslope positions (25, 12, 0% survival for ridge, midslope and valley, respectively, at age 13) ($p < 0.0001$, max. likelihood test). In contrast, white ash showed persistent survival in the valley and high mortality in the upper slope positions (0% survival by age 5 and 8 for midslope and ridge positions, respectively) ($p = 0.02$, max. likelihood test). Sugar maple and red maple only survived beyond year 10 in the valley and midslope positions, respectively, although neither effect was significant. White oak survival was relatively similar between the midslope and ridge positions where it was found. Low sample sizes likely limited the power of the analyses for sugar maple, red maple and white oak.

3.4. Growth

Average seedling heights generally increased with age for all species (Fig. 5). Average height growth was generally less than 1 cm/year for all species, and appeared to be slowest in the midslope positions, intermediate in the ridge positions, and highest in the valleys. Site specialists white oak and sugar maple exhibited the highest estimated growth in their associated sites, ridge and valley positions, respectively. Shoot dieback was common, particularly in the oaks, and contributed to negative growth in some years. Height

appeared to be positively related to long-term survival (Fig. 6).

3.5. Site association index (SAI)

Strong trends in site association were predicted for equal sized cohorts of the five species. White ash showed the most rapid trajectory towards site association (Fig. 7), surviving only in valley positions by year 8. By year 11, sugar maple also became completely associated with the valley position. In contrast, white oak and red oak were associated more strongly with the ridge position, although red oak showed a stronger directional trend towards association with the ridge position than did white oak. Red maple showed an intermediate association, persisting only in the midslope position beyond year 9.

4. Discussion

There were clear topographic patterns in the establishment, survival and growth of advance regeneration in these mixed hardwood forests of southern New England. As evident in other studies (e.g. Shibata and Nakashizuka, 1995; Collins and Carson, 2004), patterns of establishment generally reflect topographic patterns in overstorey distribution and the generally understood site affinities of the different species. However, it is also evident that survival and growth, at least for red oak and white ash, are lower in positions considered to be less optimal based on topographic associations of the overstorey. This suggests that, while poor dispersal may limit establishment in positions where a species is less frequent (e.g. Ashton et al., 1998), poor growth and survival reinforce these topographic patterns.

Establishment by the species in this study showed large year-to-year variation, as expected for masting species that produce seed crops only intermittently. This corresponds with other longer-term studies of understory seedling banks (e.g. Boerner

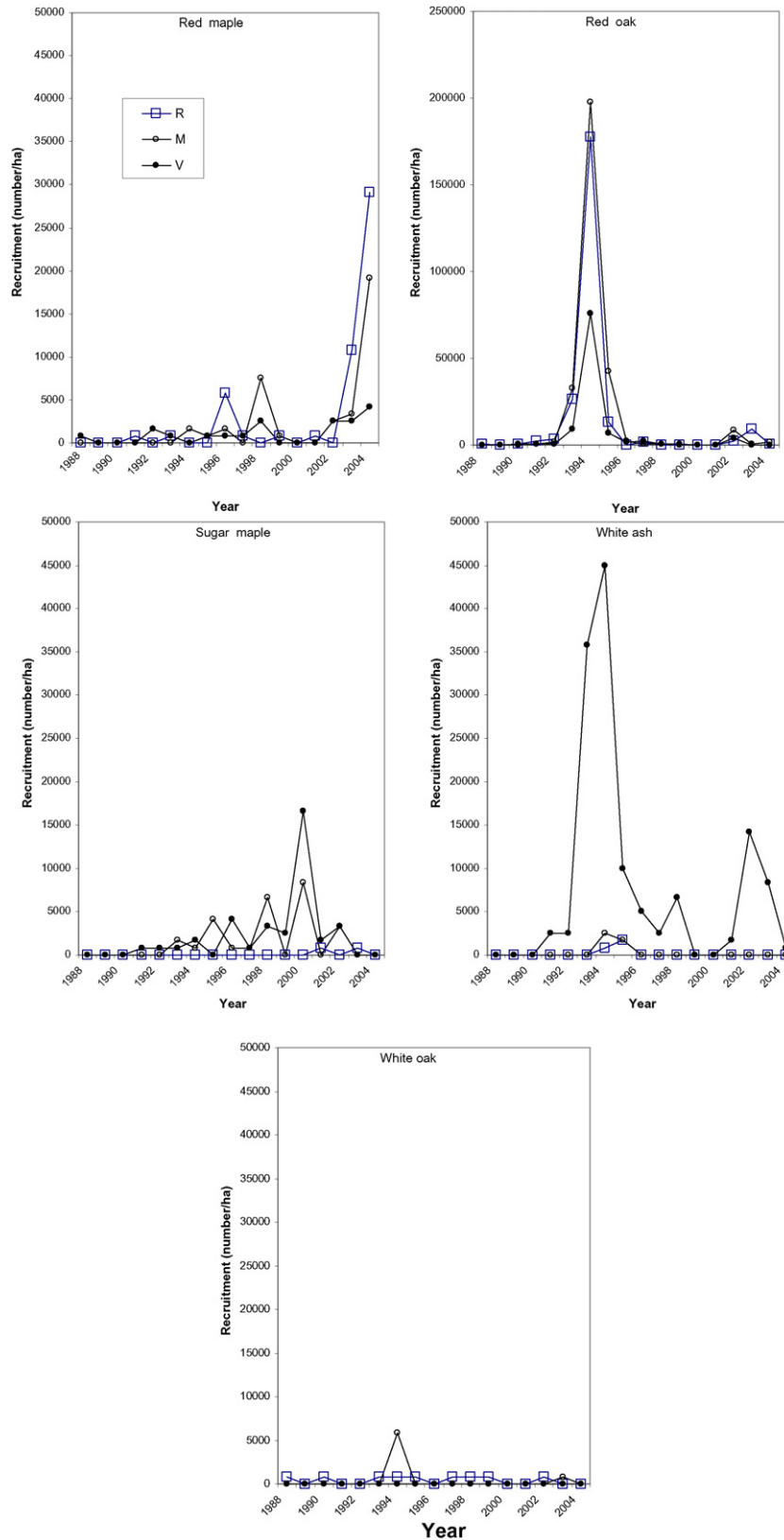


Fig. 2. Annual recruitment (seedlings/ha) by position for red maple, red oak, sugar maple, white ash, and white oak. Note the different scale for red oak.

and Brinkman, 1996; Marks and Gardescu, 1998; Gracia et al., 2001) that have documented large variation in annual recruitment of masting species of oak, ash and maple. There were also extreme differences in establishment density between

species. Red oak established at very high densities (>200,000 seedlings/ha in upper slope positions), greater than all the other species combined, and dominated the composition of the seedling bank for the duration of the study. This contrasts

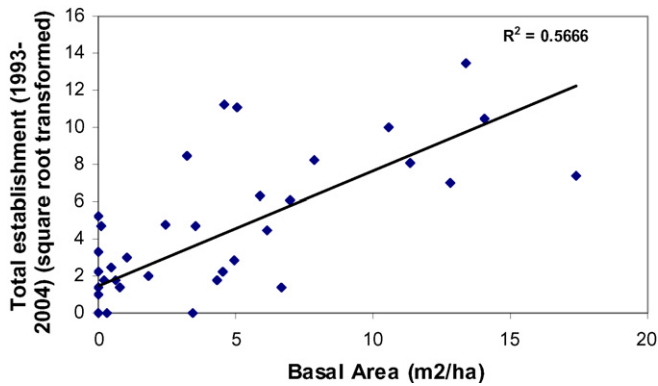


Fig. 3. Regression of total establishment (1993–2004) against basal area (m^2/ha). Total establishment square root transformed.

with earlier studies in the region that observed more balanced composition and much lower densities (<2500 seedlings/ha) among advance regeneration of red maple, sugar maple and red oak (Kittredge and Ashton, 1990). Although establishment in the valley positions was more balanced between red oak, sugar maple and white ash, densities still fluctuated substantially over the study period. Large temporal and spatial variation in establishment densities suggests caution must be used in interpreting regeneration data acquired from a single sampling time.

Survival patterns of understory seedlings generally corresponded with overstory composition, with species showing higher levels of mortality where they do not predominate in the canopy. Highest survival was thus evident for red oaks in the upper slope positions, for red maple in the midslope, and for white ash and sugar maple in valleys, in topographical correspondence with their adult distribution. Topographic associated patterns of survival likely reflect trade-offs in shade tolerance and drought tolerance among the different species. Of the species included in the study, sugar maple is considered to be highly shade tolerant, followed by the mid-tolerant red maple and red oak, and less shade tolerant white oaks and ash (Burns and Honkala, 1990; Smith and Ashton, 1993; Kobe et al., 1995; Ashton et al., 1999). As differences in light-driven mortality become evident below 5% light (Kobe et al., 1995), we expected differences to be most pronounced in the valley position where light levels averaged 3% of open conditions (Fladeland et al., 2003). Sugar maple, the most shade tolerant of the group, showed the highest survival rates under the low light conditions in the valleys. White ash and red oak, both considered less shade-tolerant than sugar maple had much lower survival rates in the valley. Nonetheless, red maple exhibited high mortality overall, suggesting that its relative high shade tolerance is not the critical factor controlling its early survival. We suspect its small initial stature makes it vulnerable to early mortality; this could explain why small red maple seedlings are commonly observed at high densities, but are much less frequent in the understory as larger seedlings (>50 cm) (Kittredge and Ashton, 1990). In the upper slope positions, light conditions of 9% of open were unlikely to drive large differences in mortality (Kobe et al., 1995). Rather we suspect drought tolerance became more important, causing the

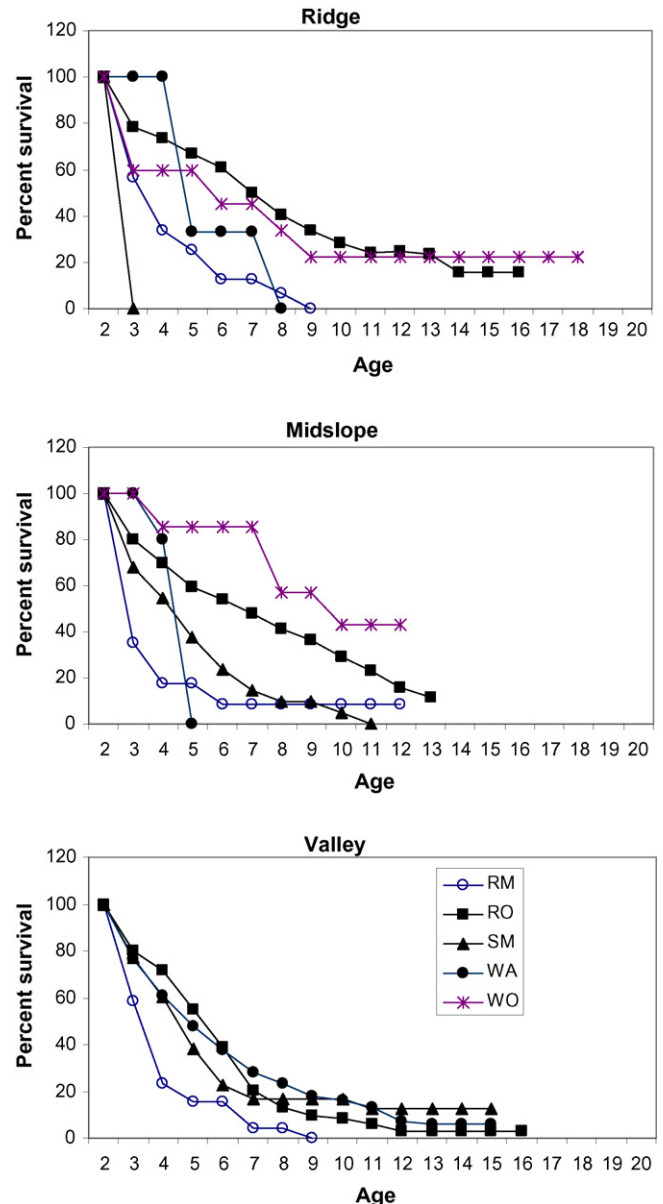


Fig. 4. Percent survival across slope positions for all species normalized by age.

relatively moisture demanding white ash seedlings to rapidly die out in the upper slope positions. In contrast oak survival was high in the upper slope positions, reflecting greater drought tolerance associated with high allocation of growth below-ground (Ashton and Larson, 1996). Finally, lower nutrient availability in upper slope positions (Ashton et al., 1998) could be limiting for white ash and sugar maple, thus contributing to their reduced survival, however, these mechanisms need to be directly tested in future studies.

Height growth also varied topographically, largely paralleling the survival patterns of the different species. Growth was highest for white oak in the ridge, and sugar maple and white ash in the valleys, corresponding to their site affinities and likely reflecting their respective tolerances to soil moisture limitation (white oak) and shade tolerance (sugar maple). Furthermore, while the oaks (red and white) accrued height

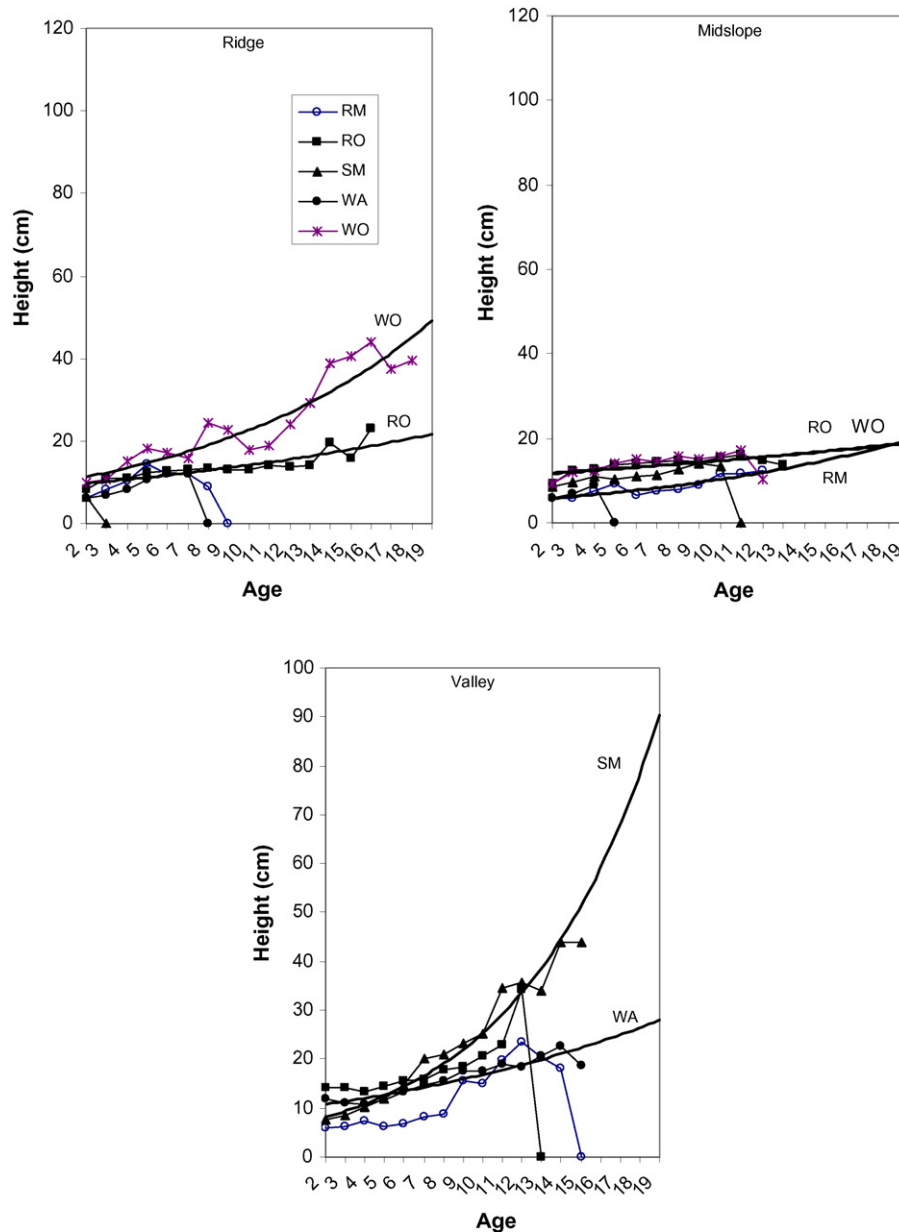


Fig. 5. Growth patterns for all species by position. Exponential curves fitted to surviving species (for comparison only).

growth in the midslope position, it was relatively higher for red maple and sugar maple. Thus, while the larger seeds of oaks may confer an early height advantage relative to the smaller seeded maples and white ash, this advantage is not maintained. There was some evidence to support the hypothesis that higher light conditions on the ridges favour higher growth, at least for the white oaks, if not for the red oaks. In red oaks, growth is preferentially allocated to the root system in upper slope positions (Ashton and Larson, 1996), which could offset height growth that typically occurs with increasing light availability (Crow, 1992; Marks and Gardescu, 1998). Overall, height growth was limited, rarely exceeding 1 cm/year, but only for sugar maple in the valleys and white oak in the ridge position. Weak height growth is common in understory seedlings, as observed in other long-term studies (e.g. Crow, 1992; Marks and Gardescu, 1998). The limited height growth and high

degree of dieback/terminal damage (particularly in the oaks) may reflect the impacts of high deer densities and browsing in this region (Kittredge and Ashton, 1995).

Browsing and acorn consumption by deer may have been an important factor affecting establishment, growth and survival dynamics over the course of the study. Regionally deer densities (Connecticut Zone 4 and 5) increased over the course of the study period, averaging 8.2 deer/mile² in 1993, 16.4 mile⁻² in 1996, 20.2 mile⁻² in 1999, and 18.5 mile⁻² in 2003 (Gregonis, 1993, 1996, 1999, 2003). As acorns of white and red oaks are an important diet component of white-tailed deer in New England (Pekins and Mautz, 1987), increasing deer population may thus have reduced oak seedling establishment over the study period. Growth and survival trends may also reflect the activity of deer, as seedlings of a number of species including red oak are an important source of browse (Pekins and Mautz, 1987; Kittredge

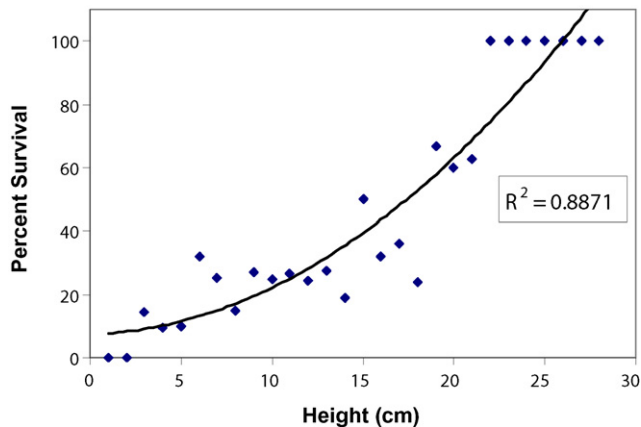


Fig. 6. Regression of survival by height (1 cm height classes) for all seedlings that established before 1996.

and Ashton, 1995). Persistent low growth of understory seedlings has been attributed to browsing pressures in other regions (Boerner and Brinkman, 1996). That said, in this region deer generally avoid seedlings of maple species, and average deer densities were also below the 23 mile^{-2} threshold suggested to negatively impact understory regeneration in these forests (Kittredge and Ashton, 1995). Furthermore, a concurrent study (Ashton et al., unpublished data) tracking the growth and survival of planted oak seedlings protected from browsing confirms the same general topographic effect of higher survival on the ridges and lower survival in the valleys for oak. Thus, while it is likely deer activity influenced establishment, growth and survival of seedlings to at least some degree, it is unlikely driving the topographical differentiation in establishment and survival.

Given persistent survival and limited upward growth observed over the course of the study, all species could be considered to form seedling banks (Grime, 1979; Marks and Gardescu, 1998). As indicated by our results, the dynamics of seedling banks vary between topographic positions, at least for some species. But there is an important temporal dimension to their dynamics as well. Based on the large variation in annual

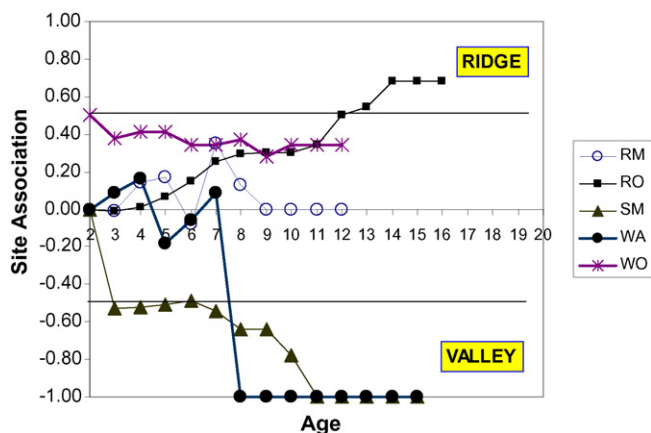


Fig. 7. Index of site association over time for equal sized cohorts of red maple, red oak, sugar maple, white ash, and white oak seedlings. Site association trends based on survival data, with a value of 1 indicating exclusive survival in the ridge position, and -1 indicating exclusive survival in the valley position.

establishment, it appears that masting behaviour is a critical driver of long-term fluctuations in seedling bank population densities. The red oak cohort establishing in the 1993–1995 period dominated population dynamics over the course of the study, and the lack of significant new recruitment events in the subsequent years has resulted in a substantial decline in seedling densities over time (also see Ward et al., 1999). Whether this is a function of smaller red oak masts in more recent years, or other factors such as poor germination conditions or high seed predation is not clear from the study. However, it may be that establishment, at least for red oak, fluctuates over longer cycles, particularly if favourable conditions for germination and establishment do not coincide with good mast years. Based on flush-aging at the start of the study in 1996, the seedling bank pre-1993 was substantially smaller ($<10,000$ seedlings/ha) than observed at any time during our study period. It may be that seedling dynamics are driven by longer (decadal) cycles reflecting the interaction of temporal variations in masting behaviour and conditions for germination and establishment.

5. Management implications

Many of these species are capable of rapid height growth given increased light availability associated with gap formation in the overstory. Species such as sugar maple and red oak can persist for decades before overstory disturbance provides opportunities for growth into the canopy (Burns and Honkala, 1990; Marks and Gardescu, 1998). However, as our results indicate, persistence in the understory varies topographically, at least for some species. In the absence of overstory disturbance, topographic positions with higher rates of mortality will be less capable of sustaining their advance regeneration. The timing of overstory disturbance relative to the timing of recruitment of advance regeneration thus becomes a critical determinant of regeneration processes. In practical terms, this has significant site-specific implications for the type and timing of silvicultural interventions aimed at stand regeneration. For red oak, lower initial densities in the valley, coupled with higher rates of mortality, suggest a shorter window of opportunity for ensuring adequate regeneration should these valley sites be harvested. One cut shelterwoods may be most suitable, although competition from other hardwood species such as white ash and sugar maple needs to be considered in these richer sites (Ward, 1992), as cuts that increase light levels above 20% may stimulate competitors to the disadvantage of red oak seedlings (Kaelke et al., 2001). In upper slope positions, where advance regeneration of oaks is more persistent, there is greater opportunity for delaying overstory removal, perhaps in favor of preharvest treatments that can enhance establishment and survival of understory seedlings (Larsen and Johnson, 1998) (e.g. progressive removal of the overstory through multi-staged shelterwood cuts).

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