Modeling tree regeneration height growth after an experimental hurricane

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Abstract: Annual height growth rates for six species of tree seedlings were modeled during the first 10 years of cohort initiation following an experimental hurricane in central Massachusetts. Selected canopy trees in a second-growth, transition oak – northern hardwoods forest were pulled over with a winch in a 50 m × 160 m area. Regeneration height growth did not follow the species-specific patterns anticipated if the disturbance had been stand replacing. Instead, the temporal increase in shade from crown expansion and sprouting of residual trees slowed cohort development and resulted in a variety of annual height growth patterns among species. Height development was followed separately for advance regeneration and new seedlings of red maple white ash, black cherry, black and yellow birch, paper birch, and red oak. All species had increasing height growth rates for 3 years followed by either decreasing or unchanged (flat) rates except red maple and ash advance regeneration, which had increasing rates throughout the measurement period. After 10 years, black and yellow birch, and red maple are the most numerous species and compose the majority of the tallest regeneration. Red oaks, which dominated the original stand, are few and unlikely to emerge to the canopy of the new cohort.

Résumé : Le taux de croissance annuelle en hauteur des semis de six espèces d'arbre a été modélisé pendant les 10 premières années qui ont suivi l'établissement d'une nouvelle cohorte à la suite d'un ouragan expérimental dans le centre du Massachusetts. Des arbres dominants ont été sélectionnés dans une forêt de transition de seconde venue, composée de chênes et de feuillus nordiques, et renversés à l'aide d'un treuil sur une superficie de 50 m × 160 m. La croissance en hauteur de la régénération n'a pas suivi le patron propre à chaque espèce comme cela aurait été le cas après une perturbation de nature à entraîner le remplacement du peuplement. Au lieu de cela, l'augmentation de l'ombre avec le temps, à cause de l'expansion des cimes et la production de rejets par les arbres résiduels, a ralenti le développement de la cohorte et provoqué une variété de patrons de croissance annuelle en hauteur parmi les espèces. La croissance en hauteur a été suivie séparément pour la régénération préétablie et les nouveaux semis d'érable rouge, de frêne blanc, de cerisier tardif, de bouleaux noir et jaune, de bouleau blanc et de chêne rouge. Le taux de croissance en hauteur de toutes les espèces a augmenté pendant trois ans suivi soit par une diminution, soit par un taux qui ne changeait pas (plat), à l'exception de la régénération préétablie d'érable rouge et de frêne dont le taux de croissance a continué à augmenter pendant toute la période de mesurage. Après 10 ans, les bouleaux noir et jaune et l'érable rouge sont les espèces les plus nombreuses et constituent la majorité de la régénération la plus haute. Les chênes rouges, qui dominaient le peuplement original, sont peu nombreux et ont peu de chances d'émerger dans la canopée de la nouvelle cohorte.

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Introduction

Modeling the growth response of forest vegetation to a range of disturbances is useful for interpreting ecosystem dynamics and informing management decisions. Accurate documentation of natural disturbance effects is difficult because studies tend to occur after the event yet predisturbance vegetation structure plays an important role in determining damage susceptibility and postdisturbance ecosystem recovery (Canham and Marks 1985; Foster 1988; Oliver and Larson 1996; Canham et al. 2001). In addition, postdisturbance sampling and analysis of plant population trends are complex because remeasurements on the same plots or individuals are confounded by the dynamic nature of spatial and temporal growth variation in the field (Lesica and Steele 1996).

Most forest ecosystems are disturbed frequently relative to the life span of the dominant species. For example, studies in central and southern New England suggest that much of the second-growth forest structure and development was strongly influenced by periodic wind damage from hurricanes and other storms. Low-intensity winds that cause only some canopy trees to blow down or break branches occur as frequently as every 20–40 years, while major events occur every 100–150 years (Boose et al. 2001).

In mature forests, hurricanes primarily uproot tall trees with large crowns and (or) cause stem and branch breakage in others. Small trees and forest floor vegetation can be

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crushed, broken, or buried by windthrow mounds as larger canopy trees fall. Hurricanes typically cause spatial alterations in the forest floor, as overturned trees create mound-and-pit microrelief, expose mineral soil, mix upper soil horizons, and spatially remove or expose buried seed (Stephens 1956; Henry and Swan 1974; Oliver and Stephens 1977; Schaetzl et al. 1990). The increase in light, water, and soil nutrients may cause a growth response from residual vegetation, sprouting from broken stems, seedlings, and larger trees, and germination of new individuals. After a stand-replacing wind event, growth of the regeneration follows the general model of single-cohort development (Bray 1956; Peet and Christensen 1987; Oliver and Larson 1996). After partial blowdown (classified as a minor disturbance, Oliver and Larson 1996), the influence of older trees varies spatially across the disturbed area (Cooper-Ellis et al. 1999) and may modify or prevent new cohort development.

In eastern deciduous forests, stem analysis has been used to reconstruct the height growth of mixed-species, single-cohort stands after disturbance (Oliver 1978; Clatterbuck and Hodges 1988; Tift and Fajvan 1999; Nyland et al. 2004). These studies demonstrate that certain species grow directly to the overstory, while others are more likely to become suppressed and either die, or grow slowly in shaded, lower canopy strata. However, these models do not predict species' growth response across the gradient of resource availability created by minor disturbances. For example, in northern latitudes, light varies strongly across forest openings (canopy gaps) (Marquis 1965; Canham 1988; Poulson and Platt 1989; Sipe and Bazzaz 1994, 1995), which influences understory growth as well as surface soil moisture (Pacala et al. 1994; Smith et al. 1997). Adaptation to disturbance types and intensity can influence intraspecific competition more than overall species densities (Hibbs 1982; Canham 1988; Connell 1989; Poulson and Platt 1989; Gottschalk 1994; Pacala et al. 1994). When growth rates are similar among species, features such as branch and limb stiffness and strength allow some species to maintain canopy dominance over others (Oliver 1978; Kelty 1986; Clatterbuck and Hodges 1988).

Field monitoring of tree seedling growth response to disturbance is important for predicting the composition of the next cohort. Growth rates have been inferred from comparisons of mean tree size at different measurement periods (Smith and Ashton 1993; Peterson and Pickett 1995; Nyland et al. 2000), regression models comparing mean size with disturbance intensity (Loftis 1990; Spetich et al. 2002), and temporal comparisons of seasonal growth changes (Palmer et al. 2004). Because all of these studies monitored the same individuals or plots through time, the observations are not independent but possess a particular correlation structure that affects the estimate of the growth response (Meredith and Stehman 1991). Therefore, studies like these must first fit an appropriate covariance model to the data to account for the correlations between measurements. Regression models can then be fit to examine growth rate trends and to test the significance of the growth responses to overstory disturbance.

The objectives of our study were to fit correlation structures to repeated measurements of tree seedling heights to model growth response to a wind disturbance. We also examined the relationships between postdisturbance plot location and regeneration height structure across a north–south environmental gradient. The study utilized an experiment designed to simulate the effects of hurricane winds on a mature deciduous forest (Foster 1988; Cooper-Ellis et al. 1999). After the hurricane simulation, the area had a partial cover of residual vegetation. In addition, 80% of the damaged trees releafed in the first growing season (Cooper-Ellis et al. 1999) creating an abundance of low shade. Soil disturbance from uprooted trees created four predominant microsites for germination (Carlton and Bazaaz 1998): open sites (40% of the disturbed area) (Carlton 1993), uprooted boles (12.8%), and pits and mounds (8.3%, Cooper-Ellis et al. 1999). Under these conditions, we expected a broad suite of species to regenerate leading to a diverse new cohort of trees.

Methods

Study area

The Harvard Forest in north-central Massachusetts lies in the New England Upland physiographic region and is characterized by moderate local relief, ranging from 120 to 410 m above sea level. The climate is cool temperate (July mean 20 °C, January mean –7 °C), with average precipitation of 110 cm distributed evenly throughout the year (Spurr 1957). Soils at the study site are moderately well-drained stony loams derived from glacial till overlying schist bedrock on a gentle northwest slope (Simmons 1939–1940; Zen 1983). A discontinuous hardpan at a depth of ~60 cm inhibits root penetration (Lyford et al. 1963).

In 1990, the experiment was initiated in a 75-year-old northern hardwoods forest dominated by red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.). A single 50 m × 160 m rectangular area was established on a west-facing slope with the long axis oriented east to west. Although the area was fenced to exclude deer, some low browsing was evident. All trees ≥5 cm dbh were tagged, mapped, and characterized by species, dbh, canopy position, and condition. Before manipulation, the stand basal area consisted of 67% red oak and 13% red maple; paper birch (*Betula papyrifera* Marsh.) and white ash (*Fraxinus americana* L.) each occupied 5%.

Because previous research has identified the importance of light gradients on forest dynamics at northern latitudes (Canham 1988), the experiment was designed to sample vegetation across the north to south light gradient. Although some large canopy trees remained after the manipulation, there was still a potential influence of light gradients on vegetation development. Three, 120 m long transects were established parallel to the east–west axis. The central transect (T2) was equidistant (25 m) from the southern and northern edges, and the north (T1) and south (T3) transects were located 10 m from the center. Twenty-four 2 m × 5 m rectangular plots (short axis oriented E-W) were randomly established on each transect. The purpose of the plots was to have fixed locations within each transect to monitor understory vegetation dynamics in response to position within the opening. All seedlings, and seedling sprouts >30 cm tall and <5 cm dbh were tagged and measured (total height, basal and bole diameter) before the manipulation (1990), and again in 1991, 1993, 1996, and 1999. Seedlings

Table 1. Data for 1999 residual tree density and regeneration age, and correlations of 1999 mean plot ages with mean plot heights and correlations of Gini coefficients with mean plot ages.

Transect	No. of plots	Mean residual basal area (m²/ha) (SD)	Mean regeneration age (SD)	Age–height correlation	Gini coefficient	Gini–age correlation
T1	24	18.58 (16.04)	7.31 (1.10)	0.726 ($p < 0.0001$)	0.481	–0.071 ($p = 0.743$)
T2	24	17.63 (8.53)	7.87 (1.21)	0.498 ($p < 0.01$)	0.440	–0.356 ($p = 0.087$)
T3	24	16.08 (7.68)	8.43 (0.94)	0.735 ($p < 0.0001$)	0.451	–0.607 ($p = 0.002$)

that established before the manipulation are referred to as advance regeneration (Smith et al. 1997). Advance regeneration and new seedlings were not counted until they reached 30 cm tall, when they were tagged, measured, and aged by counting internodes. Beginning in 1993, sprouts from damaged trees were also measured but lacked sufficient numbers to be included in our analyses.

Analyses

Height models

The large scale of this manipulation prevented replication, but provided an opportunity to examine vegetation community reorganization after a large canopy disturbance and make comparisons with smaller (replicated) canopy manipulations (Schindler 1998). At each measurement period, there is one independent replication of each transect (treatment), and the variance associated with each observation describes growth differences only within this manipulated site.

We expected that the differences among transects (treatments) would change with time and we tested for the interaction of time with treatment. In addition, because the understory tree population is dynamic — new individuals recruited and established trees grew or died between subsequent measurements — each seedling was considered an independent observation or replicate, nested within each treatment. Therefore, we collapsed the within-transect variation in height by accounting for inter-tree variation and the correlation among successive measurements on each tree by fitting a covariance function (Potvin et al. 1990; Meredith and Stehman 1991). For example, two height measurements taken at adjacent time intervals are typically more highly correlated than two measurements taken several time points apart (Apiolaza and Garrick 2001).

Six of the 20 species found on the plots occurred in adequate numbers to model height growth. Because of inadequate sample size of yellow birch (*Betula alleghaniensis* Britt.) on two transects and difficulty in distinguishing small yellow birch from black birch (*Betula lenta* L.), these species were combined. Each tree had up to five potential height measurements depending on origin year, size at each measurement, and longevity. Individuals were included in the analysis regardless of the number of measurements. Height growth analyses were conducted separately for each species and regeneration type (seedlings and seedling sprouts or advance regeneration).

Trends in height growth were analyzed using a general linear mixed model with fixed terms for the main effects of TRANSECT, TIME, and their interaction. TIME was considered the repeated-measures factor, and total HEIGHT at each time period was the dependent variable. Individual

trees (subjects) are considered random, and error terms are included for the effects of trees nested within transects. Height data were positively skewed and were log transformed before analyses. Covariance structures were modeled using the REPEATED statement in the PROC MIXED procedure with SAS software (Carriere 1994; SAS Institute Inc. 2004).

The best model for the covariance structure included the lowest number of independently fitted parameters and hence the lowest values for likelihood ratio tests (Berk 1987; Apiolaza and Garrick 2001). Because of the slight inequality in remeasurement intervals for some species and (or) regeneration types, covariance structures that actually imposed a mathematical structure on the data were not examined. Four covariance structures (compound symmetric, heterogeneous compound-symmetric, first-order antedependence, and unstructured) were tested. HEIGHT was then modeled as a polynomial function of TIME to test whether there were different temporal height growth trajectories for each species and (or) regeneration type group in each transect.

Assessment of height structure

Variation in growth rates among seedlings due to their increasing density and crown expansion, age differences, genetic variation, resource heterogeneity, and the effect of herbivores typically cause height data to become positively skewed over time because of increasing dominance of fewer, larger individuals (White and Harper 1970), and to large variation in individual sizes (Weiner and Solbrig 1984). Seedling height structure was assessed on the 24 plots established in each transect to compare variations according to residual tree basal area on each plot. Inequality in regeneration height was evaluated by calculating a Gini coefficient (G) for the frequency distributions of height in each plot according to the following formula (Weiner and Solbrig 1984):

$$[1] \quad G = \sum_{i=1}^{n} \sum_{j=1}^{n} \left| x_i - x_j \right| / 2n^2 \bar{x}$$

where x_i and x_j are heights of the ith and jth stem on a plot, respectively, and n is the total number of stems, and $\bar{x}$ is the mean stem height. Gini coefficients were calculated for each plot using the heights of new seedlings, seedling sprouts, and advance regeneration. The value of G is dimensionless and ranges from 0 (where all individuals are equal in height) to a theoretical maximum of 1 (ultimate inequality; all individuals have different heights). Our hypothesis was that average G values on all transects would increase over time as the variation in heights increased. Spearman's rank correlation was used to examine the temporal relationship among

Table 2. Mean heights (m) in 1999, SE, n of seedlings, seedling sprouts, and advance regeneration ≥3 m tall by transect with percentage of total regeneration present that was ≥3 m tall, and the number of plots per transect where each species was first or second tallest.

	Red maple			Black–yellow birch			Black cherry			Paper birch			White ash			Red oak		
	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3
Height	4.86	5.76	5.55	6.06	6.43	6.52	na	4.13	4.94	4.47	5.06	6.74	na	5.35	5.46	na	na	4.2
SE	0.24	0.21	0.33	0.39	0.35	0.41		0.41	0.27	0.33	0.43	0.64		0.26	0.34			0.00
n	12	24	26	26	36	75		11	14	15	16	9		2	3			1
% ≥3 m	34	50	51	32	43	54		19	30	19	49	38		6	5			5
Tallest																		
1st	3	5	4	9	12	16	1	0	1	2	1	2	1	0	0	0	0	0
2nd	2	4	5	6	6	13	0	4	3	5	5	1	3	0	1	0	1	0

Note: Other species not included in this study (*Pinus strobus* L., *Castanea dentata* (Marsh.) Borkh., *Prunus pensylvanica* L.f., *Ostrya virginiana* (Mill.) K. Koch, *Acer saccharum* Marsh., *Carya glabra* (Mill.) Sweet, *Fagus grandifolia* Ehrh.) were tallest on 14 of the 72 plots.

plots within transects of both G and mean regeneration height, with regeneration density, age, and residual tree basal area (residual trees ≥2.54. cm dbh) per plot.

We also established a height threshold to indicate which species were dominant in the new cohort after 10 years. We determined the percentage of individual stems of each species that had attained a height of ≥3 m by 1999. We inferred that these would likely become a component of the overstory canopy under a single-cohort development scenario (Oliver 1978; Palik and Pregitzer 1993; Tift and Fajvan 1999). We compared our threshold results with the species, height, and regeneration type of the two tallest individuals on each plot.

Results

Age and height structure of regeneration

Before the hurricane treatment, T3 had 67% more advance regeneration than T1 and 30% more than T2. By 1999, 50% of the advance regeneration on each transect was still alive, as was 34%–48% of the 1991 and 1992 cohorts. Transect 1 had the highest survival rate for 1991–1992 seedlings and seedling sprouts, and 38% and 46% fewer seedlings established in 1991 compared with T3 and T2, respectively. By 1999, there was a significant positive correlation between mean stem age and mean stem height for all transects (Table 1). Correlation coefficients were similar for T1 and T3 but lower for T2.

By 1999, black–yellow birch had the highest density of regeneration ≥3 m tall and was the tallest species on 51% of all plots sampled. On T2 and T3, 40%–50% of all red maple, black–yellow birch, and paper birch regeneration were ≥3 m tall, and these three species had the highest representation as the first or second tallest species per plot (Table 2). White ash and red oak had the lowest densities of regeneration ≥3 m tall and together with black cherry (*Prunus serotina* Ehrh.) were the tallest species on only 4% of the plots across the site (Table 2).

For T1 and T3 there were no significant correlations between residual tree basal area per plot and mean regeneration height or Gini coefficient. On T2, residual tree basal area per plot in 1999 was negatively correlated with mean regeneration height in 1999 ($r = -0.44$, $p = 0.0302$), which could help explain the lower correlation between height and age that existed on this transect (Table 1). On T2, Gini coefficients were significantly and positively correlated with residual tree basal area per plot in 1990 ($r = 0.63$, $p = 0.007$) and 1991 ($r = 0.48$, $p = 0.0370$).

Gini coefficients were similar among transects and increased slightly with time, indicating that heights were becoming more variable (relatively less equal heights among stems) (Table 3). Correlations of Gini coefficients with 1999 plot age indicated a significant negative correlation only on T3 where stems averaged about a year older and were taller than on T1 or T2 (Table 1) probably because of the high percentage of advance regeneration.

Modeling height as a polynomial function of time

The unstructured covariance structure provided the best model for all species and regeneration types, except for red oak seedlings. Examination of the correlation matrix of each species produced by the unstructured covariance model indi-

Table 3. Gini coefficients ± SE (no. of plots with tree regeneration >30 cm tall) for each transect and measurement year.

Transect	1990	1991	1993	1996	1999
1	0.367±0.041 (10)	0.363±0.038 (16)	0.375±0.021 (23)	0.423±0.019 (24)	0.481±0.021 (24)
2	0.356±0.040 (17)	0.344±0.026 (19)	0.380±0.014 (23)	0.398±0.018 (24)	0.440±0.019 (24)
3	0.406±0.030 (24)	0.387±0.029 (23)	0.393±0.016 (24)	0.439±0.016 (24)	0.451±0.024 (24)

cated a general pattern of decreasing correlations with increasing time between measurements. In addition, the covariance matrix for each species indicated increasing variances over time. Differences in the mean height variances between the first and last measurement times increased 70%–90% for all species and regeneration types, except for advance regeneration of red maple (36% increase) and red oak (54% increase) (Tables 4, 5).

The compound symmetric structure was the only model that met the convergence criteria for the red oak seedling data. The model indicated an overall difference in height growth rate over time, but the rate did not differ among transects. The linear coefficients were not significant, hence growth was essentially flat (no growth rate change) and no growth models were developed. Red oak seedling heights (Table 4) showed little variation among transects and over time.

The results of the tests of fixed effects, used to determine the best model to represent height growth trends over time, differed among species and regeneration types. Neither the linear nor the quadratic coefficients for T1 are significant for black–yellow birch, white ash, and black cherry seedlings (Table 6), because the 1996 and 1999 heights were still increasing at about the same rate as between the 1991 and 1993 measurements. Hence, the height profile is basically flat (Figs. 1b, 1c, 1d). Generally, mean heights were lower on T1 compared with the other transects, except for white ash and red oak, which averaged shorter trees on all transects (Table 4). The quadratic coefficient is not significant for black–yellow birch on T2 and not significant for white ash on T3.

Height growth rates of red maple and paper birch seedlings slowed for all transects. The quadratic coefficients are significant and negative (Table 6) indicating that height growth was not increasing as rapidly at later times compared with earlier measurements (Figs. 1a, 1e). The paper birch models were developed with measurements from 1993 to 1999, because there were no seedlings >30 cm tall in 1991. Black cherry seedlings have significant, negative quadratic coefficients on T2 and T3, as do white ash seedlings on T2, and black–yellow birch seedlings on T3 (Table 6), because height growth rates were slowing (Figs. 1b, 1c, 1d).

Regression tests of the fixed effects for advance regeneration of red maple and white ash indicated that quadratic coefficients were not needed in the model. All transects showed significant, positive slopes (Table 6) because height growth increased at a faster rate after 1993 compared with earlier measurements for these species (Figs. 2a, 2c). The only exception was for white ash on T1, where the linear coefficients were not significant, and growth was essentially flat.

Height growth rates for black–yellow birch slowed on all transects (Fig. 2b); rates for black cherry slowed on T2 and T3 and remained unchanged on T1 (Fig. 2d). There were no black cherry stems ≥3 m tall on T1 (Table 2). Red oak advance regeneration did not have a large enough sample of tagged (>30 cm tall) seedlings until 1993, so growth rates were only modeled for 6 years. Height models indicated that red oak had significant, negative quadratic coefficients for T1 and T3. On T2, neither the linear nor quadratic coefficients were significant (Table 6; Fig. 2e).

Discussion

Plot location effects on height growth

We interpret the modeled height growth trends to be a response to treatment effects and not random, environmental influences (e.g., temporal changes in precipitation) that we did not measure (van Mantgem et al. 2001). Our results suggest that the high (overstory) and low (understory) shading from the residual trees and resprouting vegetation probably had more of an influence on spatial and temporal gradients of light than edge effect. There was no correlation among height growth patterns and the light gradients associated with transect position in the treatment area (Marquis 1965; Matlack 1994). T3 was established near the zone of shading (within 10 m of the southern edge), and without residual trees, these plots would have received full sunlight for most of the day in the early years following the disturbance. As tree crowns along the gap edge expanded into the gap space over 10 years, structural edge effects would have extended into the stand decreasing gap size and probably increasing shading of T3 (Matlack 1994). However, we observed no edge effect; height growth rates on T3 and T2 slowed similarly over time.

Variation in basal area of residual trees among transects did influence height growth patterns. T1 had the highest basal area of residual trees at each measurement period. Basal areas for T2 and T3 were lower and similar, which probably contributed to their higher initial height growth rates and taller regeneration in 1999 compared with T1. Only on T2 were significant positive correlations found between plot basal areas and Gini coefficients for 1990 and 1991, indicating that plots with relatively high residual basal areas had more variation in regeneration height. T2 had 100 fewer stems of advance regeneration counted on the plots in 1990 compared with T3, but a similar number of seedlings established in 1991. By 1999, only 11 of the 24 plots on T2 had a stem of advance regeneration origin as the tallest tree compared with 17 and 20 plots on T1 and T3, respectively. There was also a significant negative correlation between plot basal areas and 1999 mean regeneration height on T2. However, T2 was the only transect where black–yellow birch seedlings demonstrated positive linear height growth (Table 6).

Table 4. Mean heights, variance, SE, and number (n) of seedlings and seedling sprouts by transect and measurement year.

Year	Red maple			Black–yellow birch			Black cherry			Paper birch			White ash			Red oak		
	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3	T1	T2	T3
1991																		
Mean height (m)	0.35	0.58	0.59	0.53	0.65	0.60	0.43	0.59	0.68									
Variance	0.01	0.04	0.06	0.03	0.06	0.03	0.00	0.06	0.07									
SE	0.05	0.08	0.07	0.06	0.06	0.06	0.03	0.06	0.06									
n	(4)	(6)	(10)	(8)	(15)	(7)	(3)	(15)	(21)									
1993																		
Mean height (m)	1.09	1.57	1.41	1.03	0.94	1.02	0.57	0.98	1.17	0.84	1.07	1.06	0.78	0.66	0.45	0.37	0.43	0.36
Variance	0.37	0.97	0.59	0.41	0.43	0.34	0.06	0.37	0.73	0.39	0.58	0.44	0.36	0.30	0.02	0.006	0.02	0.00
SE	0.13	0.13	0.13	0.11	0.06	0.05	0.06	0.09	0.11	0.07	0.08	0.07	0.24	0.15	0.06	0.05	0.10	0.03
n	(23)	(56)	(38)	(33)	(116)	(131)	(17)	(47)	(58)	(70)	(97)	(100)	(6)	(13)	(5)	(3)	(2)	(2)
1996																		
Mean height (m)	1.28	2.31	2.23	1.30	1.75	1.73	0.74	1.31	1.90	1.35	1.98	2.52	0.69	0.94	0.56	0.42	0.64	0.42
Variance	0.96	2.02	1.79	1.40	1.55	1.77	0.41	0.98	2.64	1.31	1.99	2.83	0.12	1.37	0.10	0.02	0.20	0.03
SE	0.19	0.20	0.24	0.16	0.14	0.14	0.13	0.15	0.26	0.12	0.18	0.26	0.09	0.32	0.07	0.04	0.12	0.05
n	(25)	(48)	(32)	(54)	(74)	(97)	(23)	(46)	(38)	(86)	(58)	(43)	(13)	(13)	(19)	(9)	(14)	(12)
1999																		
Mean height (m)	2.14	3.58	3.33	1.88	2.75	2.43	0.91	1.37	2.41	1.86	3.21	3.45	0.57	1.12	0.57	0.45	0.67	0.48
Variance	2.67	4.40	5.24	3.57	5.01	4.24	0.84	1.57	3.88	2.73	4.94	8.38	0.14	2.91	0.15	0.05	0.12	0.05
SE	0.37	0.38	0.48	0.24	0.29	0.23	0.21	0.20	0.36	0.19	0.39	0.59	0.08	0.44	0.08	0.07	0.10	0.07
n	(19)	(31)	(23)	(62)	(59)	(82)	(20)	(38)	(30)	(77)	(33)	(24)	(24)	(15)	(23)	(11)	(12)	(11)

Table 5. Mean heights, variance, standard error, and number (n) of advance regeneration by transect and measurement year.

Year	Red maple T1	T2	T3	Black–yellow birch T1	T2	T3	Black cherry T1	T2	T3	White ash T1	T2	T3	Red oak T1	T2	T3
1990															
Mean height (m)	1.84	1.87	1.69	0.69	1.61	1.00	0.43	0.70	0.56	0.76	0.81	0.53			
Variance	4.38	2.60	2.19	0.12	2.37	1.15	0.02	0.54	0.09	0.39	0.24	0.21			
SE	0.54	0.28	0.25	0.07	0.32	0.13	0.04	0.11	0.04	0.16	0.13	0.12			
n	(15)	(34)	(34)	(23)	(23)	(68)	(16)	(42)	(57)	(15)	(14)	(14)			
1991															
Mean height (m)	2.07	1.31	1.64	0.72	1.71	1.01	0.45	0.60	0.59	0.54	0.59	0.59			
Variance	5.39	1.54	1.88	0.26	2.51	0.83	0.04	0.14	0.10	0.13	0.18	0.34			
SE	0.64	0.23	0.23	0.11	0.34	0.11	0.05	0.06	0.04	0.08	0.13	0.16			
n	(13)	(30)	(37)	(23)	(22)	(64)	(18)	(42)	(57)	(20)	(10)	(14)			
1993															
Mean height (m)	1.79	1.82	1.78	1.58	2.29	2.19	0.61	0.91	0.94	0.53	0.61	0.60	0.43	0.43	0.74
Variance	4.19	2.22	2.09	1.58	3.57	2.13	0.12	0.33	0.41	0.08	0.10	0.23	0.01	0.02	0.67
SE	0.47	0.27	0.22	0.25	0.35	0.17	0.07	0.09	0.08	0.06	0.07	0.07	0.04	0.05	0.37
n	(19)	(31)	(43)	(25)	(29)	(72)	(26)	(42)	(62)	(28)	(21)	(46)	(6)	(7)	(5)
1996															
Mean height (m)	2.18	2.81	2.84	3.22	4.00	4.16	0.85	1.70	1.47	0.58	1.09	1.10	0.71	0.61	1.04
Variance	4.62	4.12	4.80	4.23	7.26	4.97	0.41	1.14	1.53	0.17	0.29	1.39	0.05	0.10	1.30
SE	0.48	0.41	0.37	0.46	0.54	0.29	0.14	0.21	0.21	0.08	0.13	0.19	0.08	0.09	0.43
n	(20)	(25)	(35)	(20)	(25)	(58)	(20)	(25)	(34)	(24)	(17)	(37)	(9)	(11)	(7)
1999															
Mean height (m)	2.93	3.87	3.69	4.59	5.17	6.27	1.27	2.06	2.20	0.62	1.24	1.49	0.75	0.88	1.15
Variance	7.43	7.12	6.84	11.40	12.82	9.65	0.47	1.50	3.51	0.24	0.81	2.68	0.08	0.17	1.95
SE	0.68	0.65	0.49	0.75	0.72	0.41	0.21	0.27	0.45	0.11	0.23	0.30	0.11	0.15	0.53
n	(16)	(17)	(28)	(20)	(25)	(57)	(11)	(20)	(17)	(21)	(15)	(29)	(7)	(8)	(7)

Table 6. Coefficients for height models (HEIGHT = B_1 + B_2 * TIME + B_3 * TIME * TIME) of seedlings and seedling sprouts and advance regeneration by transect and species.

	Red maple			Black–yellow birch			Black cherry			Paper birch			White ash		
Parameter	T1*	T2*	T3*	T1	T2	T3*	T1	T2*	T3*	T1*	T2*	T3*	T1	T2*	T3
Seedlings and seedling sprouts															
B_1	0.3468	0.4590	0.3385	0.3454	0.4109	0.3343	0.3088	0.2948	0.2923	0.1129	0.2814	0.1294	0.4927	0.2616	0.0962
B_2	0.1035	0.1373	0.1726	0.0371	0.0706	0.1103	0.0265	0.0990	0.1272	0.1451	0.1542	0.2270	0.0138	0.0684	0.0911
B_3	0.0069–	0.0085–	0.0106–	0.0006–	0.0031–	0.0069–	0.0021–	0.0091–	0.0109–	0.0072–	0.0093–	0.0154–	0.0000–	0.0058–	0.0067–
Advance regeneration															
B_1	0.6179	0.7402	0.6952	0.3326	0.6044	0.3177	0.2922	0.3859	0.3439	0.4052	0.4330	0.2977	0.1186–	0.2815	0.0089
B_2	0.0379	0.0337	0.0489	0.1463	0.1129	0.2036	0.0479	0.0599	0.0730	0.0006	0.0321	0.0249	0.0175	0.0241	0.1540
B_3				0.0062–	0.0049–	0.0093–	0.0034–	0.0041–	0.0069–				0.0118–	0.008	0.0095–

Note: An asterisk indicates that the model had significant ($\alpha \leq 0.05$) linear or quadratic coefficients. A minus sign next to a coefficient indicates that the value is negative.

A partial canopy plus shade from uprooted trees created an irregular distribution of sunlight and soil growing space for newly germinating individuals (Carlton and Bazaaz 1998). Residual trees and foliage on low sprouts from damaged trees and former understory trees probably reduced seedling survival and growth. T1 had the most red maple sprouts from damaged trees, and the highest basal area of residual stems, which may have affected regeneration height growth and resulted in lower percentages of trees ≥3 m tall in 1999 (Table 2).

On T2 and T3, white ash and red maple advance regeneration showed height growth acceleration after 1993. However, it seems that only the red maple crowns were able to grow above the canopy of fallen debris, understory plants, and releafing crowns. By 1999 very few ash seedlings were ≥3 m tall, yet 50% of red maple regeneration was in this height class (Table 2). On T1 both red maple and black–yellow birch had >30% of regeneration ≥3 m tall, but only red maple advance regeneration still had increasing height growth on this transect (Fig. 2*a*). Other species had increasing temporal variation in height distributions and decreasing or unchanged growth rates for both advance regeneration and seedlings.

Species ecological roles after disturbance

If site conditions and age are assumed to be uniform, then species variations in juvenile height growth patterns are caused by differences in shoot types, regeneration mechanism (new seedlings versus advance regeneration), genetics, and interspecific competitive pressure. Our analysis supports this hypothesis. For example, paper birch growth rates slowed significantly between 1996 and 1999, whereas black and yellow birch seedlings only slowed on T3 (Table 6). Black and yellow birch advance regeneration also showed a decreased growth rate after 1996. However, their larger initial size and higher 1990–1996 growth rate resulted in the most tall (>3 m) stems in 1999 (Table 2). Paper birch has rapid height growth in full sun, providing there is adequate moisture for root growth during seedling establishment (Marquis 1966). In shade, paper birch shoot and root growth is more affected than yellow and black birch, therefore it grows more slowly (Logan 1965; Smith and Ashton 1993; Carlton and Bazzaz 1998).

Maximum potential height growth rates are inherently lower in seedlings of more shade-tolerant species (Loach 1970), yet red maple and paper birch seedlings had similar mean heights and growth rates. Shade-intolerant paper birch seasonally maximizes its shoot extension growth (indeterminate), whereas red maple is shade tolerant and also has indeterminate shoots (Marks 1975). Red maple is also a heterophyllous species (Kramer and Kozlowski 1979) with shoot development and leaf arrangement suited to good light absorption (Wilson 1966) and rapid growth in both highly disturbed, high light conditions (Tift and Fajvan 1999) and low disturbance (canopy gap) low light conditions (Sipe and Bazzaz 1994). However, paper birch seedlings may be more competitive because they were the tallest on five plots, whereas no seedling origin red maple was tallest. Even though red maple was tallest on 12 plots, these individuals were either seedling sprouts or advance regeneration.

White ash seedlings and seedling sprouts are surviving but

Fig. 1. Seedling and seedling sprout height profiles resulting from modeling HEIGHT as a polynomial function of TIME. Height data were log transformed before analysis. Graphs depict the changes in the rate of height growth by transect and species; mean heights are found in Table 4.
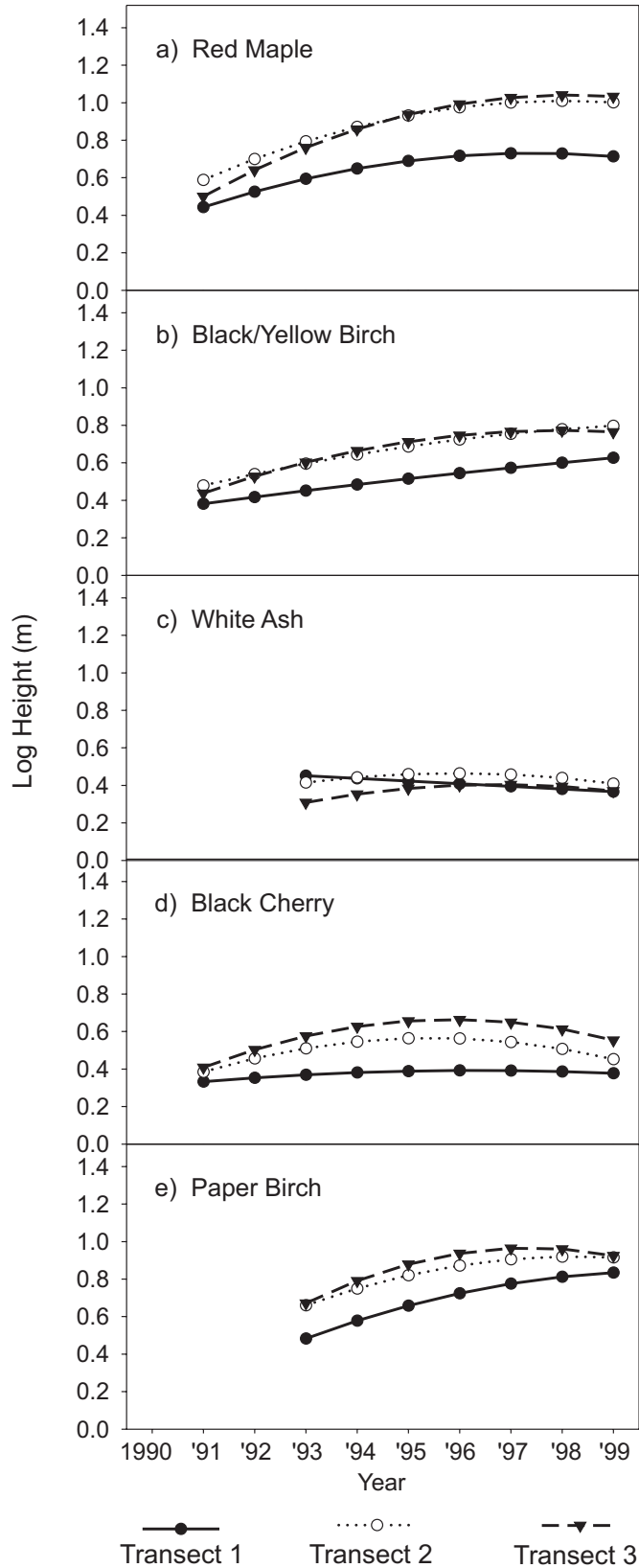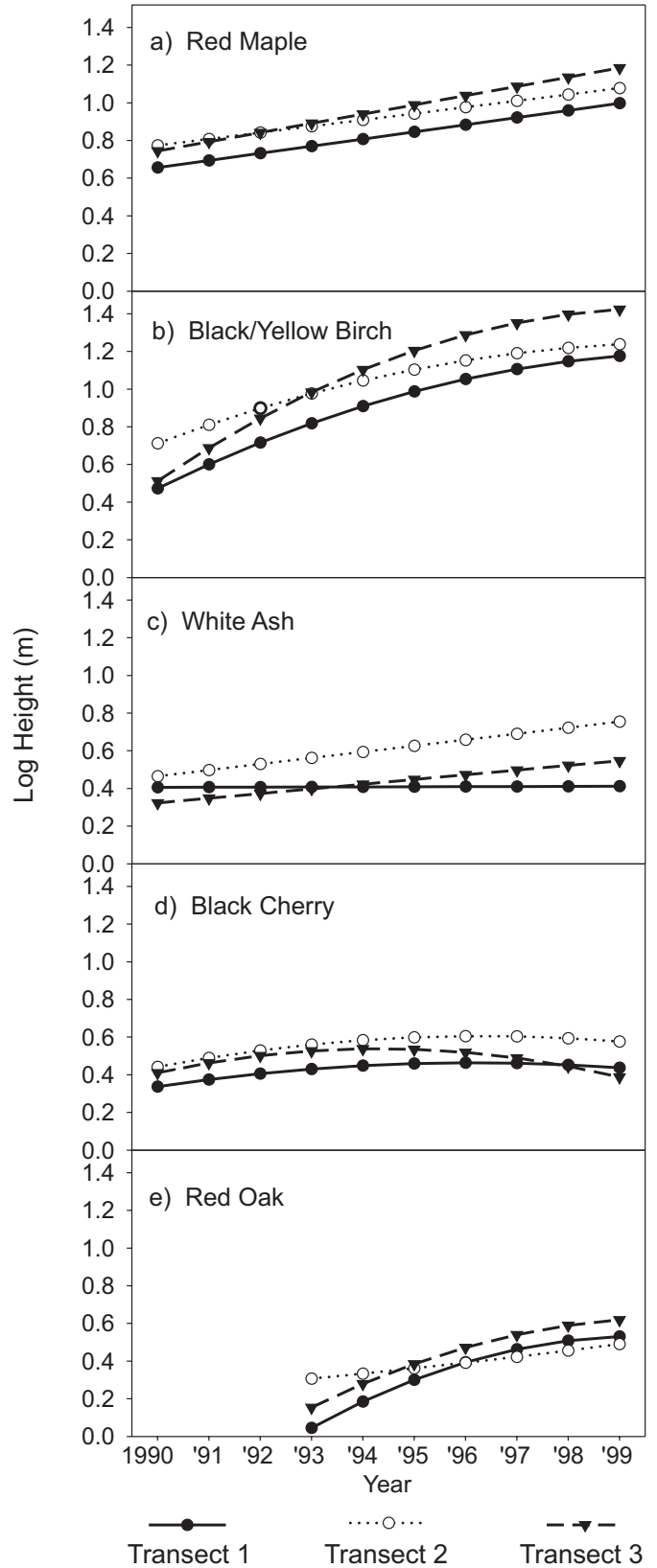
Fig. 2. Advance regeneration height profiles resulting from modeling HEIGHT as a polynomial function of TIME. Height data were log transformed before analysis. Graphs depict the changes in the rate of height growth by transect and species; mean heights are found in Table 5.

barely growing. Advance regeneration showed positive growth on two transects (Fig. 2c), but only five stems were ≥3 m tall by 1999. White ash is classified as a determinate (Marks 1975), shade-intolerant species that requires full sunlight to achieve overstory canopy dominance. However, seedling shoot elongation appears to follow an indeterminate pattern with continuous growth until the end of the growing season (Gill 1971). This physiological trait may be responsible for ash's high shade tolerance as a seedling (Schlesinger 1990) and subsequent rapid growth following release from overstory shade (Nyland et al. 2004). In our study, the initial shade from residual trees and the temporal increase in shade from new growth is likely hindering ash growth.

Black cherry seedlings had similar height growth rates as red maple on T2 and T3 but grew more slowly than red maple on T1. By 1999, red maple heights averaged at least 1 m greater than black cherry on all transects. Like red maple, black cherry also has indeterminate shoot growth; however, it is shade intolerant, and seedlings can survive for up to 5 years under undisturbed canopies (Marquis 1990) possibly because of earlier budbreak than its associates (McGee 1986). Black cherry seedlings grew similarly to black–yellow birch seedlings on T1 and T3, whereas black cherry growth rate slowed on T2 and black–yellow birch seedling growth remained unchanged. Our findings differ from growth trends documented in a Connecticut study, where black cherry seedlings and saplings had higher height growth rates in low light than red maple, ash, and red oak, and lower growth rates than yellow birch (Pacala et al. 1994).

Red oak had the shortest seedlings and the smallest sample of trees >30 cm tall. Red oak has a semideterminate shoot growth habit (White 1992) with lag phases between growth flushes (Johnson et al. 2002). However, low light, competition from other vegetation, and low root/shoot ratio can prevent subsequent flushes during the growing season (Reich et al. 1980).

The height growth patterns modeled in our study do not necessarily reflect a gradient of light conditions but are representative of average rates sampled across a random pattern of understory light conditions created by the disturbance. Most seedlings showed an initial positive growth response to the disturbance, but as shading increased because of crown expansion and sprouting of residual trees, height growth decreased over the 10 years for most species and growth forms. The heterogeneity of understory shade conditions allowed a wider suite of growth strategies to succeed than in a stand-replacing disturbance. Species that would be expected to thrive in high-light conditions, such as paper birch, were competing with species such as red maple and yellow–black birch that are more adaptable to a variety of growth environments.

Our height models considered the correlation between successive measurements and provided a realistic representation of growth rate. All of the species examined in our study have the potential to eventually achieve overstory dominance after catastrophic disturbance, even if the regeneration was from new seedlings only (Oliver 1978; Schuler and Fajvan 1999; Tift and Fajvan 1999). However, the partial canopy removal of the hurricane simulation differed from the timber harvesting that originated the stand. Current tree sizes, den-

sities, and height growth rates indicate that stand development trajectories of the new cohort differs from that which originated the red oak-dominated second-growth stand.

Retrospective studies of red oak-dominated second-growth stands suggest several models of oak recruitment to the overstory after stand-replacing disturbance: (1) delayed height growth acceleration (Oliver 1978; Ward and Stephens 1996; Tift and Fajvan 1999), (2) equal seedling height growth rates with other canopy species (Schuler and Fajvan 1999; Tift and Fajvan 1999), (3) rapid initial height growth rates from large advance regeneration or sprouts (Loftis 1990). In old-growth stands, red oaks have been recruited to the canopy through a combination of 50-year average understory residence times and episodic recruitment in canopy gaps (Rentch et al. 2003). The common element in these various disturbance patterns and recruitment strategies is that understory environmental conditions were more or equally favorable for oak height growth compared with associated species. Our height models indicate that it is unlikely red oak will increase height growth rate under current stand conditions. The increase in understory light from the hurricane treatment benefited many regenerating species, and those with greater morphological and physiological plasticity (red maple, black–yellow birch) quickly responded to the changing conditions and gained a height advantage over others (red oak, white ash).

Typically, new cohorts developing under partial canopies have a high proportion of persistent, slower-growing, shade-tolerant species, and canopy closure takes longer than expected under the single-cohort model (Ray et al. 1999; Nyland et al. 2000). In our study, the partial overstory and releafing understory also are slowing cohort development. The variations in black cherry, ash, yellow birch, and oak height growth rates reflect their different physiological adaptations to survival and growth in low light conditions. By 2003, black birch and red maple represented over 60% of stems (>5 cm dbh) in the new cohort, whereas red oak only had three stems in this size class (Barker Plotkin et al. 2004). Our height growth models help to explain this finding and suggest that black birch and red maple will continue to dominate the disturbance-initiated cohort.

Acknowledgments

References

Apiolaza, L.A., and Garrick, D.J. 2001. Analysis of longitudinal data from progeny tests: Some multivariate approaches. For. Sci. **47**(2): 129–139.

Barker Plotkin, A., Wilson, K., and Foster, D.R. 2004. Harvard forest hurricane experiment: The next generation. *In* Abstracts from the 15th Annual Harvard Forest Ecology Symposium, 29

March 2004, Petersham, Mass. *Edited by* A. Barker Plotkin, J.S. Pallant, and L. Hampson. Harvard Forest, Harvard University, Petersham, Mass. pp. 29–32.

Berk, K. 1987. Computing for incomplete repeated measures. Biometrics, **43**: 385–398.

Boose, E.R., Chamberlin, K.E., and Foster, D.R. 2001. Landscape and regional impacts of hurricanes in New England. Ecol. Monogr. **71**(1): 27–48.

Bray, J.R. 1956. Gap phase replacement in a maple-basswood forest. Ecology, **37**: 598–600.

Canham, C.D. 1988. An index for understory light levels in and around canopy gaps. Ecology, **69**: 1634–1638.

Canham, C.D., and Marks, P.L. 1985. The response of woody plants to disturbance: patterns of establishment and growth. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press, Orlando, Fla. pp. 197–216.

Canham, C.D., Papaik, M.J., and Latty, E.F. 2001. Interspecific variation in susceptilbility to windthrow as a function of tree size and storm severity for northern temperate tree species. Can. J. For. Res. **31**: 1–10.

Carlton, G.C. 1993. Effects of microsite environment on tree regeneration following disturbance. Ph.D. dissertation, Harvard University, Cambridge, Mass.

Carlton, G.C., and Bazzaz, F.A. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecol. Monogr. **68**: 99–120.

Carriere, K.C. 1994. Incomplete repeated measures data analysis in the presence of treatment effects. J. Am. Stat. Assoc. **89**(426): 680–686.

Clatterbuck, W.K., and Hodges, J.D. 1988. Development of cherrybark oak and sweet gum in mixed, even-aged bottomland stands in central Mississippi, USA. Can. J. For. Res. **18**: 12–18.

Connell, J.H. 1989. Some processes affecting the species composition in forest gaps. Ecology, **70**: 560–562.

Cooper-Ellis, S., Foster, D.R., Carlton, G., and Lezberg, A. 1999. Forest response to catastrophic wind: Results from an experimental hurricane. Ecology, **80**(8): 2683–2696.

Foster, D.R. 1988. Species and stand response to catastrophic wind in central New England, USA. J. Ecol. **76**: 135–151.

Gill, A.M. 1971. The formation, growth and fate of buds of *Fraxinus Americana* L. in central Massachusetts. Harvard For. Pap. No. 20, Harvard Forest, Harvard University, Petersham, Mass.

Gottschalk, K.W. 1994. Shade, leaf growth and crown development of *Quercus rubra*, *Quercus velutina*, *Prunus serotina* and *Acer rubrum* seedlings. Tree Physiol. **14**: 735–749.

Henry, J.D., and Swan, J.M. 1974. Reconstructing history from live and dead plant material — an approach to the study of forest succession in southwest New Hampshire. Ecology, **55**: 772–783.

Hibbs, D.E. 1982. Gap dynamics in a hemlock–hardwood forest. Can. J. For. Res. **12**: 522–527.

Johnson, P.S., Shifley, S.R., and Rogers, R. 2002. The ecology and silviculture of oaks. CABI Publishing, New York.

Kelty, M.J. 1986. Development patterns in two hemlock–hardwood stands in southern New England. Can. J. For. Res. **16**: 885–891.

Kramer, P.J., and Kozlowski, T.T. 1979. Physiology of woody plants. Academic Press Inc., Orlando, Fla.

Lesica, P., and Steele, B.M. 1996. A method for monitoring long-term population trends: An example using rare arctic-alpine plants. Ecol. Appl. **6**(3): 879–887.

Loach, K. 1970. Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. New Phytol. **69**: 273–286.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. **36**(4): 917–929.

Logan, K.T. 1965. Growth of tree seedlings as affected by light intensity. I. White birch, yellow birch, sugar maple and silver maple. Can. For. Serv. Publ. 1121.

Lyford, W.H., Goodlett, J.C., and Coates, W.H. 1963. Landforms, soils with fragipans, and forests on a slope in the Harvard Forest. Harvard For. Bull. No. 23, Harvard Forest, Harvard University, Petersham, Mass.

Marks, P.L. 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. Bull. Torrey Bot. Club, **102**(4): 172–177.

Marquis, D.A. 1965. Controlling light in small clearcuttings. USDA For. Serv. Res. Rep. NE-85.

Marquis, D.A. 1966. Germination and growth of paper birch and yellow birch in simulated strip cuttings. USDA For. Serv. Res. Pap. NE-54.

Marquis, D.A. 1990. *Prunus serotina* Ehrh. Black Cherry. *In* Silvics of North America: 2 Hardwoods. Volume 2. *Techical Coordinators* R.M. Burns and B.H. Honkala. US Dep. Agric. Agric. Handb. 654. pp. 594–604.

Matlack, G.R. 1994. Vegetation dynamics of the forest edge — trends in space and succesional time. J. Ecol. **82**: 113–123.

McGee, C.E. 1986. Budbreak for twenty-three upland hardwoods compared under forest canopies and in recent clearcuts. For. Sci. **23**(4): 924–935.

Meredith, M.P., and Stehman, S.V. 1991. Repeated measures experiments in forestry: focus on analysis of response curves. Can. J. For. Res. **21**: 957–965.

Nyland, R.D., Ray, D.G., Yanai, R.D., Briggs, R.D., Zhang, L., Cymbala, R.J., and Twery, M.J. 2000. Early cohort development following even-aged reproduction method cuttings in New York northern hardwoods. Can. J. For. Res. **30**: 67–75.

Nyland, R.D., Ray, D.G., and Yanai, R.D. 2004. Height development of upper-canopy trees within even-aged Adirondack Northern Hardwood stands. North. J. Appl. For. **21**(3): 117–122.

Oliver, C.D. 1978. Development of northern red oak in mixed-species stands in central New England. Yale Univ. Sch. For. Environ. Stud. Bull. 91.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons Inc., New York.

Oliver, C.D., and Stephens, E.P. 1977. Reconstruction of a mixed-species forest in central New England. Ecology, **58**: 562–572.

Pacala, S.W., Canham, C.D., Silander, J.A., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. **24**: 2172–2183.

Palik, B.J., and Pregitzer, K.S. 1993. The vertical development of early sucessional forests in northern Michigan, USA. J. Ecol. **81**: 271–285.

Palmer, S.C.F., Mitchell, R.J., Truscott, A.-M., and Welch, D. 2004. Regeneration failure in Atlantic oakwoods: the roles of ungulate grazing and invertebrates. For. Ecol. Manage. **192**: 251–265.

Peet, R.K., and Christensen, N.L. 1987. Competition and tree death. Bioscience, **37**: 586–595.

Peterson, C.J., and Pickett, S.T. 1995. Forest reorganization: A case study in an old-growth forest catastrophic blowdown. Ecology, **76**(3): 763–774.

Potvin C.P., Lechowicz, M.J., and Tardiff, S. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. Ecology, **71**(4): 1389–1400.

Poulson, T.L., and Platt, W.J. 1989. Gap light regimes influence canopy tree diversity. Ecology, **70**(3): 553–555.

Ray, D.G., Nyland, R.D., and Yanai, R.D. 1999. Patterns of early cohort development following shelterwood cutting in three Adirondack northern hardwood stands. For. Ecol. Manage. **119**: 1–11.

Reich, P.B., Tesky, R.O., Johnson, P.S., and Hinckley, T.M. 1980. Periodic root and shoot growth in oak. For. Sci. **26**(4): 590–598.

Rentch, J.S., Fajvan, M.A., and Hicks, R.R., Jr. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. For. Ecol. Manage. **184**: 285–297.

SAS Institute Inc. 2004. SAS/STAT user's guide [computer program], version 9.1. Vol. 4. SAS Institute Inc., Cary, N.C.

Schaetzl, R.J., Burns, S.F., Small, T.W., and Johnson, D.L. 1990. Tree uprooting: review of types and patterns of soil disturbance. Phys. Geogr. **11**: 277–291.

Schindler, D.W. 1998. Replication versus realism: The need for ecosystem-scale experiments. Ecosystems, **1**: 323–334.

Schlesinger, R.C. 1990. *Fraxinus Americana* L., White Ash. *In* Silvics of North America: 2 Hardwoods. Vol. 2. US Dep. Agric. Agric. Handb. 654. pp. 333–338.

Schuler, T.M., and Fajvan, M.A. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. USDA For. Serv. Res. Pap. NE-710.

Simmons, C.S. 1939–1940. Soil survey of Harvard Forest. Harvard Forest Archives, Harvard Forest, Petersham, Mass.

Sipe, T.W., and Bazzaz, F.A. 1994. Gap partitioning among maples (*Acer*) in central New England: Shoot architecture and photosynthesis. Ecology, **75**: 2318–2332.

Sipe, T.W., and Bazzaz, F.A. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. Ecology, **76**: 1587–1602.

Smith, D.M., and Ashton, P.M.S. 1993. Early dominance of pioneer hardwood after clearcutting and removal of advanced regeneration. North. J. Appl. For. **10**(1): 14–19.

Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S. 1997. The practice of silviculture: Applied forest ecology. John Wiley & Sons, N.Y.

Spetich, M.A., Dey, D.C., Johnson, P.S., and Graney, D.L. 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. For. Sci. **48**(3): 504–517.

Spurr, S.H. 1957. Local climate in the Harvard forest. Ecology, **38**: 37–46.

Stephens, E.P. 1956. The uprooting of trees: a forest process. Soil Sci. Soc. Am. Proc. **20**: 113–116.

Tift, B.D., and Fajvan, M.A. 1999. Red maple dynamics in Appalachian hardwood stands in West Virginia. Can. J. For. Res. **29**: 157–165.

van Mantgem, P., Schwartz, M., and Keifer, M.B. 2001. Monitoring fire effects for managed burns and wildfires: Coming to terms with pseudoreplication. Nat. Areas J. **21**(3): 266–273.

Ward, J.S., and Stephens, G.R. 1996. Influence of crown class on survival and development of *Betula lenta* in Connecticut, USA. Can. J. For. Res. **26**: 277–288.

Weiner, J., and Solbrig, O.T. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia, **61**: 334–336.

White, D.A. 1992. Relationships between foliar number and the cross-sectional areas of sapwood and annual rings in red oak (*Quercus rubra*) crowns. Can. J. For. Res. **23**: 1245–1251.

White, J., and Harper, J.L. 1970. Correlated changes in plant size and number in plant populations. J. Ecol. **58**: 467–485.

Wilson, B.F. 1966. Development of the shoot system of *Acer rubrum* L. Harvard Forest Pap. No. 14. Harvard Forest, Harvard University, Petersham, Mass.

Zen, E. 1983. Bedrock geologic map of Massachusetts. Map scale 1 : 250 000. United States Geological Survey, Reston, Va.