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DYNAMICS IN LATE-SUCCESSIONAL HEMLOCK–HARDWOOD FORESTS OVER THREE DECADES

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Abstract. Permanent plots in old-growth hemlock–northern hardwood forests of Michigan's upper peninsula have been remeasured over periods of 16–32 yr. A gradient from hemlock (*Tsuga canadensis*) to sugar maple (*Acer saccharum*) dominance is associated with increasing soil pH and calcium. Secondary species include yellow birch (*Betula alleghaniensis*) and basswood (*Tilia americana*). From 1962 to 1994 hemlock increased in basal area and dominance in most plots. Sugar maple showed little overall change, while basswood and especially yellow birch showed sporadic but often large declines in basal area. Birch populations declined due to lack of recruitment, and sugar maple and basswood may be subject to similar decline; only hemlock showed a fairly stable size structure. Mortality rates were lowest for hemlock (0.3%/yr) and highest for yellow birch (1.6%/yr), corresponding to canopy residence times of 357 and 61 yr, respectively. Stem maps allowed assessment of neighborhood influences on growth and mortality. Growth and mortality rates were negatively correlated for all species. Growth rate was influenced by tree size and site conditions for all species, but hemlock and sugar maple growth rates were also affected by size- and distance-weighted indices of neighbor influence. Old-growth stands several centuries old continue to undergo compositional change related to both stand history and current population interactions. Yellow birch and basswood are probably maintained by significant disturbances and will decline under a disturbance regime of small gaps. Hemlock may be the ultimate competitive dominant in most sites but may require well over a millennium without major disturbance to displace sugar maple.

Key words: Acer saccharum; Betula alleghaniensis; *canopy dynamics; competition; hemlock–northern hardwood forest; long-term studies; old-growth forest; permanent plots; succession; tree demography;* Tsuga canadensis.

INTRODUCTION

Much of our understanding of late-successional forests is based on untested anecdotes and conceptual models and lacks strong empirical support. Because tree generation times exceed a century, direct measurement of community dynamics is daunting, while indirect approaches are hampered by assumptions about environmental history (chronosequence studies and inferences from current stand patterns) or limits on resolution, precision, or generalizability of data (paleoecology and historical reconstruction) (Davis 1989, Pickett 1989). New generations of simulation models (e.g., Pacala et al. 1993, 1996) may overcome some of these limitations, but are difficult to apply retrospectively. These limitations threaten the effectiveness of conservation management focused on old-growth forests. Ultimately, direct, long-term observation is critical in testing and extending hypotheses about properties of late-successional communities (Bakker et al. 1996), but few studies of late-successional forests have been maintained over more than a decade (but see Filip et al. 1960, Leak 1970, Hough 1965, Whitney 1984, Peet 1984).

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I used data from a 32-yr study of permanent plots in old-growth hemlock–northern hardwood stands in northern Michigan to interpret community and population dynamics and to assess some frequent assumptions and expectations of succession theory. Succession models often suggest that with the passage of time following stand initiation, stand composition will become more stable, community and population properties will become more fully controlled by processes and interactions internal to the stand, and stand structure and composition will become less directly attributable to particular historical events. Do late-successional stands, in fact, increase in stability? If so, what is the relevant time frame? If more than two or three generations of canopy dominants are required, infrequent major disturbances may make stable "old-growth" stands relatively rare. Do structure and composition of late-successional stands become substantially independent of the direct effects of massive disturbance (as indicated by lack of even-aged cohorts and light-demanding species), becoming increasingly shaped by processes internal to the stand?

Changes in basal area and size structure, mortality and establishment rates, and the effects of local competition on growth and mortality over three decades all suggest that successional change continues in these old-

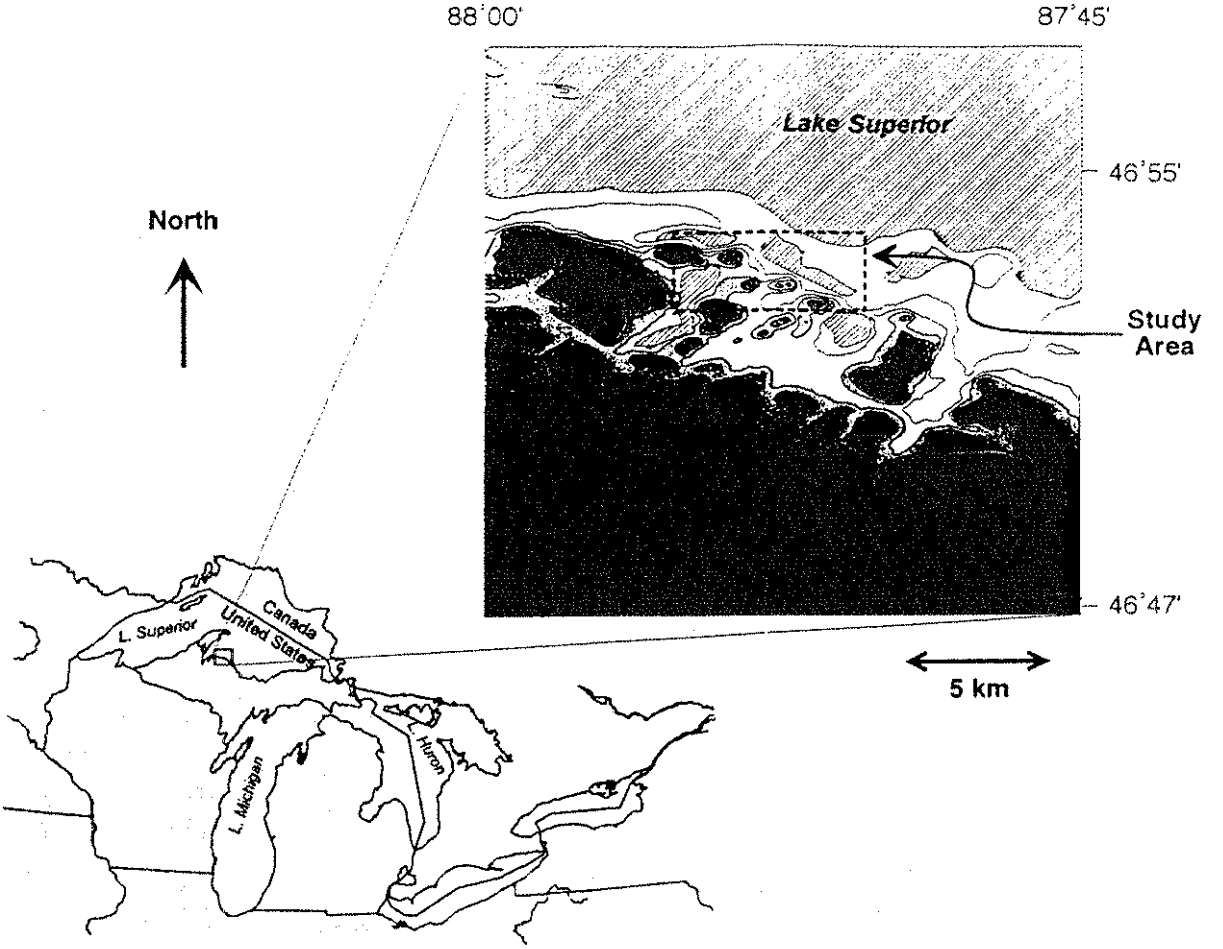

FIG. 1. Location of the Huron Mountains study site. The outline map at lower left locates the study area within the Great Lakes region of the United States and Canada. The expanded inset shows topography for an area of roughly 20 × 20 km: contour lines are at 30-m intervals. Water surfaces (Lake Superior and larger inland lakes) are hatched. Lake Superior surface elevation is ~183 m; highest elevations (~510 m) are at the southwest corner of the map. Permanent plots are distributed at several sites near the cluster of large inland lakes.

growth forests. Current composition reflects probable disturbances several centuries past, but patterns in growth and mortality are also shaped by current competitive interactions. Trends suggest an ultimate, hemlock-dominated, and potentially stable community, but only after several more centuries without major disturbance.

METHODS

Site description and field methods

The Huron Mountains, on the central south shore of Lake Superior in Michigan, USA (Fig. 1), display local relief of ~270 m above mean lake surface of 182 m. Bedrock is Pre-Cambrian granite, gneiss, and sandstones (Dorr and Eschmann 1970). Soils are generally thin and acidic, derived from rocky glacial till, with small areas of deeper till and alluvium. Research sites are located within a 2500-ha reserve in mesic forests dominated by hemlock (*Tsuga canadensis*) and sugar maple (*Acer saccharum*), with yellow birch (*Betula alleghaniensis*) and basswood (*Tilia americana*). There has been no logging within the reserve.

In 1962 E. A. Bourdo and J. A. Johnson (Michigan Technological University) established 21 circular 0.08-ha plots ("old plots") distributed across the reserve. Trees >12.5 cm diameter at breast height (dbh) were labeled and tallied by species and dbh. Selected trees were cored for ages. Trees were remeasured by the original investigators in 1967. In 1978 I established seven 0.1-ha plots (20 × 50 m) (Woods 1984). On these "new plots," all stems >1 cm dbh were measured and mapped, and several increment cores were collected from each plot. Trees on these plots were remeasured in 1984.

In 1989 I measured all stems >1 cm dbh on all 28 (new and old) plots. On old plots, stems were mapped

on polar coordinates. Distance from plot center was measured by tape (later with Sonin [Scarsdale, New York, USA] ultrasonic rangefinders), and azimuth was measured with a sight-through compass (Suunto, Helsinki, Finland). Experiment and replication indicated that maximum mapping error was <1 m. Trees were measured and mapped beyond plot boundaries to include all canopy dominants within 8 m of any stem within the plot. Mortality since the last census was noted. I repeated measurements in 1994.

In 1992, soil samples were collected from depths of 10–20 cm at two locations in each plot. Chemical analyses (P, K, Mg, Ca, Fe, Al, Mn, Zn, Cu, pH, exchange acidity, and NO_3^-) were done at the Cornell University Nutrient Analysis Laboratories. Fractions of gravel (>2 mm), sand, and clay were determined by sieving and densitometry.

Analysis

Compositional patterns and community dynamics.—Tree ages, determined by ring counts on increment cores, were used to assess stand history and to discover evidence of even-aged cohorts that might indicate past fire or other disturbance.

Association between environmental and historical variables and species composition of plots was assessed using canonical correspondence analysis (CCA: ter Braak 1986). The following environmental variables were submitted to CCA after initial inspection of patterns of variation and correlation: slope and aspect (coded as degrees from north-northeast, so that higher scores are edaphically drier); soil concentrations of P, K, Ca, Fe, Al, and NO_3^-; soil pH; and percentage sand and gravel (by mass). A dummy variable coded for three plots that burned in about 1820. CCA ordinations were performed for each sampling period, but trends were the same, and results are reported only for the 1994 data set. Detrended correspondence analysis (DECORANA: Hill 1980) ordinations of pooled sample dates were used to assess temporal patterns of compositional change and to partition the data set into compositionally defined "plot groups." Analyses of population dynamics and competitive effects were carried out for the entire data set, and also on each plot group separately where sample size was sufficient and there were statistical differences among groups.

Population dynamics and competitive interactions.—Annual mortality rates were calculated as mortality rate = $[\ln N(t_2) - \ln N(t_1)]/(t_2 - t_1)$ where $N(t_1)$ and $N(t_2)$ are stem numbers at the beginning and end of a time interval. Growth and mortality rate were summarized by size class for sampling dates and intervals and for each plot group. Stem maps were used to develop indices of potential neighborhood competition for each tree. As a measure of competitive influence of neighboring ("influencing") trees on a focal ("influenced") tree, I calculated an influence index (I_f):

$$I_f = \sum_{\mathrm{dist} < 8\ \mathrm{m}} D_n/\mathrm{dist}_{n,f}$$

where D_n is dbh of an individual neighboring tree and $\mathrm{dist}_{n,f}$ is the distance between neighboring and focal trees. The summation is over all neighbors within 8 m of the focal tree with a diameter greater than that of the focal tree (see Woods 1979, Monserud and Ek 1977, Lorimer 1983). Influence indices were calculated separately for neighbors of each dominant canopy species as well as for all species pooled.

Analyses of covariance were used to assess relationship of growth rates to dbh, influence indices, plot group, and their interactions. Logistic regressions and resampling methods (Simon 1993) were used to test whether probability of mortality was influenced by tree size, growth rate, or influence indices. In these analyses, I used growth rate for the immediately previous measurement interval (e.g., for mortality during 1989–1994, growth rate for 1967–1989 was the independent variable). Mann-Whitney tests and resampling were used to compare influence index means for trees that survived to those for trees that died (parametric comparisons of means tests could not be used because indices had highly skewed distributions and many zero values). Resampling tests were based on 1000 bootstrapped data sets created by resampling with replacement from influence indices for surviving and dying trees. Mann-Whitney and resampling tests were used to compare growth rates for trees that survived or died during each sampling interval.

RESULTS

Community composition and dynamics

Sugar maple and hemlock dominated all stands, while basswood and yellow birch were abundant in several plots (Table 1; plot numbers >7000 were assigned by the original investigators in 1962; 1 established plots 1–7 in 1978). Hop-hornbeam (*Ostrya virginiana*) occured with high frequency in the subcanopy. Canopy trees cored ranged from about 150 to 400 yr old, and there was no apparent clustering of ages within stands except in hemlock-dominated plots 7094–7096, where most stems were about 170 yr old. Stand structure (high stem density with modest maximum size) and shallow soil charcoal (not noted in other stands) suggest a stand-initiating fire in about 1820 in these three plots, which are subsequently referred to as "burned plots."

DECORANA ordination of untransformed 1994 data is typical of all ordinations (Fig. 2). The primary axis reflects gradation from sugar maple to hemlock dominance, with basswood more frequent in association with sugar maple. The second axis separates three plots (two in the burned stand) with minor, predominantly shade-intolerant species (*Pinus strobus*, *Picea glauca*, *Populus grandidentata*, *Quercus borealis*, *Thuja occidentalis*, and *Acer rubrum*). The third axis separates

TABLE 1. Basal area (m^2/ha) by species and plot for 1994.

Plot	Total	Sugar maple	Hop-horn-beam	Basswood	Balsam fir	Red maple	Yellow birch	Hemlock	Minor species÷
Group I									
7097	39.01	38.37	0.00	0.00	0.00	0.00	0.00	0.64	
7089	30.54	28.65	0.00	0.00	0.00	0.00	1.89	0.00	
7090	40.13	35.15	0.11	4.18	0.00	0.00	0.70	0.00	
7098	67.22	63.72	0.36	0.00	0.00	0.00	0.14	3.00	
7100	31.97	28.91	0.49	1.32	0.00	0.00	0.00	1.24	
7	28.44	24.40	0.09	3.40	0.00	0.00	0.56	0.00	
7088	29.76	23.61	0.00	3.72	0.00	0.00	2.42	0.00	
Group II									
7101	49.00	37.66	0.00	11.34	0.00	0.00	0.00	0.00	
7103	45.32	29.34	0.75	10.69	0.00	0.00	1.42	3.11	
1	50.60	36.45	1.30	3.38	0.11	0.00	1.45	7.92	
7099	45.29	23.21	1.26	10.69	0.91	0.00	7.83	1.39	
2	52.10	28.87	0.58	9.94	0.00	0.00	3.20	9.51	
7102	55.56	27.28	0.23	8.06	0.00	0.00	5.80	14.19	
7104	47.92	25.14	0.91	2.12	0.97	0.00	2.48	16.30	
3	60.71	30.16	0.43	5.12	0.00	0.00	4.46	20.54	
6	58.23	18.08	0.91	19.88	0.00	0.00	1.40	17.96	
Group III									
4	55.68	21.21	0.07	9.79	0.00	3.14	0.25	20.96	acpe = 0.27
5	55.04	17.57	0.31	2.22	0.00	0.00	8.84	25.93	thoc = 0.16
7091	59.07	11.83	0.00	4.65	0.00	0.00	18.24	24.34	
7105	54.12	14.58	0.00	1.11	0.00	0.00	0.31	38.12	
7092	68.07	11.64	0.00	9.02	0.00	0.00	0.00	47.40	
7086	53.15	8.29	0.00	0.00	0.64	2.12	4.63	37.47	
7106	55.87	9.62	0.07	1.26	0.05	7.30	4.90	24.35	ulam = 0.77, pigl = 1.46, pogr = 2.9, pist = 3.2
7093	71.09	5.44	0.00	1.98	0.00	0.00	12.40	51.27	
7085	42.53	0.59	0.00	0.00	0.11	0.00	6.27	35.55	
Group IV (burned)									
7096	63.21	11.36	0.06	17.43	0.00	0.00	1.78	26.35	pigl = 0.64, qubo = 4.88, pist = 0.7
7094	63.53	10.21	0.37	0.00	0.00	0.71	4.17	48.07	
7095	65.33	1.25	0.00	0.00	0.00	3.69	1.64	47.83	pogr = 9.34, thoc = 1.58

÷ Codes for minor species: acpe = *Acer pensylvanicum*, pigl = *Picea glauca*, pist = *Pinus strobus*, pogr = *Populus grandidentata*, qubo = *Quercus borealis*, thoc = *Thuja occidentalis*.

plots with higher basal area of the two secondary dominants, basswood and yellow birch. Yellow birch is broadly and irregularly distributed, but reaches greatest importance in some of the hemlock-dominated stands. In the subcanopy, hop-hornbeam is largely restricted to maple-dominated stands.

CCA ordinations showed similar compositional structure (Fig. 3). Burned plots are at extremes on all axes, and the "fire" variable is heavily weighted. Sugar maple-dominated stands had high pH and NO_3^- and low total acidity as compared to hemlock-dominated stands. Soil Ca was positively correlated with pH and NO_3^-, while Al and percentage gravel were negatively correlated with the same variables. Soil K and Mg were associated with the third axis and positively correlated with basswood basal area. Ordinations and soil characteristics were subjectively used to assign plots to the following four groups for demographic analyses (Fig. 2, Table 1):

Group I.—Plots strongly dominated by sugar maple on fine-textured alluvial soils with relatively high moisture-holding capacity and cation exchange capacity (Marquette County Soil Survey, *unpublished data*).

Group II.—Plots dominated by sugar maple with basswood, yellow birch, and hop-hornbeam on well-drained sandy alluvial soils (plots 1, 7099–7104) or relatively deep glacial drift (plots 2, 3, 6).

Group III.—Mixed hemlock–hardwood to hemlock-dominated plots, often with yellow birch, on glacial till-derived soils of varying depth and drainage.

Group IV.—The three burned sites, site characteristics similar to Group III.

Over 32 yr, hemlock dominance increased except in the most strongly sugar maple-dominated plots. In ordination space (Fig. 4), plot trajectories converge on the center of hemlock distribution except in regions of maple dominance (left side of field). Hemlock basal area and total basal area increased in most plots with initial hemlock presence (plot groups II–IV). Sugar maple basal area increases were proportionately smaller and less consistent. Overal basal area declines for yellow birch and basswood are a consequence of several

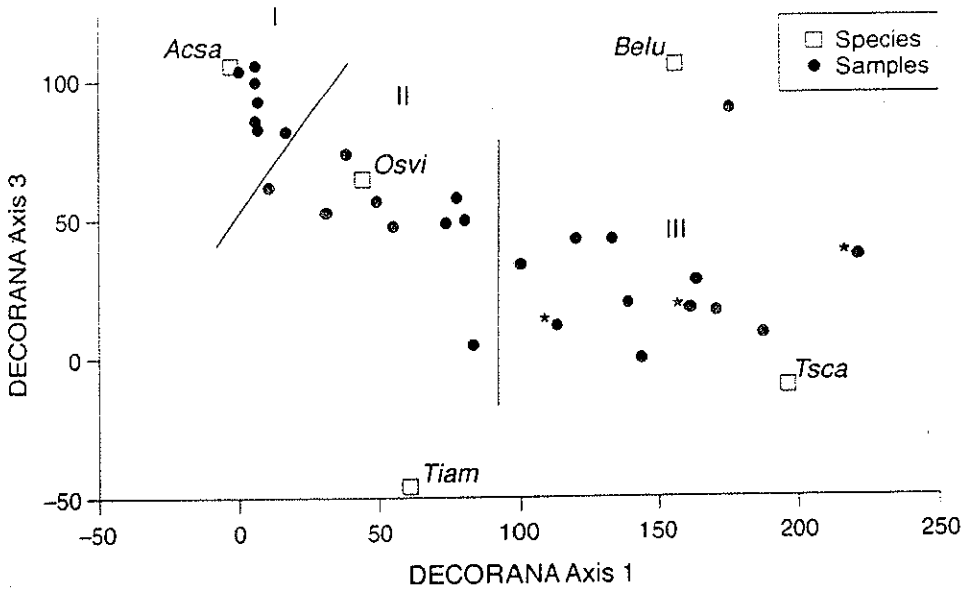

FIG. 2. DECORANA ordination of 1994 data, showing first and third axes. Sample ordination (solid dots) is based on basal area, unweighted, for all species. Species ordination (open squares) is shown for dominant species: *Acer saccharum* (*Acsa*), *Betula alleghaniensis* (*Belu*), *Ostrya virginiana* (*Osvi*), *Tilia americana* (*Tiam*), and *Tsuga canadensis* (*Tsca*). Lines separate plot groups I, II, and III used in analyses (Table 1). Asterisks indicate "burned plots" in plot group IV.

plots experiencing large declines while others changed little or increased slightly; basal area of hop-hornbeam showed large proportional increases in the majority of plots (Fig. 5). Regressions of 1994 basal area on 1962 basal area had slopes significantly differing from unity ($P < 0.05$) only for hemlock and for total basal area.

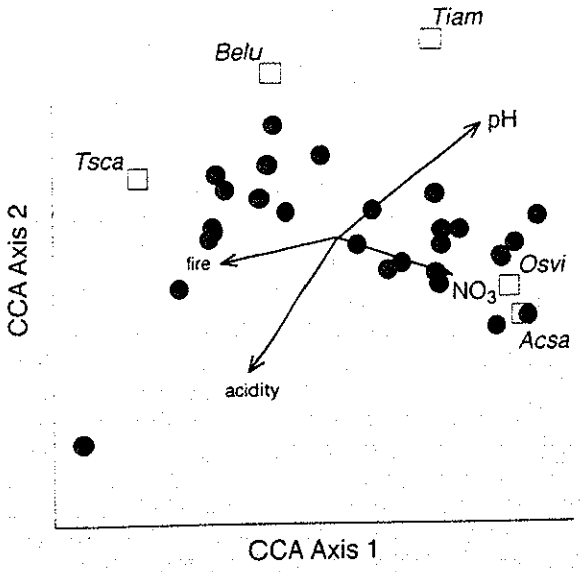

FIG. 3. Canonical correspondence analysis (CCA) biplot of 1994 data, showing first and second axes. Sample and species arrangements are indicated as in Fig. 2. Vectors indicate the strength and sign of correlation of indicated environmental variables with ordination axes (e.g., soil acidity is negatively correlated with both axis 1 and 2). "Fire" is a qualitative variable, coded 1 for plots that burned circa 1825, 0 for unburned plots.

Demography

Density of sugar maples <42 cm dbh decreased monotonically, but no density trend was evident for larger stems (Fig. 6a). Average growth rates increased with stem size, ranging from about 1.5 to 3 mm/yr. Mortality ranged from 0.5 to 1%/yr, but showed no clear trend with size class. Hemlock size distribution remained relatively constant in a smoothly decaying curve (Fig. 6b), with slight but consistent density declines in the smallest size class and comparable increases in larger classes. Growth rates were similar to those for sugar maple, but mortality rates were much lower (<0.4%/yr for size classes <62 cm dbh).

Yellow birch trees <32 cm dbh (corresponding roughly to subcanopy trees) decreased by more than 50% in density (Figure 6c). Growth rates were similar to those for sugar maple and hemlock, but mortality rates were higher, ranging up to 4% for smaller size classes and from 1–2%/yr for diameters up to 52 cm. Small basswood trees were never as frequent as larger stems, and densities of small stems declined during the study (Fig. 6d). Growth rates increased with size, but mortality estimates are uncertain due to small sample sizes.

Increased mortality rates for smaller stems, over time, are suggested for sugar maple, hemlock, and yellow birch (Fig. 6). Only hop-hornbeam and hemlock increased in stem density (new stems exceeding mortality in Table 2). Among trees of canopy size (dbh >

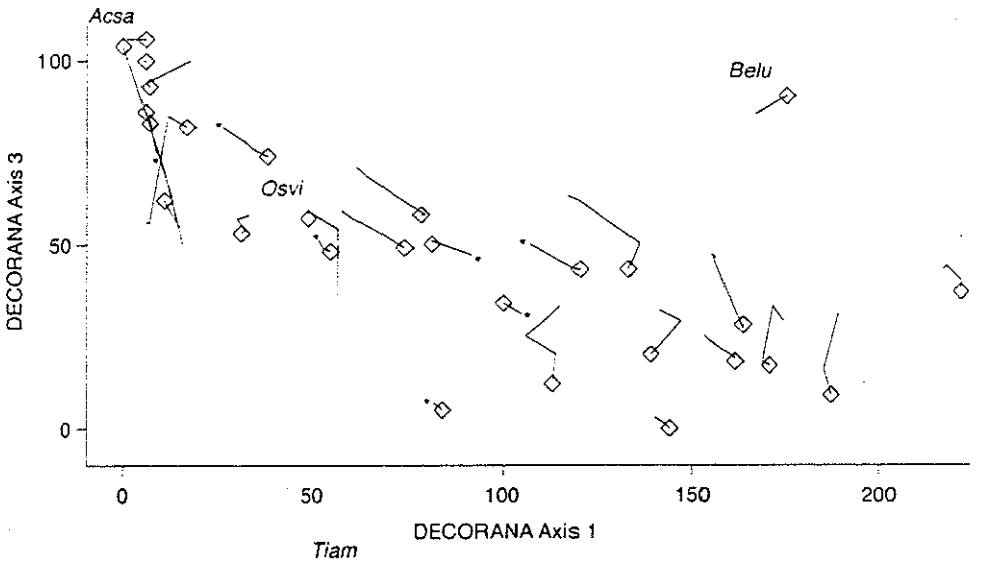

FIG. 4. Plot trajectories in DECORANA ordination space. Ordination includes all measurements of all plots. Lines connect ordinated positions for each plot for successive dates in the temporal sequence. Diamonds represent the most recent (1994) measurement. "New" plots, established in 1978, are indicated by asterisks at the origin of the trajectory. Species centers are as in Fig. 2: *Tilia americana* is centered below the displayed range on Axis 3.

30 cm), mortality was lowest for hemlock and highest for yellow birch (Table 3). Corresponding estimates of turnover time for canopy tree populations range from less than one to more than three centuries. Maples in plot group I had higher mortality than in plot groups II–IV. Hemlock canopy trees in the burned plots (group IV) experienced no mortality, but even with exclusion of these plots, canopy residence times are still estimated at 250 yr.

Growth rates for all canopy species were influenced by plot group, initial dbh, and their interaction (analysis of covariance, $P < 0.05$). Hop-hornbeam diameter growth was independent of plot group and was only slightly affected by dbh ($P < 0.10$). In comparisons among plot groups within species (Bonferroni multiple comparison of means test, $P = 0.05$), sugar maple and yellow birch grew faster in plot group I than in other groups (Table 4). Sugar maple growth in group I also showed less size dependency (Figure 7). Hemlock growth rates decreased from plot group II through IV (group I had few hemlock trees and was statistically indistinguishable from other groups). Low overall growth in group IV (burned plots) was due to slower growth in trees less than 32 cm dbh, which constitute the majority of stems in these plots (Fig. 8). Separate results for stems larger and smaller than 42 cm dbh were similar for all species, so results are given only for the more powerful overall test.

Low growth rate was associated with elevated mortality (Fig. 9). Sugar maple and hemlock trees that died by 1989 grew more slowly during 1962–1967 than did trees that survived (Mann-Whitney tests and resampling comparisons, $P < 0.05$). Average growth rates from 1967 to 1989 were lower for trees that died in the subsequent five years. A similar relationship held for yellow birch during the first time interval only. Basswood showed marginal differences for the first time interval ($P = 0.06$), but sample size was inadequate for testing in the second. Too few hop-hornbeam trees were measured in early samples to assess the relationship between growth rate and mortality.

Neighborhood effects on growth and mortality

Indices of neighborhood influence or competitive effect explained additional variation in growth rates when added to multiple analysis of covariance models. Stepwise regressions selected plot group and dbh as predictors of growth rate in all cases, but importance of neighborhood effects varied among species.

Overall, neighbor influence indices had only modest explanatory power for sugar maple growth rate, but interaction of neighbor influence index and plot group was important (Table 5). Total neighbor influence index had significant predictive power for maple growth in maple-dominated plot group I, but not in the pooled groups II–IV. Over all plots, hemlock growth was affected by both hemlock and total neighbor influence indices, as well as by interactions involving total influence index. Examined separately, hemlock growth in plot group IV (burned plots) was less affected by neighbor influence indices, while separate maple and hemlock neighbor influence indices have significant explanatory power for groups I–III pooled. Growth rates of yellow birch and basswood were unrelated to neighbor influence indices. Hop-hornbeam growth was influenced by both hemlock and maple influence index,

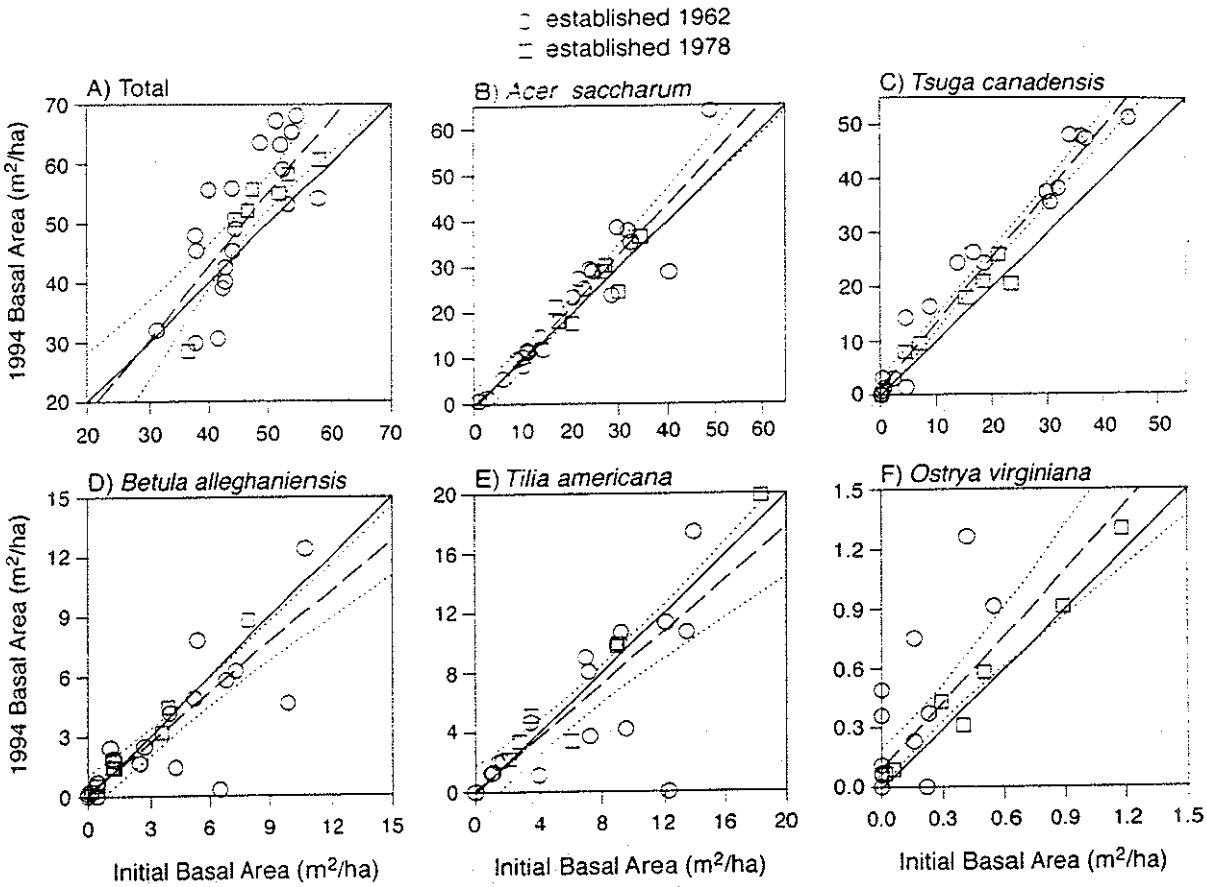

FIG. 5. Changes in basal area over study period, by species. The 1994 basal area is plotted against earliest basal area measurement (old plots are indicated by circles, new plots by squares). Solid lines indicate the locus of zero change in basal area. Dashed lines are linear regressions of 1994 basal area on initial basal area; dotted lines give 95% confidence interval for regressions.

and by total influence index in interaction with plot group and dbh.

Total neighbor influence index affected chance of mortality for all species except hop-hornbeam (logistic regression, Mann-Whitney and resampling comparisons, $P < 0.05$; all tests gave consistent results) (Fig. 10). Sugar maple influence index had no effect on hemlock mortality, but both hemlock and sugar maple influence indices affected mortality rate for sugar maple. These patterns were maintained when plot groups were examined separately. Only hemlock neighbor influence index had significant effect on mortality rate in yellow birch, and only sugar maple influence index affected mortality for basswood. No index influenced mortality rate in hop-hornbeam. All tests were conducted separately for mortality during 1989–1994 (using all plots) and mortality during 1967–1994 (using old plots only), with consistent results.

DISCUSSION

Old-growth hemlock–northern hardwood stands, centuries removed from stand-initiating disturbance, are not necessarily in demographic or compositional equilibrium. Ongoing successional change observed here reflects both competitive interactions among dominant species and long-lasting effects of moderate disturbance events. Observed rates of change, when compared with rates of environmental change and the frequency of major disturbance, suggest that equilibrial communities have rarely, if ever, been achieved during the Holocene.

Demographic patterns and population dynamics

Vital rates for tree populations at the Huron Mountains indicate that hemlock populations are expanding while other species show little change or decline. Estimated residence times for canopy trees in old-growth forests in the upper Great Lakes region range from 128 to 186 yr (Frelich and Lorimer 1991, Frelich and Graumlich 1994, Dahir and Lorimer 1996), bracketing the 149-yr estimate from this study (Table 3). Species-specific estimates vary widely. Low observed hemlock mortality (Fig. 6, Tables 2, 3) equates with canopy residence times more than twice those for other species

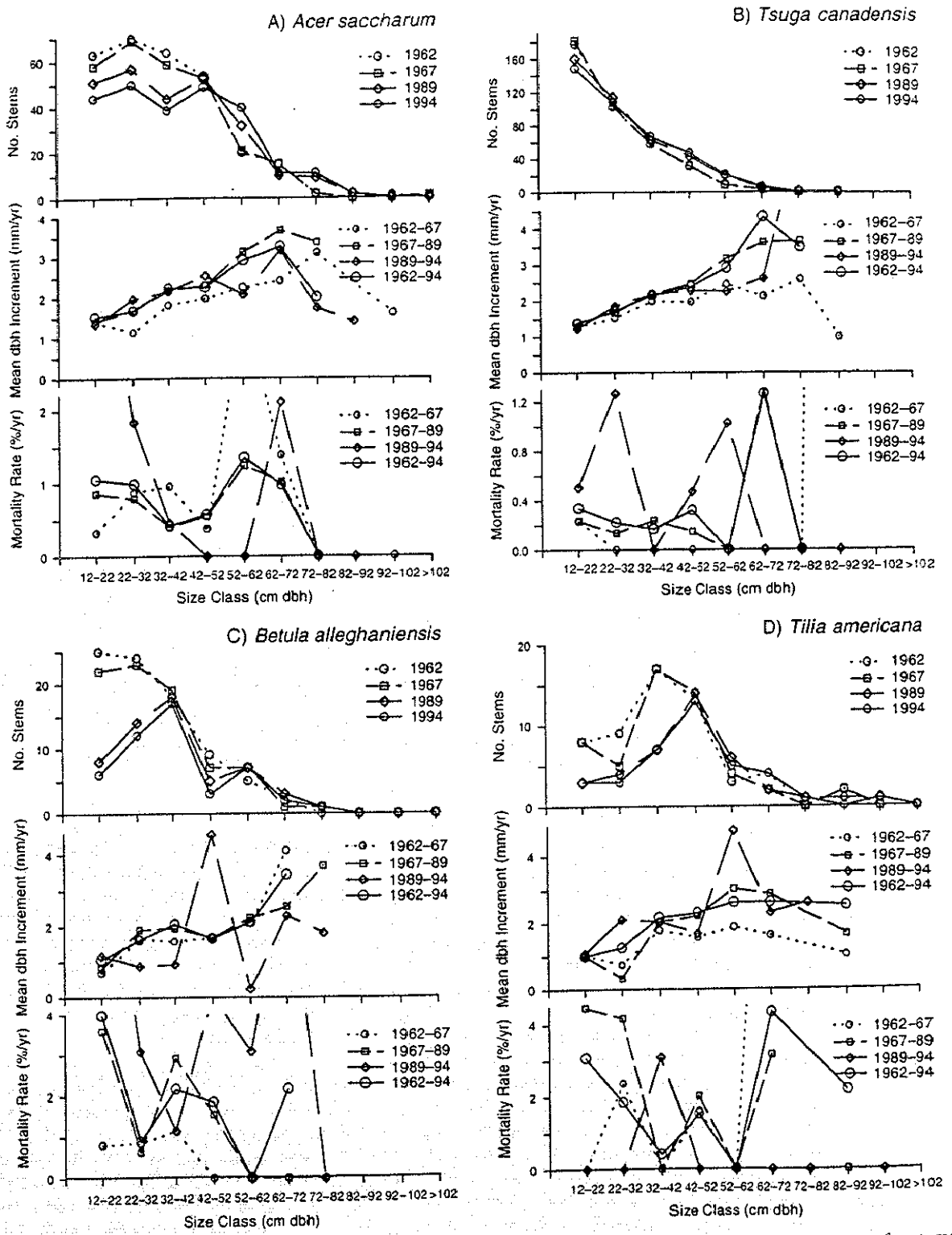

FIG. 6. Demographic patterns for dominant species, all old plots. Diameter distributions (top graph each set) for stems >12 cm dbh are shown for each sampling period. Curves for average growth rates (middle graph) by size class, as annual diameter increment, are given for each sampling period and for the entire study period (–⊖–). Mortality rates (bottom graph) are illustrated similarly to growth rates.

TABLE 2. Overall recruitment and mortality (no. stems·(decade)$^{-1}$·ha^{-1}).

Species	1962–1967	1967–1989	1989–1994	1962–1994
A) New stems >12 cm dbh				
Sugar maple	1.2	5.7	7.1	5.2
Plot group I	0	12.0	17.2	10.8
Plot groups II–IV	1.7	3.0	3.3	2.9
Yellow birch	0	0.5	1.2	0.6
Hop-hornbeam	1.2	1.4	1.2	1.3
Basswood	0	0.3	0	0.2
Hemlock	12.3	9.7	6.0	9.5
Plot groups I–III	12.7	9.5	5.6	9.3
Plot group IV	8.3	11.2	8.3	8.9
B) Mortality, all stems >12 cm dbh				
Sugar maple	13.6	11.1	20.3	11.7
Plot group I	42.0	1.9	38.1	18.7
Plot groups II–IV	3.3	11.0	14.6	9.6
Yellow birch	0	7.0	11.2	7.1
Hop-hornbeam	0	0.5	4.8	1.1
Basswood	4.8	3.8	2.4	3.7
Hemlock	3.6	4.9	14.7	6.3
Plot groups I–III	2.8	5.1	15.1	6.3
Plot group IV	8.3	3.8	17.0	6.5

(250–350 yr, depending on whether burned plots are included). Residence times estimated for yellow birch range from 61 yr in this study to 232 yr by Frelich and Graumlich (1994). The low estimate here may indicate extended regeneration failure for yellow birch at the Huron Mountains, leading to an age distribution dominated by older cohorts.

Among canopy species, recruitment rates exceed mortality only for hemlock, with highest density declines among smaller stems of hardwood species (Table 2). Further decline may be most immediate for yellow birch because of the marked decrease in the density of smaller trees. This pattern apparently results from failure of recruitment in size classes smaller than those measured here; mortality rates are not notably higher for small size classes in hardwood species, and are comparable to those observed by Leak (1970). Recruitment failure is difficult to explain without long-term data on seedlings and smaller saplings. Simulation models (Pacala et al. 1996) suggest that competition will drive replacement of hardwoods by hemlock, at least in the absence of beech, indicating that patterns observed here may be successional. If so, persistence of hardwoods (especially birch) may depend on pulses of establishment following infrequent, relatively intense disturbance.

TABLE 3. Canopy mortality rates and residence time (stems >30 cm dbh).

Species	No. stems in 1962	Stem mortality (%/yr)	Estimated residence time (yr)
Sugar maple	156	0.64	156
Plot group I	63	0.85	118
Plot groups II–IV	93	0.51	196
Yellow birch	34	1.65	61
Basswood	39	1.03	97
Hemlock	104	0.28	357
Plot groups I–III	74	0.40	250
Plot group IV	30	0	...
Total	333	0.67	149

Only small gaps, caused by the death of one or a few trees, have been observed in this study, but these have not resulted in establishment of birch trees. Catastrophic blow-downs, the primary form of intense disturbance in the study area, can foster massive regeneration of yellow birch (Dunn et al. 1983, Peterson and Pickett 1995), but have return times exceeding a millennium (Lorimer 1977, Canham and Loucks 1984, Frelich and Lorimer 1991, Seischab and Orwig 1991). Disturbances eliminating 30–50% of canopy have an estimated return time of 300 yr (Frelich and Lorimer 1991), and may allow sufficient, episodic yellow birch regeneration to account for patterns observed here. Willis and Coffman (1975) found a clustering of yellow birch around 180 yr old in the Huron Mountains. Cohorts of similar age in maple and hemlock (K. D. Woods, *unpublished data*) strengthen the suggestion of a major disturbance in the late 1700s. Basswood regeneration may also require significant disturbance, but its habit of basal sprouting allows extended site occupation (Crow 1990); only sprout regeneration was observed in this study.

Growth and mortality of seedlings and saplings in forest understories are differentially influenced by particular species in the canopy (Woods 1979, 1984, Frelich et al. 1993, Davis et al. 1994). This study suggests that growth and survival of large trees are influenced both by neighbors and by site qualities (as indicated by plot group) and tree size (Table 5). The effect of size, presumably related to access to light, is slight in hop-hornbeam, which remains in the subcanopy throughout its life. Effects of neighbors on growth were

TABLE 4. Mean diameter growth rate, 1989–1994 (mm/yr): comparisons by plot group (standard error in parentheses).

Species	Plot group I	II	III	IV
Sugar maple	2.5 (0.16)[a]	1.8 (0.14)[b]	1.8 (0.18)[b]	0.92 (0.36)[b]
Yellow birch	4.2 (1.9)[a]	0.68 (0.34)[b]	1.2 (0.24)[b]	0.62 (0.42)[b]
Hop-hornbeam	0.27 (0.41)	0.68 (0.14)	0.50 (0.13)	0.33 (0.24)
Basswood	3.6 (1.0)	2.4 (0.47)	2.9 (0.45)	1.2 (0.57)
Hemlock	2.6 (0.60)[ab]	2.5 (0.16)[a]	1.9 (0.10)[b]	0.88 (0.10)[c]

Note: Within a row (species), shared superscript letters indicate that the means do not differ significantly (Bonferroni, $P > 0.01$).

seen only in the shade-tolerant species, sugar maple, hemlock, and hop-hornbeam. Response to competition by growth reduction may be related to the mechanisms of shade tolerance (Canham 1989, Pacala et al. 1993, 1994). Even in large size classes, hemlock, the most shade-tolerant species in this study, appears to display the most response to competition in growth rate. The relationship between neighbor influence index and growth rate may be emphasized for hemlock because a large proportion of hemlock trees are in subcanopy size classes, where competitive effects are likely to be most intense. Separate analyses for hemlock trees of canopy size only (>35 cm dbh) show no affect of neighbor influence on growth rate (only dbh and the dbh × plot group interaction have significant effect). Separate analyses of small and large stems for maple showed no such differences.

Mortality rates are not strongly related to diameter for any species (Fig. 6), but both growth rate and the influence of neighboring trees appear to affect survival for all canopy species (Figs. 9, 10). Ward and Stephen (1997) also documented a correlation of growth rate and survival in successional yellow birch. Only hop-hornbeam (tested for the entire term of the study to achieve a sufficient number of tree deaths) showed no significant mortality response to neighbor influence. Consistent with its apparent competitive superiority, hemlock's growth and mortality appear to be more

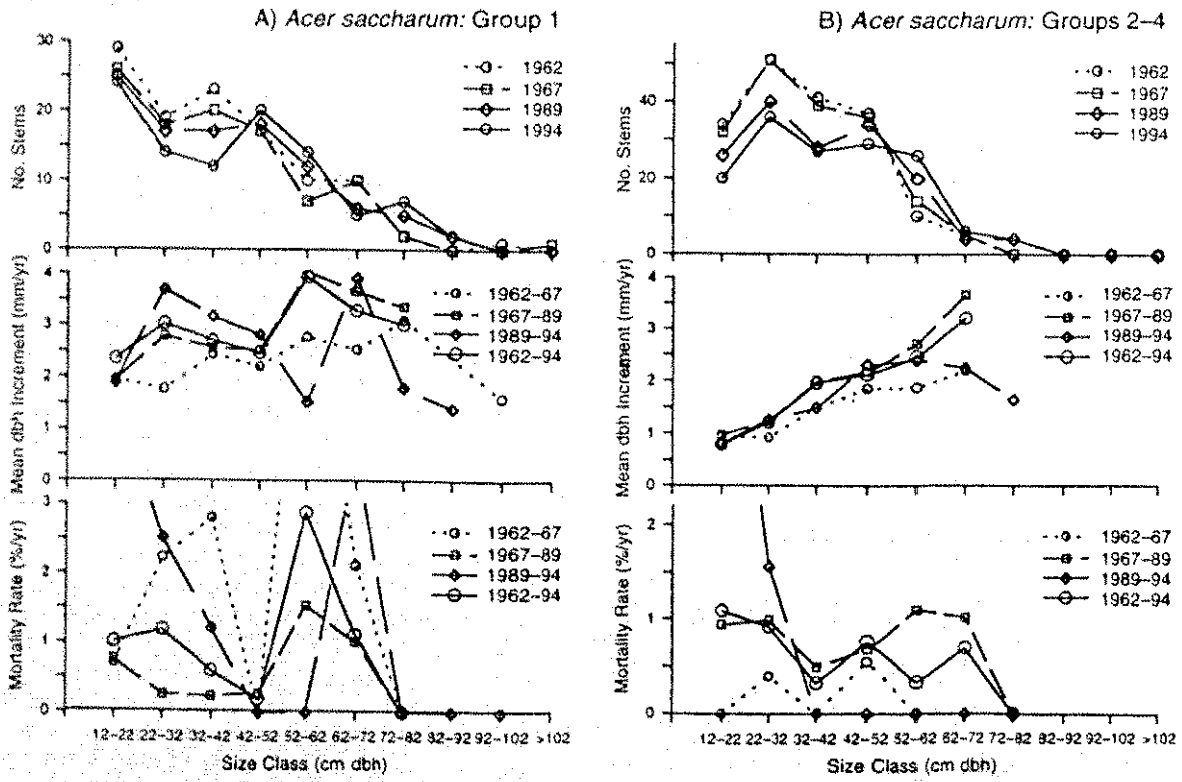

FIG. 7. Demographic patterns for *Acer saccharum* by plot groups. Data are presented as for Fig. 6. Maple-dominated plot group I is presented separately from remaining plots.

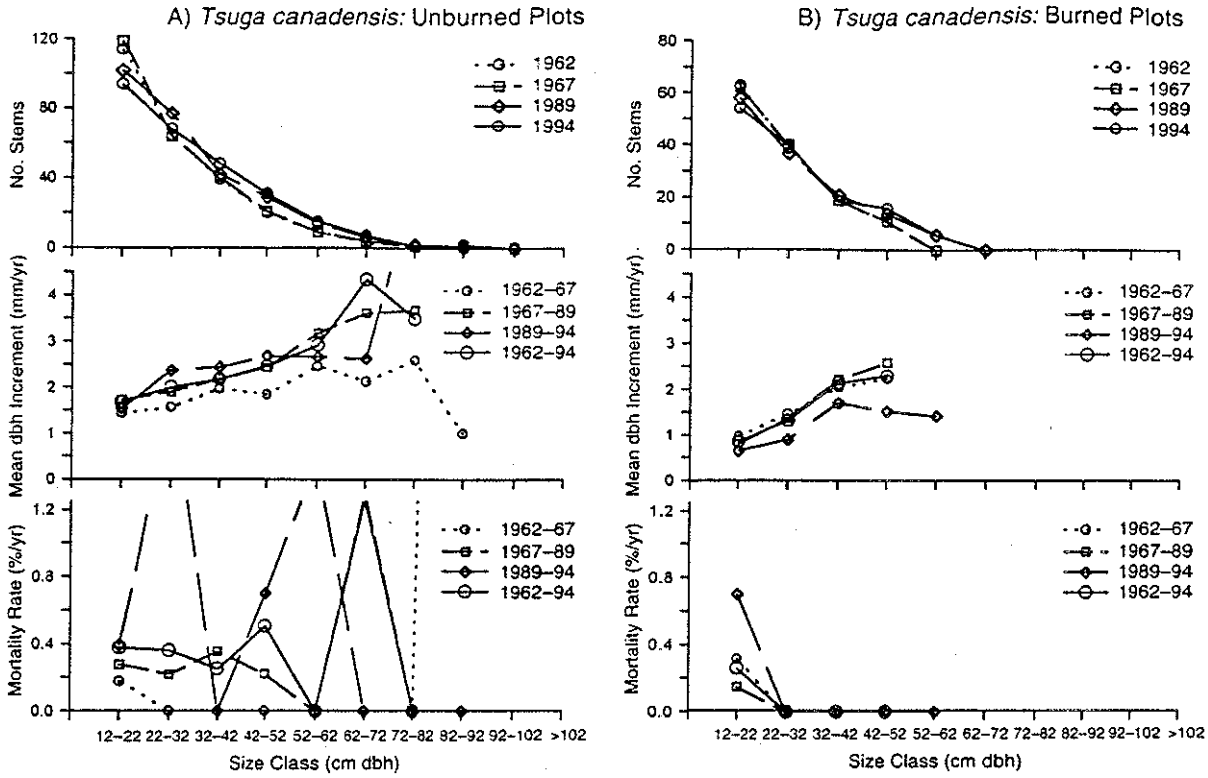

FIG. 8. Demographic patterns for *Tsuga canadensis* by plot groups. Data are presented as for Fig. 6. Burned plots (plot group IV) are presented separately from remaining plots (plot groups II and III).

strongly affected by conspecific competitors than by competition with sugar maple, while sugar maple mortality increases with both conspecific and hemlock influence.

Demographic patterns and compositional trends may be influenced by factors unrelated to the demographic and competitive processes assessed here. Deer browse can limit tree regeneration, especially for hemlock and basswood, in hemlock–northern hardwood forests (Stoeckeler et al. 1957, Webb 1957, Hough 1965, Moore and Johnson 1967, Marquis 1974, Anderson and Loucks 1979, Whitney 1984, Alverson et al. 1988). Deer browse intensity on the Huron Mountains is extreme and may have been elevated for most of this century (Willis and Coffman 1975), possibly accounting for progressive depletion of smaller size classes. Effects of deer on hemlock size structure may be relatively delayed due to the extreme shade tolerance of this tree species (Kobe et al. 1995); a large pool of suppressed saplings, <12 cm dbh but beyond the reach of deer, can survive long periods of suppression to enter measured size classes when released by canopy gaps (Whitney 1984). Climate change since the Little Ice Age may mean that current canopy trees established under cooler and moister climates than those experienced by current seedlings and saplings. Stand simulations (Davis and Botkin 1985) suggest that climate change of the magnitude experienced over the last 200 yr can alter canopy composition, but that canopy response may lag the causal climate changes by up to two centuries.

Compositional patterns and successional change

The dominant compositional gradient observed here, from hemlock dominance on thinner, acidic soils to maple dominance (with basswood and hop-hornbeam) on deeper, richer soils, has been observed in late-successional hemlock–northern hardwood forests throughout their range (Willis and Coffman 1975, Leak 1978*a*, *b*, Rogers 1978, Woods 1984, Crow 1990, Metzger 1990). However, interpretations of the successional and edaphic relationships between these two species vary. Pastor and Broschart (1990) found no difference in soils between mixed and pure hemlock and hardwood stands. Frelich et al. (1993) and Frelich and Graumlich (1994) described mosaics of hemlock and sugar maple patches that are not associated with underlying soil or site differences; they suggest that this pattern may be relatively stable.

Suggestions that hemlock may be limited to moist sites (e.g., Olson et al. 1959, Rogers 1978, 1980, Hix and Barnes 1984, Calcote 1986, Pastor and Broschart 1990) are not consistent with trends observed here or in some nearby areas (Darlington 1930, Frelich et al.

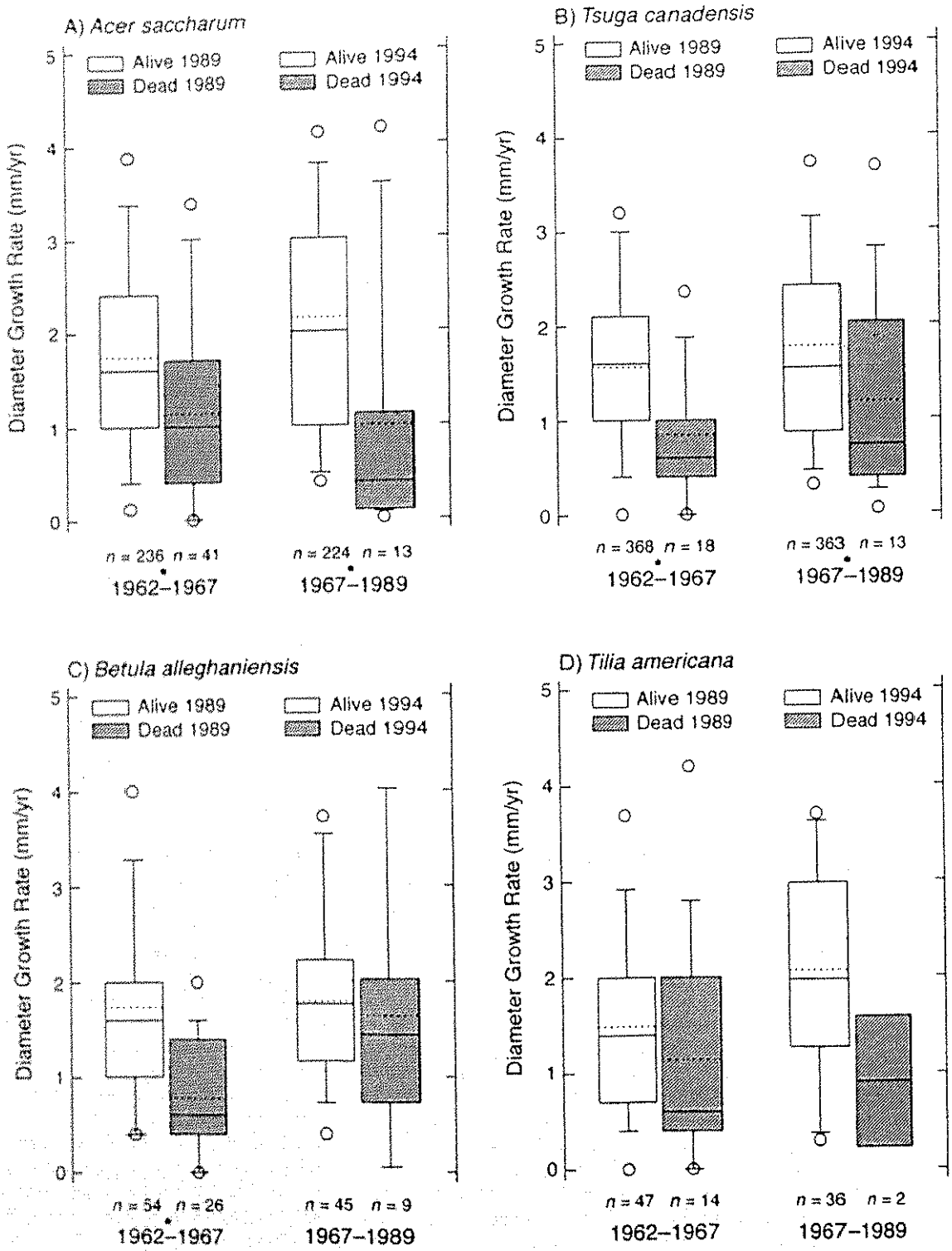

FIG. 9. Comparison of growth rates for dying and surviving stems. Pairs of box plots allow comparison of growth rates for trees that died or survived during the measurement period subsequent to growth measurement. Boxes include middle two quartiles, capped bars extend to 10th and 90th percentiles, and open circles indicate 5th and 95th percentiles. Solid horizontal bars in boxes indicate median growth rates, and dashed bars indicate mean growth rates. Asterisks indicate significant differences in growth rates between dying and surviving trees (Mann-Whitney and resampling tests, $P < 0.05$).

TABLE 5. Variables introduced in stepwise regression for growth.

Species	Multiple r^2	Group	Maple influence	Hemlock influence	Total influence	1989 dbh	Interactions‡
Sugar maple (n = 380)	0.63	***	†			***	a**, b***, c†
Group I (n = 137)	0.55	...			*	***	
Groups II–IV (n = 243)	0.58	...				***	
Yellow birch (n = 69)	0.59	*				***	b***
Hop-hornbeam (n = 77)	0.48	†	*	*		†	a**, c*
Basswood (n = 61)	0.70	*				***	b***
Hemlock (n = 584)	0.69	***		***	***	**	a***, c**
Groups I–III (n = 426)	0.67	...	***	***		***	
Group IV (n = 158)	0.44	...		*	†	***	

Note: Table shows P values associated with F ratio in final model: † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
‡ Codes for interactions: (a) Total influence × Group; (b) 1989 dbh × Group; (c) Total influence × 1989 dbh.

1993). Hemlock dominance in even-aged, post-fire stands (plot group IV) is inconsistent with suggestions that it is particularly slow in recovery following massive disturbance (Rogers 1978, Calcote 1986, Foster and Zebryk 1993, Pacala et al. 1996). However, such dominance has been observed elsewhere (Maissarow 1941, Miles and Smith 1960).

The broad and irregular distribution of yellow birch in the ordinations may be a consequence of its relative shade intolerance (Winget and Kozlowski 1965, Erdmann 1990) and dependence on canopy disturbance rather than site conditions. A tendency toward association with hemlock rather than with other hardwoods (see also Brown and Curtis 1952, Whittaker 1956, Mcintosh 1972, Leak 1975, Rogers 1978, Woods 1984) is not easily ascribed to physical environment: birch favors richer, less acidic soils than does hemlock (Erdmann 1990), and shows highest growth here in maple-dominated plot group I. Sparse advance regeneration beneath hemlock canopy may reduce competition and favor yellow birch regeneration in canopy gaps (Barden 1979, Woods 1984).

In all but the most maple-dominated stands, continuing successional change is suggested by increases in hemlock basal area averaging about 20%, while other canopy species change little or decrease. In mixed stands (plot groups II and III), hemlock is often present as discrete patches of uneven-aged (K. D. Woods, *unpublished data*) hemlock saplings and subcanopy trees beneath a hardwood canopy (see also Stearns 1951, Whitney 1990*b*). Hemlock's spread within stands may be dispersal limited (Pacala et al. 1993), which adds plausibility to the notion that patches are centers of hemlock invasion of hardwood-dominated stands. Although maple canopy (or dense populations of maple seedlings) may be unfavorable to hemlock regeneration (Tubbs 1976, Woods 1984, Frelich et al. 1993), these hemlock patches indicate that some establishment is possible. A hemlock canopy has strong inhibitory effects on advance regeneration of other species. Frelich et al. (1993) and Davis et al. (1994) suggested that the mosaic of maple- and hemlock-dominated patches at the Sylvania tract is stabilized by such canopy–understory feedbacks; data from the Huron Mountains suggest that hemlock patches can spread in a maple-dominated matrix.

Hemlock is more shade tolerant than are other species at the Huron Mountains (Godman and Lancaster 1990, Whitney 1990*a*, Kobe et al. 1995), and may have been important over a wider range of habitats in the pre-logging landscape (Rogers 1978, Calcote 1986). Darlington (1930) predicted ultimate hemlock dominance in lake-influenced forests in the nearby Porcupine Mountains, but expected hardwood dominance a few miles inland where climates are more extreme. Brown and Curtis (1952) predicted succession to hemlock in mesic northern Wisconsin forests. Simulation models (Pacala et al. 1996) predicted replacement of maple by hemlock. Hemlock has increased in other multi-decade studies in the northeastern United States (Filip et al. 1960, Whitney 1984, 1990*a*), and may be capable of sustained dominance for many centuries (Foster and Zebryk 1993). The three plots burned in the early 19th century (plot group IV) and colonized by hemlock show low growth rates of small stems; this suggests intense suppression of smaller stems and may denote the onset of self-thinning, but there is no suggestion that hemlock dominance will not be maintained.

However, some researchers have suggested ultimate dominance by maple or maple and basswood (Stearns 1949, Goff and Zedler 1972, Zedler and Goff 1973), and the successional trend from hardwood to hemlock is not apparent in all plots in this study. Hemlock has not become established in sampled stands on fine, alluvial soils (plot group I). Whether this is due to site characteristics or historical factors cannot be assessed here, but these plots are distinguished by higher pH and Ca, and Kobe et al. (1995) suggested that effective shade tolerance of sugar maple increases on calcareous substrate in New England.

Thirty-two years is still brief in the inherent time

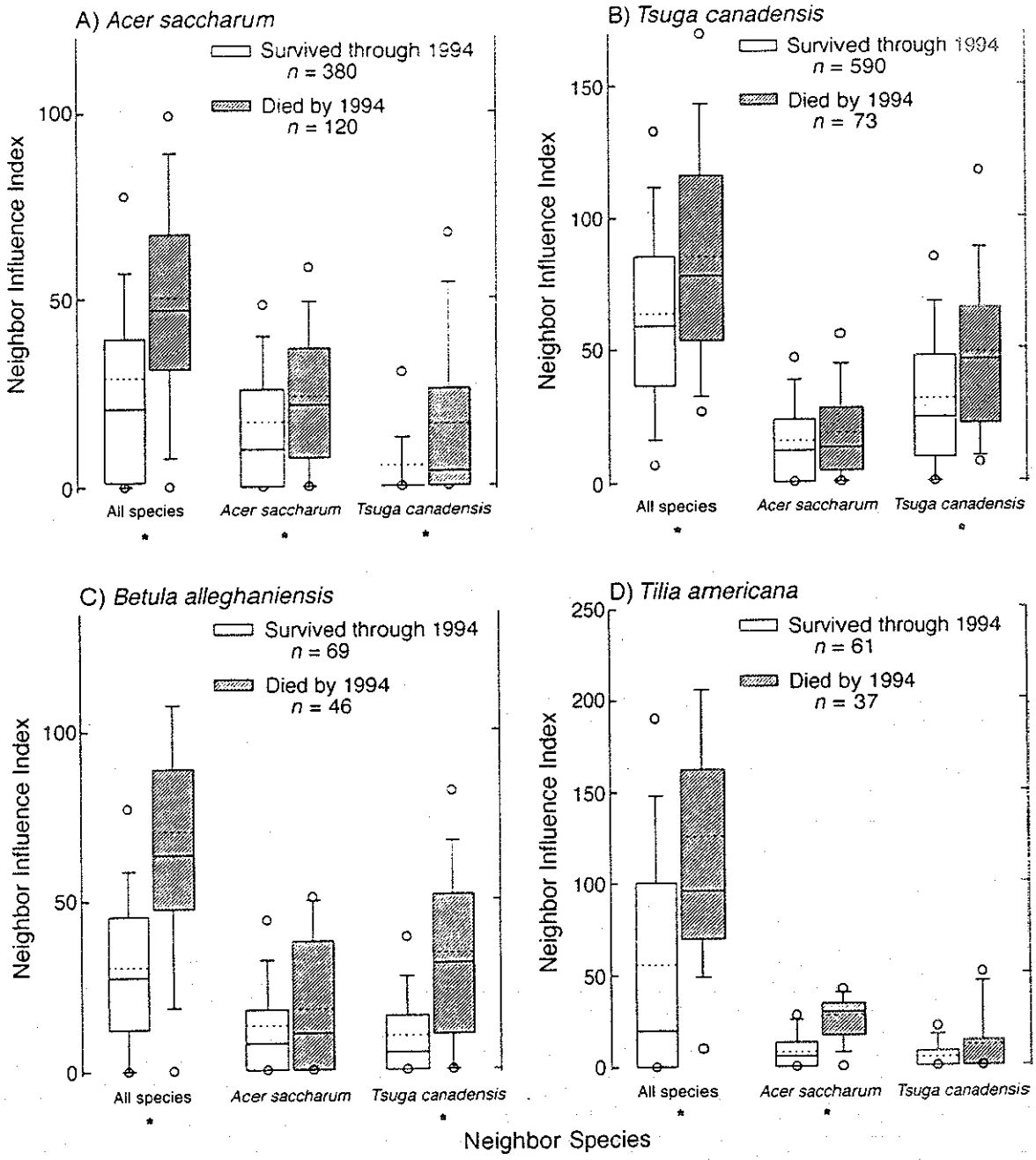

FIG. 10. Relationship between neighborhood influence indices and mortality. Box plots (see Fig. 9) allow comparison of neighbor influence, for all species combined and for *Acer* and *Tsuga* separately, on trees that died during the study period (1962–1994) and trees that survived for the entire period. Asterisks indicate cases where indices differ (Mann-Whitney and resampling tests, $P < 0.05$).

scale of these forests; projection remains risky. Dynamics inferred from current data may be (or already have been) altered by external factors, both human-induced and natural. In particular, greenhouse-induced climate change may force changes in these forests; hemlock is close to its apparently climatically determined range limit (Davis et al. 1986, Kavanagh and Kellman 1986), so modest climate change may significantly alter the competitive relationships proposed here (Davis and Zabinski 1992).

Observed trends and inferred relationships among species suggest that directional, successional change in forest composition will continue. In the absence of more intense disturbance, current patterns of regener-

ation and mortality should lead to increased hemlock dominance, further decline in yellow birch, and eventual decrease in sugar maple basal area in most stands. However, age structures and observed rates of change suggest that a period of at least 400 yr was required to reach the successional status of stands examined here. Hemlock's eventual attainment of general dominance is likely to require at least several centuries more, given canopy residence times and current demographic patterns. Time elapsed from major disturbance to full hemlock dominance may frequently be on the order of a millenium—a period similar to estimated return times for major disturbance events.

Since competition-induced changes continue over several generations of canopy trees, these stands should be considered late-successional, rather than "climax" or steady-state. However, rates of change are slow and the trajectory of change is increasingly influenced by within-stand biological interaction. In this regard these stands differ from hemlock–northern hardwood forests of New England, where relatively frequent hurricane disturbance may keep a much larger proportion of the landscape from attaining equivalently late-successional status (Henry and Swan 1974, Foster and Boose 1992). Even so, major disturbances with return times on the order of a millenium, and more frequent intermediate disturbances, appear sufficient to maintain most or all of the landscape in successional status. The time-frame for successional change in these forests appears to overlap with that for catastrophic disturbance and even climatic change, making questions about stable or climax communities of little practical consequence.

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