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Long-term change and spatial pattern in a late-successional hemlock–northern hardwood forest

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Summary

1 Tree populations were monitored for six decades on a grid of 140 permanent plots in old-growth mesic (hemlock-northern hardwood) forests in northern Michigan, USA. Multiple remeasurements allow assessment of stability of late-successional forests and analysis of spatial patterns and environmental linkages.

2 This forest is not compositionally stable. *Betula alleghaniensis* has declined with little regeneration, suggesting dependence on episodic canopy disruption for persistence. *Tsuga canadensis* and *Fagus grandifolia* have increased in dominance in all size classes independently of major disturbances. *Acer saccharum* populations have remained little changed overall. Dynamics appear to be successional in nature, even though there has been no major disturbance for at least 400 years. Different areas in the stand may have experienced different histories.

3 *Fagus grandifolia* has invaded the stand recently through range expansion, and has come to dominate regeneration in some parts of the stand.

4 Canonical correspondence analysis suggests that soil texture, chemistry, and drainage influence successional dynamics, producing strong spatial pattern. *Fagus grandifolia* has invaded only on relatively fine-textured soils with impeded drainage.

5 Trends suggest that *Fagus*, *Tsuga*, and perhaps *Acer saccharum* would, in different parts of the stand, achieve near-total dominance in the absence of large-scale disturbance, but only after elapsed time of a millennium or more. Estimated return times for major disturbance in this region are of similar magnitude.

Key-words: Acer saccharum, succession, *Fagus grandifolia*, permanent plots, *Tsuga canadensis*

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Introduction

When unlogged, mesic forests of the Great Lakes region of North America are 'slow systems', dominant trees can live for over 300 years and canopy-residence times range from 100 to over 200 years (Frelich & Lorimer 1991; Frelich & Graumlich 1994; Parshall 1995; Dahir & Lorimer 1996; Woods 2000). Catastrophic wind-throw caused by tornadoes and 'derecho' events may be the most important stand-initiating disturbances in mesic stands, but return times for such occurrences appear to exceed a millennium (Lorimer 1977; Canham & Loucks 1984; Whitney 1990; Seischab & Orwig 1991). It is therefore likely that, prior to the onset of widespread logging, large portions of the landscape were occupied by late-successional forests in which intense disturbance had not occurred for several tree generations.

Such late-successional mesic forests, dominated by combinations of *Acer saccharum* (sugar maple), *Tsuga canadensis* (eastern hemlock), *Betula alleghaniensis* (yellow birch) and *Fagus grandifolia* (American beech), have been described from remnant stands (e.g. Darlington 1930; Woods 1984; Frelich *et al.* 1993; Davis *et al.* 1994; Tyrrell & Crow 1994) and from analysis of early survey records (e.g. Stearns 1949; Smith *et al.* 1993). These forests were long assumed to be examples of a relatively stable regional 'climax' or 'potential' vegetation (e.g. Kuchler 1966) in equilibrium with climate. More recently, non-equilibrium models have gained currency, and these suggest that intense disturbances and environmental change are sufficient to prevent

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arrival at any equilibrium in temperate forests. Stand composition, therefore, always reflects history (e.g. Strong *et al.* 1984; Davis *et al.* 1986; Diamond & Case 1986; Webb 1986), although larger landscapes may maintain an equilibrium distribution of successional states (Frelich & Lorimer 1991). Nonetheless, recent discussions of succession suggest that forest succession does tend towards a recognizable steady-state (e.g. Peet 1992; Oliver & Larson 1996) that is maintained by biological interactions internal to the community.

There are, however, few empirical assessments of dynamic properties of late-successional forests, and most of these depend on data from chronosequences (Brown & Curtis 1952; Tyrrell & Crow 1994), extrapolation from within-stand patterns of regeneration and disturbance (Goff & Zedler 1972; Zedler & Goff 1973; Woods 1979, 1984; Runkle 1981; Dahir & Lorimer 1996), simulation models (Leak 1970; Davis & Botkin 1985), or palaeoecological studies (Davis *et al.* 1991, 1994; Foster & Zebryk 1993). All of these approaches are valuable but they are limited in comparison to direct, long-term observation. Only a handful of studies have monitored stand composition and tree population dynamics in late-successional northern hardwood forests for more than a decade (Woods 2000) and most of these are based on sampled areas of less than 1.0 ha. Such studies are nevertheless essential for assessing whether communities are equilibrial (and so understandable from knowledge of species properties, climate and substrate) or not (in which case historical information is also needed).

Understanding the dynamics of late-successional communities is important for both theory and management. If communities are in equilibrium, it is important to understand the mechanisms by which canopy species coexist, for instance by subdivision of niche space or resource use in space or time (e.g. Woods 1979, 1984; Runkle 1981). If they are not in compositional equilibrium, management strategies must recognize that species coexistence is unstable and dependent on occasional, large-scale disturbance. For instance, the notion put forward in conservation management that natural, late-successional communities may resist invasion by non-indigenous species becomes intuitively less plausible if non-equilibrium conditions apply.

In this paper, I draw on 60 years of data from permanent plots in old-growth *T. canadensis*–northern hardwood forests in northern Michigan, USA, to assess the dynamic properties of late-successional forests. These data allow direct evaluation of the stability of community properties and of individual tree populations. A dense array of plots (total area *c.* 12 ha) also permits analysis of the interplay of spatial and dynamic patterns. Comparison of results with a 30-year study in other old-growth stands located about 100 km away (Woods 2000) sheds light on regional patterns and the possible effects of geological factors and climate change. Finally, the location of the study area just within the recently expanded range limit of a shade-tolerant canopy dominant (*F. grandifolia*) allows assessment of the dynamics of invasion and establishment of a late-successional species in an established forest community.

Methods

SITE DESCRIPTION

The Dukes Research Natural Area (RNA), in the Hiawatha National Forest, is situated at 46° 25′ N, 87° 10′ W in northern Michigan, USA, 12 km from the shore of Lake Superior and at an elevation of about 330 m (Fig. 1). The 100 ha of the RNA has not been logged, although anecdotal histories suggest that a few trees, especially of *Pinus strobus* (white pine), may have been removed from small portions of the stand in the early 1900s, shortly after European-American settlement in the area.

There is less than 10 m of topographic relief within the RNA. Portions that are poorly drained (about half the area) support swamp forests of mixed conifers and hardwoods and are not addressed in this paper. Elsewhere in the stand, soils range from very well-drained, coarse sandy loams (alfic fragiorthods and alfic haplorthods) to fine sandy loams (entic haplorthods and aquic haploborolls) with well-developed pans (ortsteins). The RNA and areas to the east are underlain by Palaeozoic sedimentary bedrock with deep, sometimes calcareous till deposits (Dorr & Eschmann 1970). Less than 10 km west of the RNA, sedimentary formations give way to Pre-Cambrian igneous bedrock, typically with thinner and more acidic overlying till.

The north-western limit of continuous distribution of *F. grandifolia* lies only a few kilometres west of the RNA (Fig. 1). Palaeoecological studies suggest that the species has been present locally for less than 500 years (Woods & Davis 1989), and that the range limit may be at least indirectly related to the geological boundary.

Plant names used here follow Gleason & Cronquist (1991).

SAMPLING HISTORY

In 1935, 240 circular 0.2 acre (809 m^2) permanent plots were established within the RNA, on a 132 × 330 ft (*c.* 40 × 100 m) grid (Fig. 2). Plot centres were marked with a steel pipe. Trees > 5 in (12.7 cm) diameter at breast height (d.b.h.) were censussed in all plots (excepting a few that were deemed transitional between forest 'types'). In 1948, mea-

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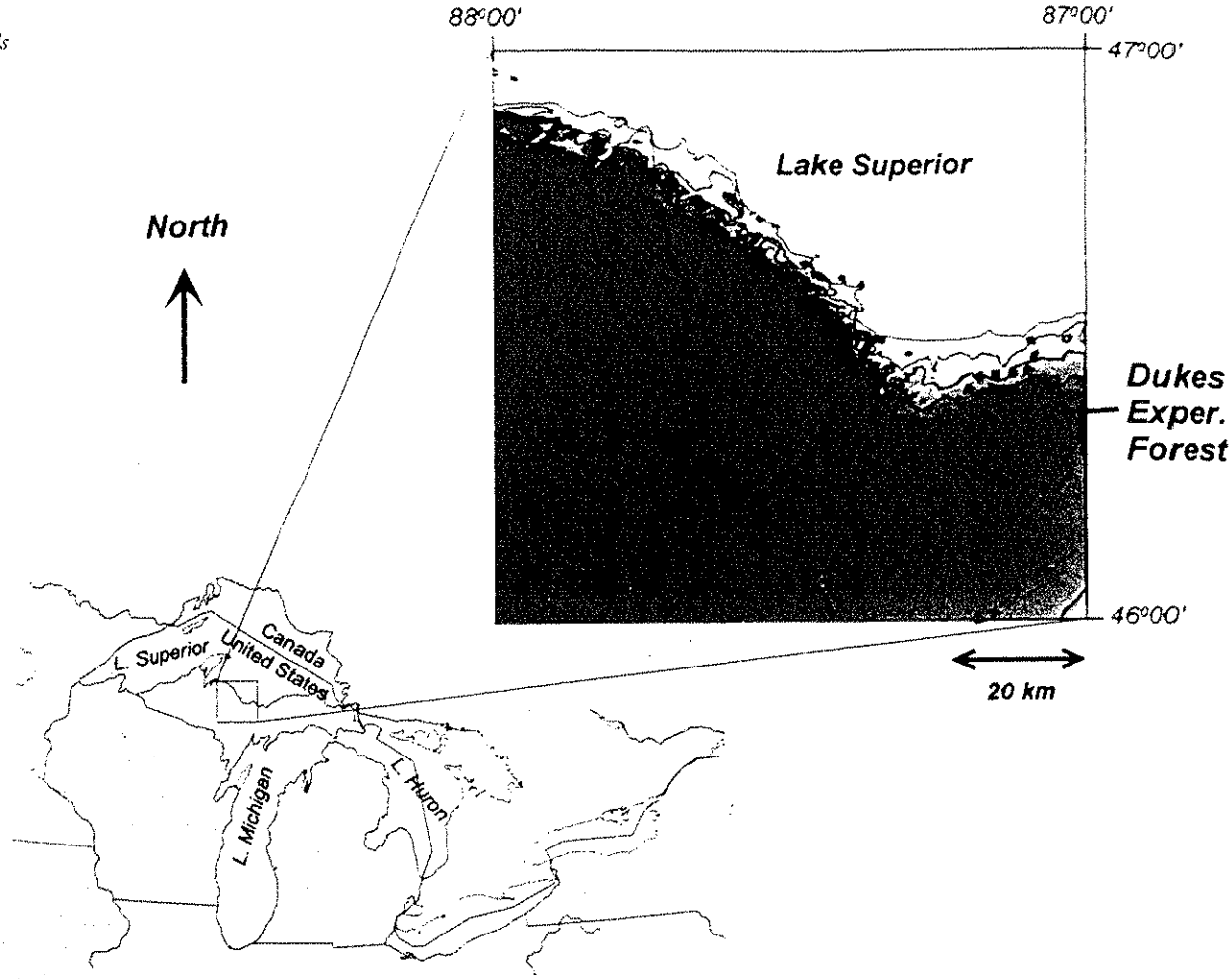

Fig. 1 Location of the Dukes Experimental Forest study site. Outline at lower left locates study area within the Great Lakes region of the United States and Canada. Expanded inset shows topography for the central Upper Peninsula of Michigan; contour lines are at 30-m intervals, and elevation ranges from 183 m at Lake Superior to *c.* 530 m. The heavy dashed line approximates the border between Pre-Cambrian granitic shield rock and Palaeozoic sedimentary rock. The heavy dotted line is the approximate western range limit of *Fagus grandifolia*.

surements were repeated for every second plot. In 1974–78, woody stems > 0.6 in (1.5 cm) were tallied in all plots under the direction of Dr Fred Metzger of the Northern Hardwoods Laboratory of the U.S. Forest Service. Data from these measurements were compiled under the direction of Dr Thomas Crow of the U.S. Forest Service.

In 1992–94, I remeasured all upland plots, some of which also contained wetland species (a total of 139 plots; Fig. 2). Original plot centres were located for 138 plots (sometimes using a metal detector to relocate the steel pipe) and in the remaining plot a new centre was established by survey from adjacent plots. I measured all stems > 5 cm d.b.h. within the original plot and stems 2–5 cm d.b.h. in a centred subplot of 8 m radius (201 m^2).

I described soil profiles from 77 plots distributed over the stand. Pooled soil samples for each plot were collected from approximately 10–20 cm depth (below organic humus horizon but within rooting zone) at four predetermined locations. Basic soil chemistry and nutrient analyses were done by Cornell University Soil Science Labs. I assessed soil texture by densitometric analysis and conducted loss-on-ignition measurements for subsamples.

ANALYSES

Data from different years were cross-checked for consistency of total basal areas and size distributions of trees. In several instances, plots were either misidentified or data were incomplete. If data could

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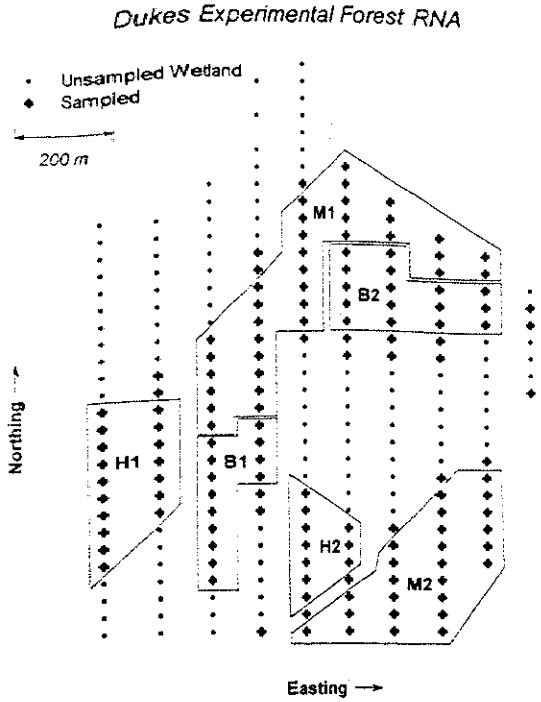

Fig. 2 Distribution of permanent plots in the Dukes Experimental Forest RNA. Dots are plots in wetland forests (swamp conifer and black ash), not resampled 1992–94. Crosses are upland and marginal plots resampled during 1992–94. Outlined portions of the stand correspond to plot groups in Table 1 and text. Groups M1 and M2 are strongly dominated by *Acer saccharum*, groups B1 and B2 by mixed hardwoods (including *Fagus grandifolia*) and *Tsuga canadensis*, groups H1 and H2 by *Tsuga*, with *Pinus strobus* in group H1.

not be confidently reconciled, particular plot measurements were discarded.

Compositional patterns were assessed with detrended correspondence analysis (DECORANA: Hill 1980) and nonmetric multidimensional scaling (MDS) ordinations. The complete data set from 1935 was used to assess the full range of composition and relationships between upland and wetland forests. Analyses of 1992–94 data were used for more detailed examination of compositional patterns within upland stands. Associations between composition and soil characteristics (primary nutrients, texture, depths of A_0, A_1, and A_2 horizons, presence of cemented layers, and presence and depth of mor humus) were examined using canonical correspondence analysis (CCA: Palmer 1993).

Population size structures were compared over measurement intervals. Ordinations of multiple plot measurements over time (up to four per plot) allowed examination of plot trajectories in ordination space and patterns of community change. As 1935 and 1948 measurements only include stems > 11 cm d.b.h., smaller stems were excluded in comparisons involving these dates. To assess spatial variation in population dynamics, spatially contiguous groups of compositionally similar plots were developed using multidimensional scaling classification and maps of ordination scores. Changes in population structure were examined for each species for each plot group.

Results

GENERAL COMPOSITIONAL PATTERNS

Ordination of all 240 plots (1935 or 1948 measurements) shows continuous variation in composition across a broad range from swamp to upland forests (Fig. 3). Dominant species shape the ordination field, three plot clusters corresponding to near-complete dominance of *A. saccharum*, *Thuja occidentalis* (white cedar), and *T. canadensis*. The first axis corresponds to a continuum from upland (*A. saccharum*) to wetland (*T. occidentalis*) stands. Soil chemistry may shape the second axis; *Fraxinus nigra* and *Tilia americana*, at low values on the axis, occur primarily in moist to wet sites of high pH and soil Ca, while *T. canadensis* and *F. grandifolia* are found predominantly on more acidic soils. *B. alleghaniensis* and *Acer rubrum*, widely distributed on soils of diverse character, are positioned near the centre of the ordination field. The third axis (not illustrated) is influ-

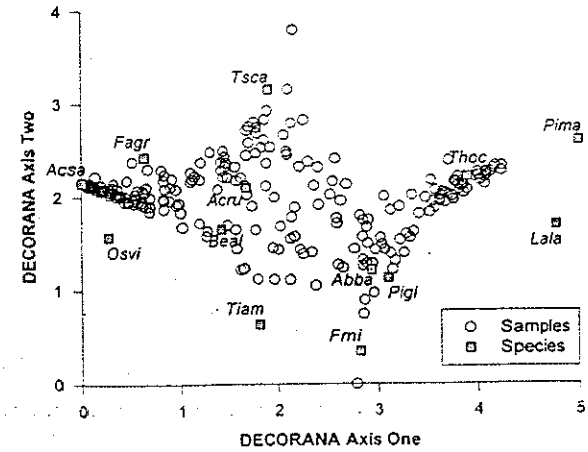

Fig. 3 Detrended Correspondence Analysis ordination of 240 plots measured in 1935 or 1948. Data are 1935 measurements except for 15 'transitional' plots which were not measured in 1935, but for which 1948 data were available. Filled circles are plot locations on first two axes of DCA ordination. Squares show DCA ordination of primary species on same axes. Species codes are: Abba = *Abies balsamea*, Acru = *Acer rubrum*, Acsa = *Acer saccharum*, Beal = *Betula alleghaniensis*, Lala = *Larix laricina*, Fagr = *Fagus grandifolia*, Frni = *Fraxinus nigra*, Osvi = *Ostrya virginiana*, Pigl = *Picea glauca*, Pima = *Picea mariana*, Thoc = *Thuja occidentalis*, Tiam = *Tilia americana*, Tsca = *Tsuga canadensis*.

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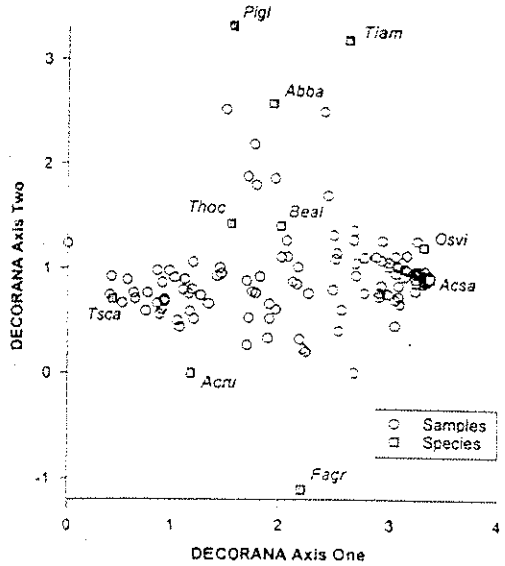

Fig. 4 Detrended Correspondence Analysis ordination of 138 plots measured in 1992–94. Symbols and species codes as in Fig. 3.

enced primarily by a few plots with shade-intolerant species (*Quercus rubra and P. strobus*).

Ordinations of upland plots alone (1992–94 measurements) extract a dominant axis from *A. saccharum* to *T. canadensis* dominance (Fig. 4). *Ostrya virginiana* is associated with *A. saccharum* dominance. The second axis separates plots with significant representation of *F. grandifolia* (and, to a lesser extent, *A. rubrum*) from plots with *T. occidentalis* and other swamp conifers. *B. alleghaniensis* is broadly distributed.

CCA ordination extracts a similar first axis, and first axis scores are negatively associated with pH and depth of A_1 horizon and positively associated with depth of A_2 horizon and development of a mor humus (Fig. 5a & b). Second axis scores are correlated with basal area of *F. grandifolia and* with soil chemistry. *F. grandifolia* achieves greatest importance on finer soils with a well-developed cemented horizon, at high values on the third axis (Fig. 5b). Ca concentrations are positively correlated with both *A. saccharum* and *F. grandifolia* basal area, but negatively correlated with *T. canadensis*. There were strong spatial patterns in these soil characteristics (Fig. 6).

Plot groups derived from classification of 1992–94 data on the basis of canopy composition tended to be spatially coherent (Fig. 2). Basal areas by plot groups and species are shown in Table 1. Soil properties show related spatial patterns (Fig. 6) and vary among plot groups (Table 2). These results are consistent with results of CCA ordinations. The following plot groups are used in subsequent analyses.

M1: maple-dominated plots on fine-textured soils with little pan development and relatively high Ca and pH. Other species (particularly *B. alleghaniensis*) are more important than in M2, and the understorey is comparatively diverse, with strong representation of spring ephemeral herbs.

M2: maple-dominated plots on well-drained sandy soils of high Ca content (south-east section). *A. saccharum* dominance is nearly total in these stands, and the understorey is of relatively low diversity and dominated by maple seedlings.

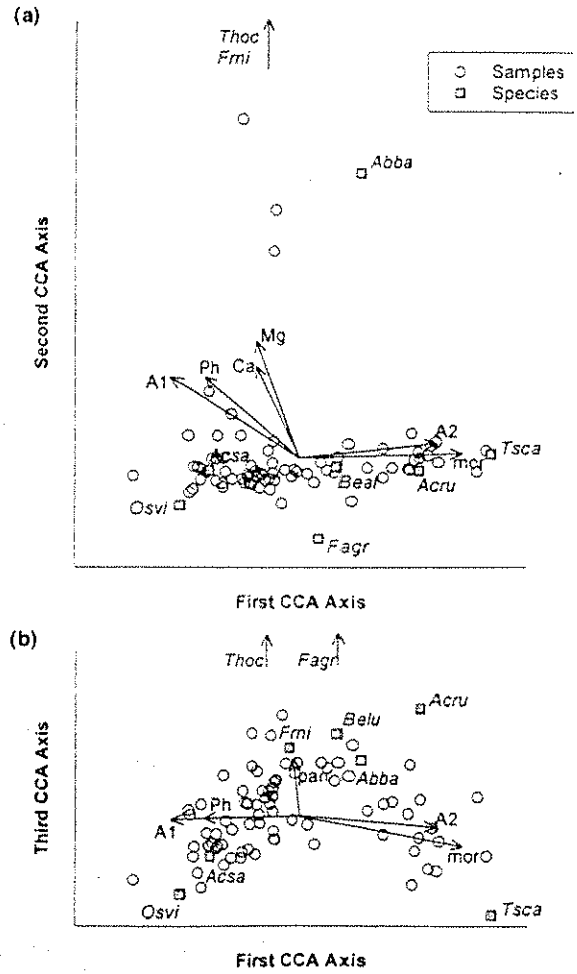

Fig. 5 Canonical Correspondence Analysis ordination of 77 plots, with environmental data, measured in 1992–94. (a) axes 1 and 2, (b) axes 1 and 3. Open circles show positions of plots in ordination, open squares position of species. Species codes are as in Fig. 3. Vectors indicate strength and sign of correlation of indicated soil variables with ordination axes. 'mor' refers to depth of mor humus layer, 'A1' and 'A2' to depth of indicated soil horizons, 'pan' to degree of development of cemented ortstein horizon, 'Ca' and 'Mg' to untransformed concentrations of these elements, and 'pH' to untransformed soil pH.

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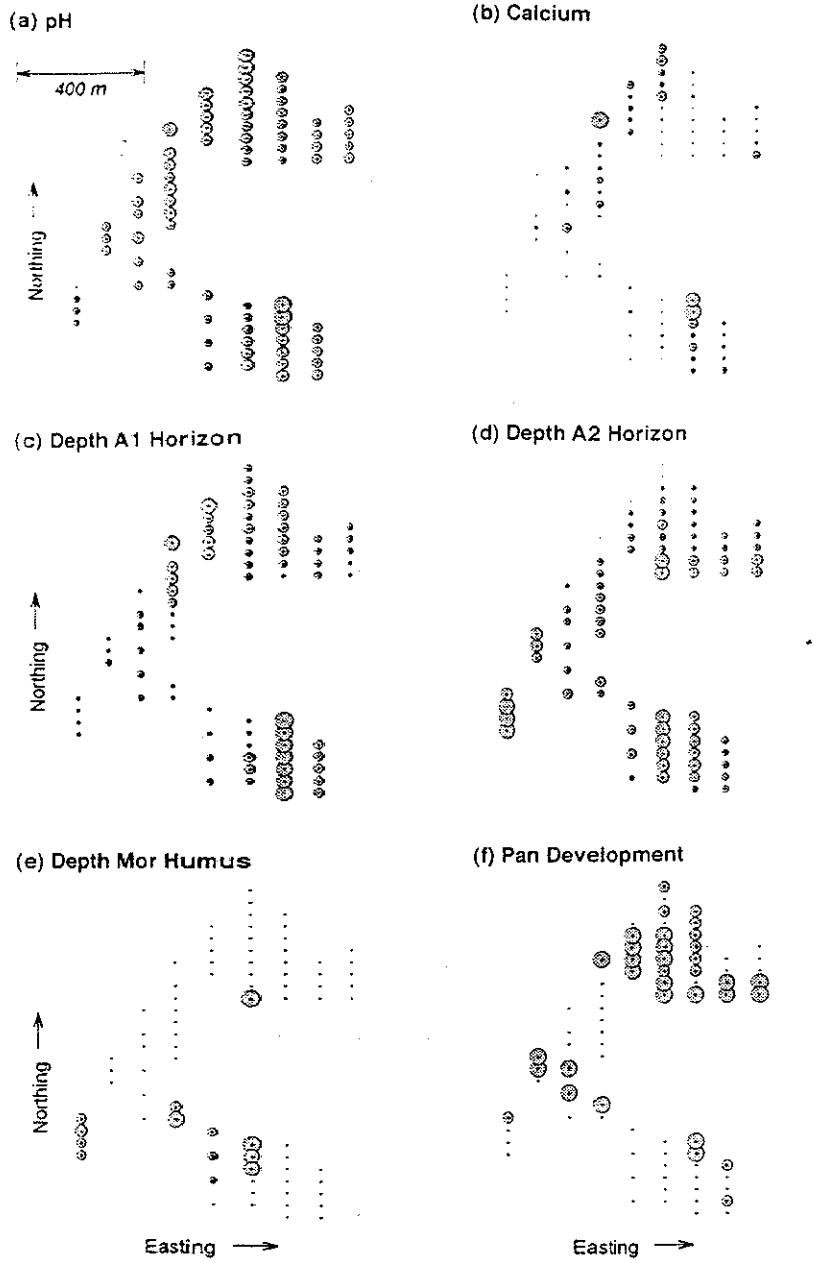

Fig. 6 Maps of sampled plots (see Fig. 2 for plot groups), with symbol area scaled to values for measured soil parameters. All plots for which soils were sampled are shown; small crosses indicated measured value of zero. See Table 2 for ranges and mean values. (a) pH at *c.* 10 cm depth; (b) Ca concentration at *c.* 10 cm depth; (c) depth of A_1 horizon; (d) depth of A_2 horizon; (e) depth of mor humus; (f) degree of ortstein or pan development (assigned to three classes).

B1: *mixed maple-beech-hemlock plots* on fine-textured soils with some pan development. Both *B. alleghaniensis* and *A. rubrum* are significant canopy components. Understorey communities are variable.

B2: *mixed maple-beech-hemlock plots* compositionally similar to B1 but with strong pan development. Low areas often retain standing water. There is abundant *F. grandifolia* regeneration, and understorey communities are of low diversity.

H1: *hemlock-dominated plots* with coarse, excessively drained soils, and significant presence of *P. strobus* in the canopy.

H2: *hemlock-dominated plots* with deep mor humus and strongly developed podzol, generally along margins of wetlands.

Unassigned plots are either along margins of swampy areas, with significant canopy representation of such species as *T. occidentalis and F. nigra*,

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Table 1 Basal area ($m^2 ha^{-1}$) by year, plot group, and species

Plot group	No. of plots	*Acer saccarum*	*Tsuga canadensis*	*Betula alleghaniensis*	*Fagus grandifolia*	*Acer rubrum*	*Ostrya virginiana*	*Abies balsamea*	*Picea glauca*	*Thuja occitalis*	*Fraxinus nigra*	*Pinus strobus*	*Tilia americana*	Other species*	Total
1935															
M1	35	27.14	0.17	4.97	0.38	0.45	0.40	0.28	0.01	0.00	0.02	0.00	0.11	0.09	34.04
M2	24	29.44	0.10	4.82	0.01	0.15	0.36	0.07	0.01	0.06	0.00	0.00	0.13	0.09	35.24
B1	13	13.75	9.84	10.27	0.87	4.52	0.06	0.33	0.04	0.10	0.01	0.00	0.00	0.00	39.80
B2	16	9.92	7.66	10.41	3.41	4.65	0.05	0.63	0.02	0.02	0.03	0.00	0.00	0.29	37.08
H1	12	1.56	17.54	9.59	0.11	4.29	0.03	1.01	0.32	2.71	0.69	3.76	0.00	0.59	42.21
H2	8	1.14	39.71	9.49	0.10	3.75	0.00	1.09	1.83	1.72	0.50	0.00	0.14	0.32	59.78
UN	22	4.80	5.77	10.35	0.23	1.55	0.30	1.30	1.23	6.19	3.61	0.04	0.57	1.15	37.09
1946															
M1	18	25.39	0.16	4.44	0.44	0.46	0.41	0.19	0.00	0.00	0.00	0.00	0.15	0.01	31.64
M2	12	32.21	0.00	3.17	0.00	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.31	0.11	36.15
B1	6	10.13	10.17	11.03	1.39	3.91	0.00	0.32	0.03	0.21	0.00	0.00	0.00	0.00	37.19
B2	8	9.58	5.87	11.53	3.62	4.23	0.00	0.09	0.00	0.08	0.13	0.00	0.00	0.05	35.16
H1	9	3.18	16.95	9.09	0.02	4.17	0.00	0.91	0.14	1.70	0.44	2.04	0.00	0.51	39.14
H2	5	1.14	39.71	9.49	0.10	3.75	0.00	1.09	1.83	1.72	0.50	0.00	0.14	0.32	59.78
UN	12	4.24	6.45	10.23	0.38	2.12	0.23	1.27	1.94	7.21	3.18	0.10	0.66	0.85	38.85
1976															
M1	34	29.72	0.14	4.89	0.34	0.37	0.13	0.05	0.01	0.02	0.00	0.00	0.22	0.01	35.91
M2	25	30.25	0.01	3.62	0.02	0.20	0.14	0.02	0.05	0.48	0.09	0.00	0.02	0.48	35.38
B1	12	12.74	7.90	13.48	1.04	5.53	0.06	0.25	0.02	0.12	0.00	0.00	0.00	0.42	40.26
B2	16	9.90	6.91	10.00	5.82	4.64	0.01	0.06	0.00	0.00	0.05	0.00	0.00	0.06	37.45
H1	17	2.63	19.90	9.31	0.07	5.56	0.00	0.29	0.28	1.58	0.28	2.92	0.01	0.02	42.83
H2	10	1.28	28.71	8.15	0.41	3.43	0.00	0.13	0.46	1.25	0.14	1.07	0.00	0.67	45.69
UN	22	6.99	7.00	9.95	0.25	1.95	0.04	0.81	1.31	6.08	1.82	0.10	1.43	1.50	39.25
1993															
M1	35	32.01	0.16	2.90	0.48	0.29	0.21	0.09	0.01	0.03	0.00	0.00	0.21	0.02	36.21
M2	25	32.38	0.01	1.50	0.06	0.34	0.40	0.01	0.04	0.43	0.04	0.00	0.04	0.00	35.21
B1	13	14.96	9.85	12.39	2.56	4.09	0.10	0.21	0.08	0.11	0.00	0.00	0.32	0.00	44.35
B2	16	12.54	8.39	8.05	7.89	4.85	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	41.75
H1	17	3.96	20.89	8.37	0.58	7.00	0.00	0.66	0.19	2.23	0.18	3.17	0.01	0.00	47.24
H2	10	1.47	32.85	8.00	0.97	5.26	0.00	0.19	0.45	0.42	0.18	1.11	0.00	0.03	50.92
UN	23	7.89	8.83	9.95	0.71	2.26	0.30	1.04	1.22	6.96	1.84	0.11	1.62	0.41	42.84

*Other species include (with basal areas for 1993):Group M1: *Quercus rubra* 0.02Group H2: *Quercus rubra* 0.03, *Prunus pensylvanica* 0.01Group UN: *Quercus rubra* 0.31, *Fraxinus americana* 0.03, *Ulmus americana* 0.01

Table 2 Soil properties (mean ± standard deviation, range) by plot group

Plot group	*n*	Mor horizon (cm)	A_1 horizon (cm)	A_2 horizon (cm)	Mg ($mg\,kg^{-1}$)	Ca ($mg\,kg^{-1}$)	pH
All	77	2 ± 5	3 ± 2	8 ± 6	22.0 ± 38.0	169 ± 234	5.0 ± 0.5
		0–21	1–8	0–25	4.4–256.5	15–1238	4.0–7.2
M1	27	0	3 ± 1	4 ± 2	21.2 ± 18.6	202 ± 155	5.2 ± 0.4
		0–0	1–6	0–7	6.1–80.6	22–607	4.5–5.9
M2	13	0	7 ± 4	10 ± 5	37.8 ± 65.1	262 ± 310	5.3 ± 0.6
		0–0	2–5	4–20	4.4–256.5	32–1238	4.8–7.2
B1	3	3 ± 5	2 ± 0.5	8 ± 2	11.1 ± 3.0	46 ± 8	4.7 ± 0.1
		0–10	1–2	5–1	6.9–13.9	34–53	4.5–4.8
B2	16	1 ± 5	2 ± 0.7	8 ± 5	10.9 ± 7.0	68.5 ± 70.7	4.8 ± 0.2
		0–21	1–3	3–20	5.7–36.8	23–330	4.4–5.2
H1	8	5 ± 5	0.3 ± 0.4	17 ± 6	7.2 ± 2.4	44 ± 28	4.5 ± 0.3
		0–12	1–2	10–25	4.4–11.3	22–114	4.0–4.8
H2	8	8 ± 7	2 ± 0.7	12 ± 6	9.1 ± 1.3	48 ± 26	4.6 ± 0.2
		0–20	1–3	3–20	7.7–12.2	15–95	4.1–4.9

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or compositionally intermediate between groups defined above.

DYNAMICS

Basal area changes

There was a slight but significant tendency towards an increase in stand basal area in the 139 plots remeasured in 1992–94, over both the full interval of nearly six decades (Fig. 7a) and for each of the intervals between measurements (Table 1). Stands of initially low basal area tended to increase while stands of initially high basal area were more likely to decrease.

Basal area dynamics varied among dominant species and, in some cases, suggest directional changes, although *T. canadensis* and *A. rubrum* showed no strong directional trends overall (Fig. 7c & d, respectively) or for any of the sampling intervals. *A. saccharum* showed a small but significant increase in basal area over the full range of basal areas only when the full 58 years was considered. The scatter of points for *A. rubrum* appears broader than for either *A. saccharum* or *T. canadensis*, suggesting more rapid population change: by the 1992–94 remeasurement, *A. rubrum* basal areas in some plots had declined by as much as $7\,m^2\,ha^{-1}$ while others increased by up to $10\,m^2\,ha^{-1}$.

B. alleghaniensis and *F. grandifolia*, by contrast, showed pronounced directional trends in basal area. *B. alleghaniensis* (Fig. 8) declined during all measurement intervals, but declines were much greater during the last interval (17 years of the total of 58; Fig. 8c). Some plots experienced modest growth in basal area, but declines were both more frequent and often of much larger magnitude (up to $20\,m^2\,ha^{-1}$). *F. grandifolia* occurred in fewer plots but showed consistent and large basal area increases (Fig. 9). Maximum *F. grandifolia* basal area increased from *c.* $6\,m^2\,ha^{-1}$ in 1935 to over $15\,m^2\,ha^{-1}$ in 1992–94. On average, basal areas approximately doubled over the study period, and several plots lacking *F. grandifolia* in 1935 had basal areas as great as $4\,m^2\,ha^{-1}$ in 1992–94. Rates of increase were not constant, so that, even accounting for its greater length, the period from 1948 to 1976 showed greater proportional increases.

Trends are more difficult to assess for minor species. All three subcanopy species (*Abies balsamea*, *Picea glauca*, and *O. virginiana*) showed inconsistent patterns among measurement intervals, but overall declines in basal area were recorded. However, since comparisons involve only stems > 11 cm d.b.h.

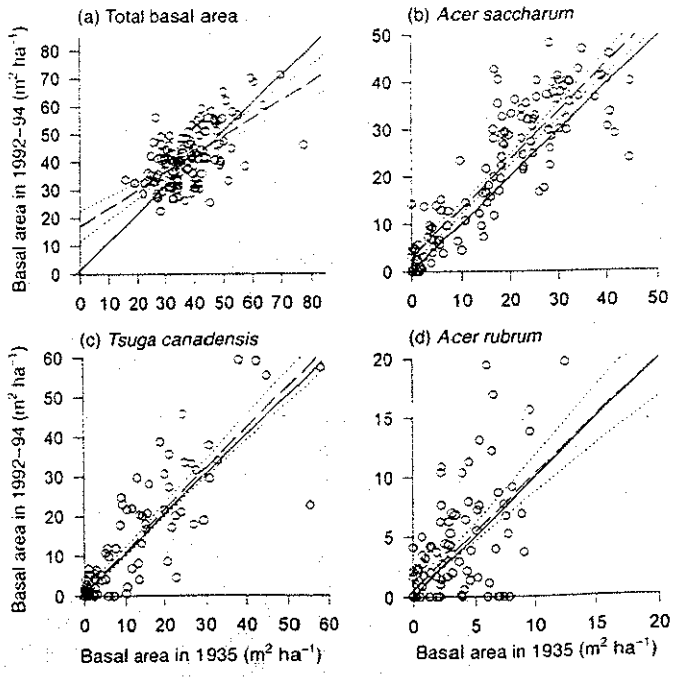

Fig. 7 Changes in basal area from 1935 to most recent measurement. Each symbol represents one sample plot. Only the 139 plots remeasured in 1992–94 are shown. Solid lines at 1 : 1 slope show locus of no change; dashed lines are linear regression of later measurement on earlier measurement; dotted lines are 95% confidence interval for regression. (a) Total plot basal area. (b) *Acer saccharum*. (c) *Tsuga canadensis*. (d) *Acer rubrum*.

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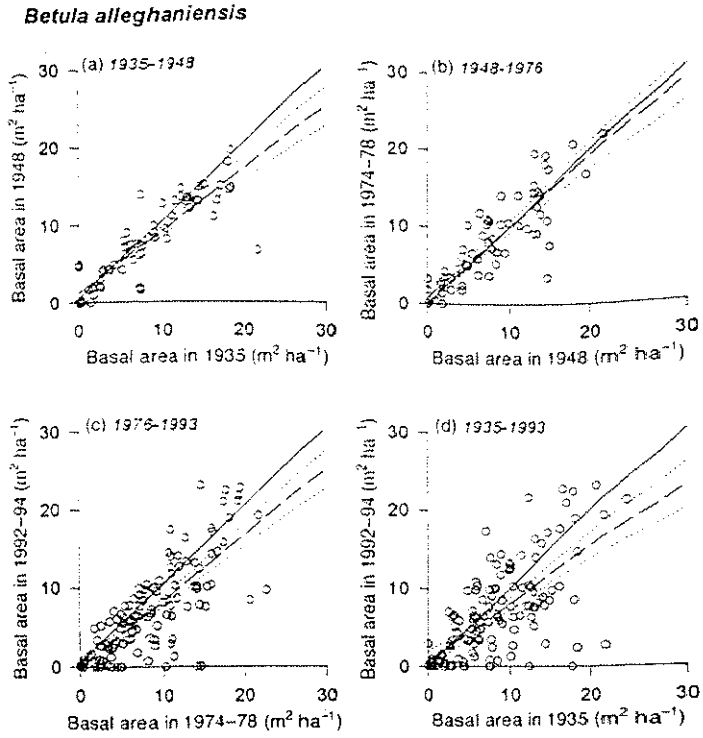

Fig. 8 Changes in basal area for *Betula alleghaniensis* by measurement period, (a) to (d). Symbols represent sample plots. Number of plots varies among intervals.

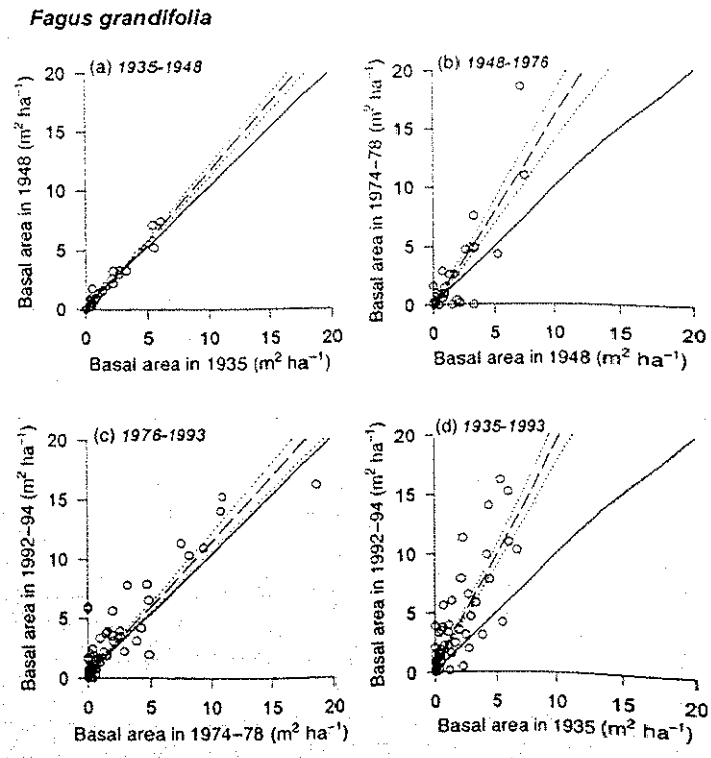

Fig. 9 Changes in basal area for *Fagus grandifolia* by measurement period, (a) to (d). Symbols represent sample plots. Number of plots varies among intervals.

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(relatively large for these species) apparent fluctuations may be artefacts of sampling.

Spatial patterns of change

Comparisons of spatial distributions from 1935 and 1992–94 measurements (Fig. 10) show that population dynamics are related to patterns of community differentiation discussed above. *T. canadensis* and *A. saccharum* show strong spatial segregation, and show only modest basal area changes without evident spatial clustering. *A. rubrum* is distributed relatively concordantly with *T. canadensis*; basal area shows little overall trend, but may be consistent within plot groups (compare group B1 and H1 with reference to Fig. 2). *B. alleghaniensis* is broadly distributed in the stand. Large declines in basal area occur throughout, but are especially notable in the south-east, maple-dominated area (group M2). *F. grandifolia*, although increasing rapidly in basal area, remains patchily distributed in the stand.

Size distributions

A. saccharum size distributions changed little and showed little difference among plot groups (Fig. 11a). Stem densities were relatively uniform in size classes from 20 to 60 cm (generally subcanopy and canopy status), while stems of 2–12 cm d.b.h. (measured only in the last two sampling periods) had densities approximately an order of magnitude greater. Densities fell off rapidly above about 70 cm d.b.h. *T. canadensis* size distributions also changed little over time but differed in having lower densities in the smallest size classes and a relatively constant

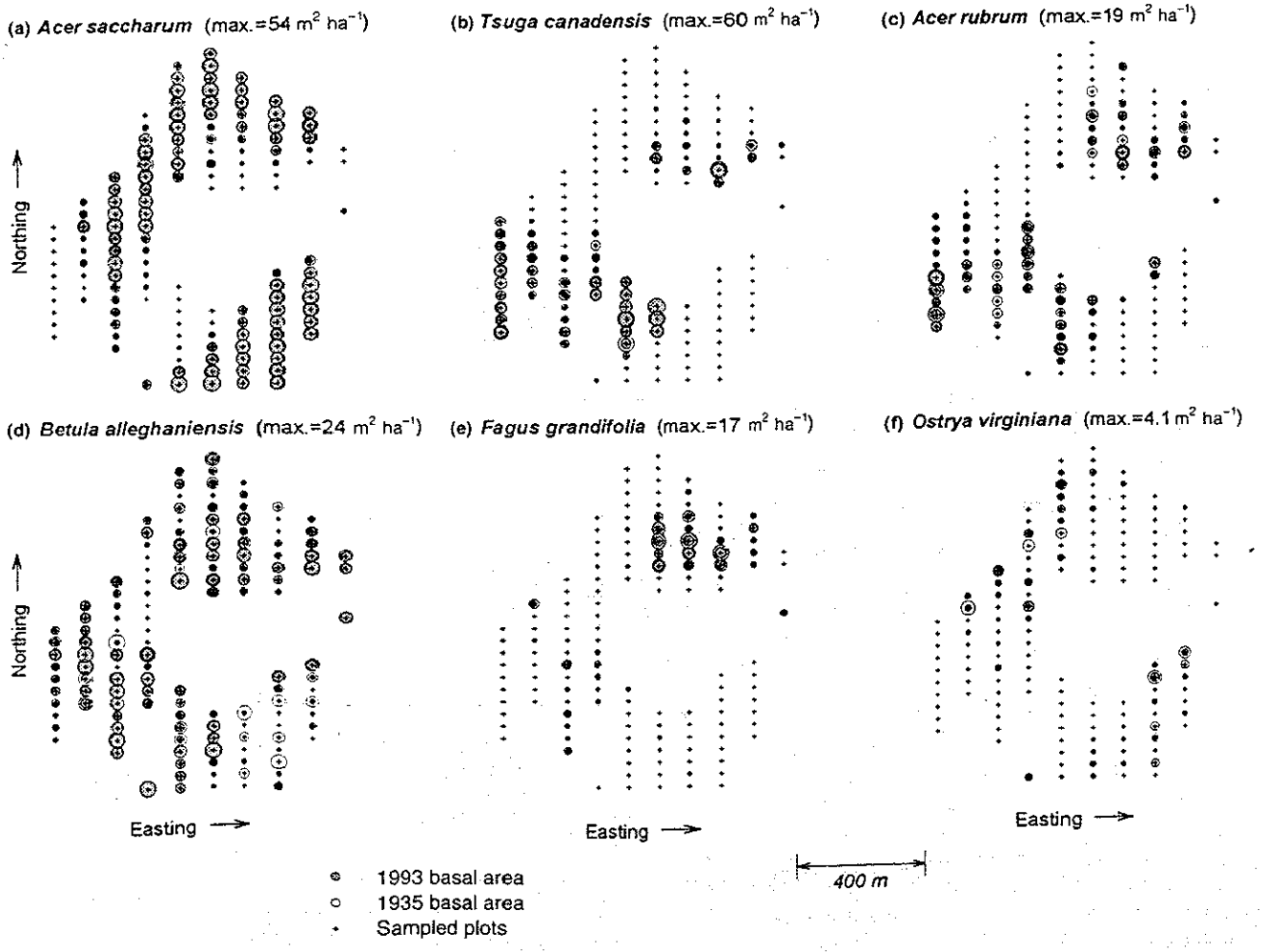

Fig. 10 Basal area changes mapped over stand (see Fig. 2 for plot groups) for six tree species, (a) to (f). Area of symbol for each plot is scaled to basal area. Crosses alone show measured plots where species concerned was not present. Shaded circles indicating 1992–94 basal area are superimposed on open circles indicating 1935 basal area (or 1948 basal area in those plots not measured in 1935). Basal area change is therefore indicated by 'bull's-eyes': those with unshaded outer rings indicate declines in basal area, while shaded outer rings indicate increases in basal area.

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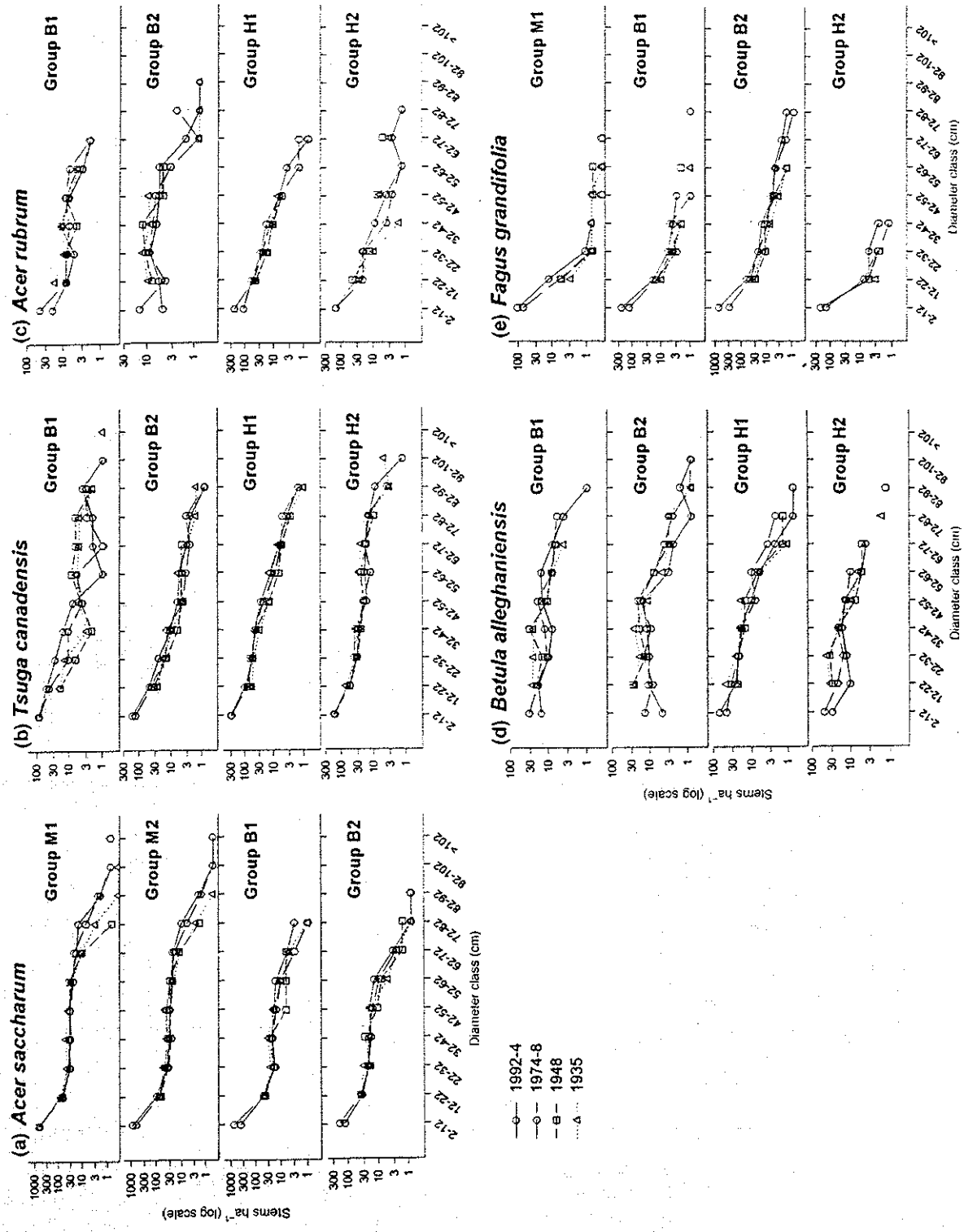

Fig. 11 Changes in size distributions over plot groups and sampling periods for five tree species, (a) to (e). Log-transformed stem densities are plotted over 10-cm diameter classes. Stems in smallest size class were measured only for the last two measurement intervals. Plot groups are as in Table 1 and Fig. 2.

proportional decline in density with size over a wide range of size diameters (Fig. 11b).

A. rubrum size distributions were more variable among measurement periods and among plot groups (Fig. 11c). Curves in plot groups B1 and B2 resembled those for *A. saccharum* in shape, although densities were lower, and there is some suggestion that densities for stems below 50 cm d.b.h. declined over time. In *Tsuga*-dominated plots (H1 and H2), *A. rubrum* densities were higher overall and time-invariant, but showed a much sharper and proportionally constant decline with size.

B. alleghaniensis was present in all plot groups, with lowest densities in plot groups M1 and M2, and highest densities in hemlock-dominated areas (H1 and H2). In all plot groups except H1, size classes < 50 cm d.b.h. declined more or less continuously over the course of the study (Fig. 11d). This decline was most marked in the smallest diameter classes in maple-dominated areas (not illustrated). *F. grandifolia* size distributions remained constant in form (Fig. 11e), but overall density increased in all size classes, typically by two-fold or more. Small trees were markedly more abundant than larger stems and density declined continuously with increasing size.

Community change

Plot time-trajectories in ordination space reflect overall compositional changes (Fig. 12). Patterns are complex and noisy, but some trends are visible. Many plot trajectories are directed towards the lower centre of the ordination field, their direction influenced by increasing *F. grandifolia* basal area. *Tsuga*-dominated plots, clustered at the right side of the ordination field, appear to converge on the region of maximum *T. canadensis* importance. There is little indication of convergent trajectories for *A. saccharum*-dominated plots, at the left side of the ordination, but these trajectories seem to be strongly confined within a neighbourhood defined by strong *A. saccharum* dominance.

Discussion

COMMUNITY PATTERNS

Compositional patterns at the scale of tens to hundreds of metres are strongly correlated with spatial variation in soil chemistry and structure (Figs 6 & 10). *A. saccharum* achieves maximum dominance on well-drained soils of high pH and Ca content (plot group M1). *F. grandifolia* is confined largely to soils of finer texture, particularly where drainage is impeded by pan development (plot group B2), where *A. rubrum* is also more abundant. *T. canadensis* is dominant, often to the near-exclusion of other species, on soils of low pH and with a mor humus and well-developed A_2 horizon, generally near the margins of wetter areas of the RNA. These patterns may reflect both influences of soil properties on species distributions and, especially with respect to chemical properties, influences of canopy composition on soil properties.

B. alleghaniensis is widely distributed across soil types and plot groups. This is consistent with a relatively opportunistic life history: occurrence may be more reflective of disturbance history than current environmental patterns. Greater abundance of *B. alleghaniensis* in stands of *T. canadensis* dominance (also see Brown & Curtis 1952; Whittaker 1956; McIntosh 1972; Leak 1975; Rogers 1978; Woods 1984) might indicate overlapping environmental preferences or differences in disturbance dynamics, but Woods (1984) suggested that the very low density of

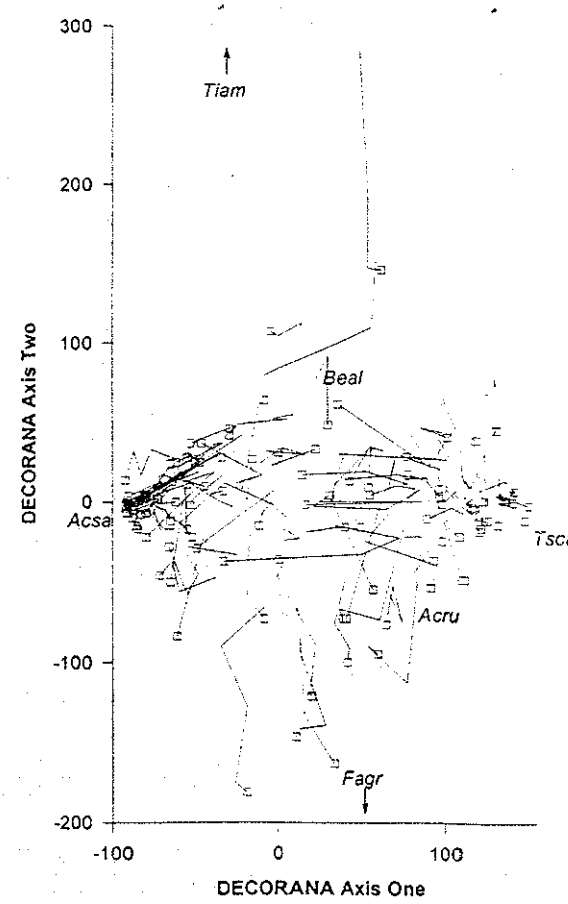

Fig. 12 Plot trajectories in DCA ordination space over time. Ordination includes all measurements of all plots. Square symbols indicate position in ordination for measurements in 1992–94; lines connect these symbols with ordinated positions for the same plots at previous dates (ordination positions for earlier positions are typically indicated by inflections in line). Directionality of compositional trajectories should be seen as along lines toward the squares. Note that actual time elapsed for trajectories shown varies since not all plots were measured in 1935. Species distributional centres are shown as in Figs 3 & 4.

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suppressed saplings of *B. alleghaniensis* in *T. canadensis* stands could favour *B. alleghaniensis* regeneration in gaps.

Canopy species do not show concordant distributions within the study area, but subcanopy species are significantly associated with particular canopy species. *O. virginiana* is strongly associated with *A. saccharum* canopy dominance. *A. balsamea* and *P. glauca* are more widely distributed, but both are strongly correlated with *T. canadensis*. The coincidence of phenological strategies – deciduous with deciduous and evergreen conifer with evergreen conifer – may reflect common response to physical environment, or it may be due to environmental constraints imposed by canopy type.

Total plot basal areas are high compared to other studies in northern hardwood forests: studies cited by Keddy & Drummond (1996) have basal areas ranging from 23 to 40 $m^2 ha^{-1}$. Higher basal area in *Tsuga*-dominated plots (Table 1) is consistent with observations in other studies, but reasons for the difference are not apparent.

Community variation is continuous and strongly associated with environmental variation. There is no evidence of distinct canopy types or recognizable clusters within ordinations (Figs 3 & 4), except in the conceptually trivial instances of single-species dominance by *A. saccharum* and, to a lesser degree, *T. canadensis*.

DYNAMICS

There is no overall trend in plot basal areas over the six decades of the study. The tendency of plots with initially high basal areas to show declines and those with initially low basal areas to increase in basal area (Fig. 7a) is consistent with stand-level biomass equilibrium maintained by fine-scale disturbance and recovery typical of patch or gap models of equilibrial old-growth forests (e.g. Forcier 1975; Runkle 1981). Patches of high basal area (i.e. high densities of large, mature canopy trees) are more likely to experience mortality of large individuals and consequent sharp declines in basal area. Plots of low basal area are generally dominated by smaller trees, presumably colonists in old canopy gaps, where accretion of basal area more than balances less frequent mortality.

Individual species dynamics, however, do not conform to equilibrium models. The current dominants, *A. saccharum* and *T. canadensis*, show only modest trends in biomass or size distributions, but basal areas of both appear to be increasing. *A. rubrum* basal areas fluctuate relatively rapidly at the plot level but show no trend. Equation of size distribution and age structure is risky for shade-tolerant trees, but these patterns, along with unpublished increment core data, suggest that populations of these three species are relatively stable. The suggestion of relatively high mortality among the smallest size classes of *A. saccharum* and much lower initial mortality (and density) of smaller *T. canadensis* trees (Fig. 11) is consistent with other research (Kobe *et al.* 1995; Woods 2000). Decreases from the 1970s to 1990s in the smallest size classes for *A. saccharum* in mixed stands (groups B1 and B2) may foreshadow eventual increases in relative *T. canadensis* or *F. grandifolia* dominance.

B. alleghaniensis populations, on the other hand, are clearly changing in basal area and size structure. Large basal area declines have increased in frequency over the course of the study and are not matched by increases in other plots. Size structures suggest a population with very little regeneration: small trees dying or growing into larger size classes are not being replaced, so the trend of declining basal areas with the death of current canopy trees is likely to continue. *B. alleghaniensis* is relatively shade-intolerant and therefore depends on canopy gaps for establishment (Erdmann 1990). Patterns at the Dukes RNA suggest a population dominated by a cohort, or cohorts, established during some period of disturbance and now experiencing increasing mortality with age. There has been a lack of successful establishment in recently formed gaps of up to 400 m^2 (personal observation), suggesting that *B. alleghaniensis* requires more intense disturbance for regeneration. Increment cores from the Dukes stand suggest that current *B. alleghaniensis* cohorts date to the last decades of the 1700s, perhaps indicating the most recent major stand-wide disturbance. Near-total loss of *B. alleghaniensis* from plot group M2 (Figs 2 & 10) suggests a pattern distinct from the remainder of the stand: either the *B. alleghaniensis* in this part of the stand date from an earlier disturbance, or the life expectancy of *B. alleghaniensis* is lower on the sandy, well-drained, high-Ca soils of this area.

The Dukes site is within a few km of the northwestern range limit of *F. grandifolia*, and palaeoecological data (Woods & Davis 1989) indicate local arrival only within the last 500 years. The rapid population expansion observed here may be part of this ongoing invasion. Increment cores suggest an age distribution consistent with size distributions, strongly weighted to classes less than 150 years old and a maximum age of just over 200 years. Population growth over the last six decades has been very rapid for a slow-growing, late-successional canopy dominant, and has occurred without major disturbance; there is no evidence of higher disturbance intensity in the portions of the stand where *F. grandifolia* has increased the most. The presence of many apparently vigorous saplings and subcanopy trees beneath intact canopy is consistent with the extreme shade-tolerance of this species (Poulson & Platt 1989, 1996; Pacala *et al.* 1993, 1994, 1996; Kobe *et al.* 1995). *F. grandifolia* populations might

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grow faster with more intense canopy disturbance, but there is no suggestion here of 'community resistance' to invasion (Elton 1958).

The trigger for the current expansion of *F. grandifolia* is obscure. Woods & Davis (1989) show that the species was present as close as 50 km to the east by 2500 years ago, indicating that its recent arrival at the Dukes site is not solely a consequence of dispersal limitation. They suggest that water relations have played a role in determining the western range limit of the species. Petty *et al.* (1995) suggest that broad establishment of *F. grandifolia* in the region was delayed until a combination of soil development and climate change led to the development of drainage-impeding ortsteins in certain soils. At Dukes, *Fagus* is most abundant in areas of finer soil, often with cemented horizons and impeded drainage.

COMPARISONS AND PROJECTIONS

Sixty years remains a brief interval – less than a single generation of canopy trees – in the relevant time scale for stand dynamics in these forests. However, if observed trends are extrapolated, they suggest a community that, although conforming to definitions of 'old-growth' forest, continues to undergo successional change. *B. alleghaniensis*, a major component of the canopy 60 years ago, is likely to be largely lost within the next few decades.

Among shade-tolerant species, the expansion of *F. grandifolia* is a strong directional trend. Long-term studies in old-growth forests in the Huron Mts, *c.* 80 km north-west of the Dukes site and beyond the range-limit of *F. grandifolia*, suggest that, in the absence of intense disturbance, stands will gradually diverge towards dominance by either *T. canadensis* or *A. saccharum* (Woods 2000). Trends observed here (Fig. 12) suggest a similar pattern at Dukes, with the addition of a third 'basin of attraction' in the region of *F. grandifolia* dominance. Simulations of northern hardwood forests in New England (Pacala *et al.* 1996) predict eventual dominance by *F. grandifolia*, but it is not clear how geographically generalizable such results are. Relative shade-tolerance may change with site conditions (Kobe *et al.* 1995), and in this stand, *F. grandifolia*, near its range limit, may be competitively dominant only in relatively moist locations. However, observational studies in southern Michigan (Poulson & Platt 1996) and in New Hampshire (Forcier 1975) suggest that *F. grandifolia* may tend towards competitive dominance when disturbance is limited to small gaps.

Trends, even though slow, towards local single-species dominance suggest that within-stand processes invoked to explain sustained canopy diversity may prevail for only limited periods. Forcier (1975) and Woods (1979, 1984) suggested that the influence of the canopy on microsite conditions might determine survival of seedlings and saplings such that, in some cases, replacement patterns sustain co-dominance (particularly between *F. grandifolia* and *A. saccharum*). Observations of regeneration in canopy gaps have led to similar projections (e.g. Runkle 1981). Observed patterns here do not deny the existence of these processes, but suggest that, if they exist, they are not fully balanced and only delay the final outcome of competitive interactions.

Other data support the notion that *B. alleghaniensis* populations in late-successional forests consist typically of a few cohorts dating from intense disturbances. At the Huron Mts, *B. alleghaniensis* shows similar size structures and declines, and increment core ages cluster at slightly over 200 years (Willis & Coffman 1975; Woods 2000). These ages are close enough to those observed at the Dukes site to suggest that the same intense wind event was responsible for the disturbances at both sites.

This study, with the parallel study at the Huron Mts (Woods 2000), suggests that old-growth forests several centuries old may not be characterized by meaningful community equilibrium or compositional stability. Cores from trees in the Dukes stand approaching four centuries in age show that they were subject to strong suppression when young; together with the near-absence of shade-intolerant species, this suggests that a minimum of five centuries has elapsed since stand-initiating disturbance. Results here suggest that this may be insufficient time for resolution of competitive interactions among shade-tolerant species, and the slow trends observed may not permit competitive displacement to be achieved in the time expected between catastrophic disturbances. If periods much greater than half a millennium are required for the completion of observed successional processes, climatic change and soil development are also likely to intervene, leading to changed competitive dynamics and successional patterns. For example, the recent arrival of *F. grandifolia* at the Dukes site has changed the likely course of succession and delayed the attainment of potential compositional stability by several centuries.

In light of these conclusions, it is probably best to completely discard the notion of an end-point to successional change and simply consider stands such as the Dukes site 'late-successional'; they are removed from stand origination by more than a generation of trees, but successional change continues. Successional change in such stands may well be slower than in earlier succession simply because of the longer life expectancies of the species involved; scaling of rates of change to generation time of dominant trees is needed to clarify this issue. If these generalizations hold, it is inappropriate to consider stability as a distinguishing ecological characteristic in defining 'old-growth' forests.

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