Bulletin of the Torrey Botanical Club 121(2), 1994, pp. 130–139

Fifty years of change in an upland forest in south-central New York: General patterns[1]

Jay J. Fain, Timothy A. Volk and Timothy J. Fahey
Department of Natural Resources, Cornell University, Ithaca, NY 14853

ABSTRACT

FAIN, J. J., T. A. VOLK AND T. J. FAHEY (Department of Natural Resources, Cornell University, Ithaca, NY 14853). Fifty years of change in an upland forest in south-central New York: General patterns. Bull. Torrey Bot. Club 121: 130–139. 1994.—Long-term changes in the composition and structure of an upland hardwood forest in south-central New York were quantified by resurvey of 22 permanent plots originally established in 1935. In 1935 most of the forest consisted of stands recovering from disturbance by logging in the late 19th century, and most of the plots underwent timber stand improvement in 1934 that reduced basal area by an average of about one-third. Average basal area nearly doubled during the 50 year period, and basal area of the individual plots converged from widely disparate values in 1935 to about 32 m^2/ha in 1985. Size structure of the forest changed markedly over the 50-year period reflecting high recruitment of the shade tolerant species—sugar maple, beech, hemlock—as well as a significant decline in density of suppressed sub-canopy trees (10–20 cm DBH) mostly as a result of mortality. Although basal area of the mid-tolerant species—white ash, red maple, basswood—remained high, recruitment of these species was limited and in the continuing absence of large-scale disturbance the forest appears to be moving towards a composition dominated by the highly shade tolerant species.

Key words: Allegheny northern hardwoods, mortality, recruitment.

Long-term changes in the composition and structure of eastern deciduous forests have been documented by a variety of techniques including stand reconstruction from living and dead stems (Henry and Swan 1974; Oliver and Stephens 1977; Oliver 1978), interpretation of early surveyors' notes (Stearns 1949; Canham and Loucks 1984; Whitney 1986) and contemporary chronosequence comparisons (Christensen and Peet 1981). The most precise way to document these changes is the periodic remeasurement of permanent plots (Hough and Taylor 1946; Wilson 1953; Leak and Solomon 1977), but because of the limited set of available plots, few of these studies have extended beyond two decades (Della-Bianca 1983; Hibbs 1983; Leak 1987; Stephens and Ward 1992).

To gain a better understanding of long-term change in forest structure and composition in an eastern deciduous forest we remeasured permanent plots established in 1934–1935. Our objective was to describe the long-term changes in species composition, basal area, and diameter-density distributions in second-growth, Allegheny northern hardwoods.

STUDY AREA. The study was conducted at the Arnot Teaching and Research Forest located at the boundary between Tompkins and Schuyler County, in Cayuta, New York. Situated on the northern Allegheny Plateau physiographic province, the Forest occupies the southeast section of the Alpine Quadrangle of the 7.5 minute U.S.G.S. topographic map series (42°15″N and 76°40″W; Fig. 1). Bedrock consisting of shale, siltstone, and sandstone of the Upper Devonian Period underlies the forest. The province is characterized by deep, U-shaped valleys and flattened ridgetops resulting from glacial action in the dissected landscape. Elevation ranges from 370 m in valley bottoms to 615 m on the ridgetops.

The climate of west-central New York is temperate continental with a mean temperature of −4°C in January and 22°C in July (Thompson 1966). Precipitation is 100 cm per year, with slightly higher amounts in summer than winter. Frost penetration in forest soils is usually minimal due to persistent snow cover in the winter (Diebold 1938).

Soils of the Arnot Forest, especially those on the hillslopes that comprise the majority of the study area, consist mainly of acidic Dystrochrepts and Fragiochrepts of the Lordstown-Vol-

[1] For their assistance in various phases of this research the authors wish to thank John Kelley, Jim Lassoie and Peter Marks. Support was provided through the New York State Agricultural Experiment Station with McIntire-Stennis funds.

Received for publication July 19, 1993, and in revised form November 6, 1993.

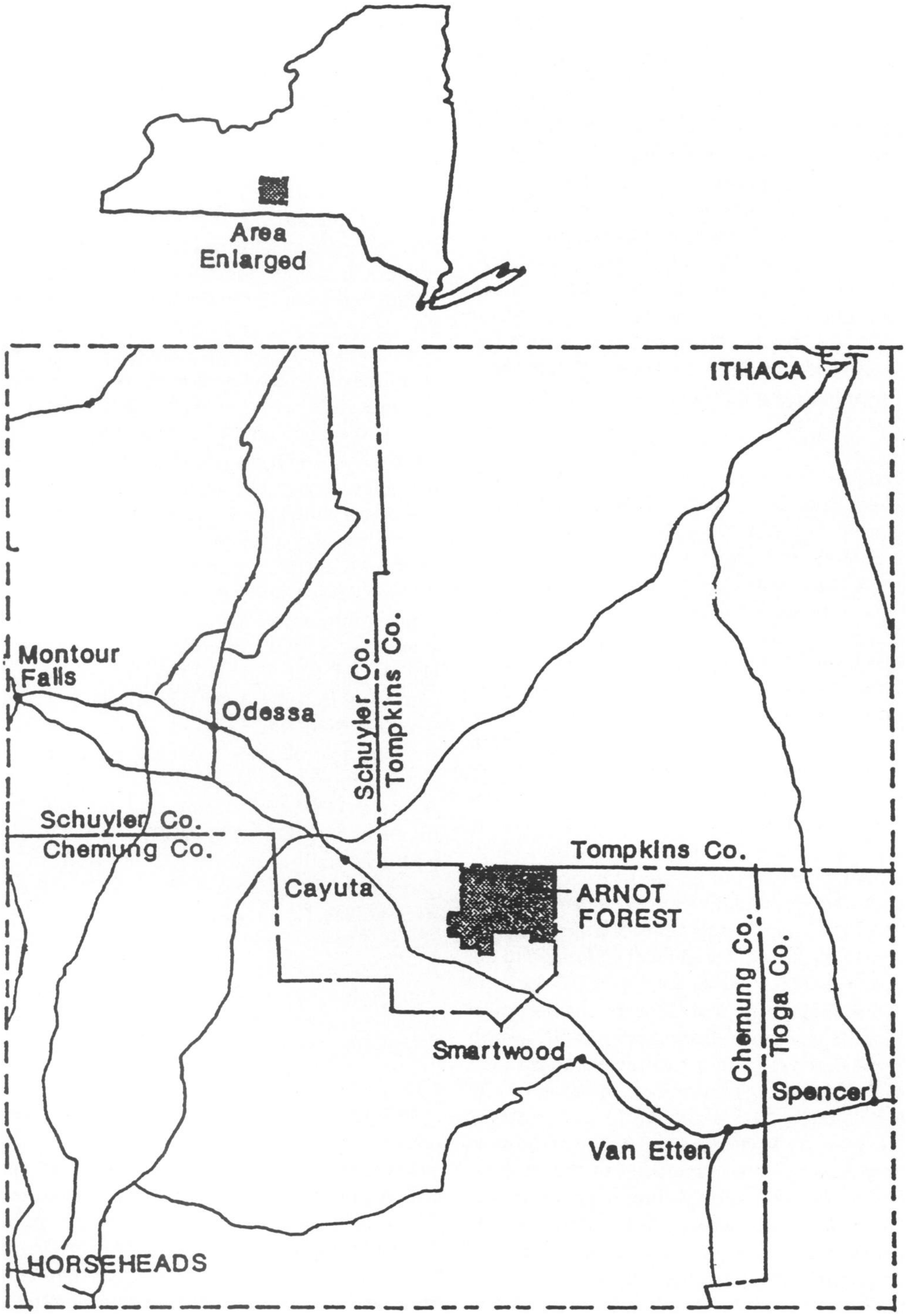

Fig. 1. Location of the Arnot Forest in south-central New York.

usia-Mardin Series (Cline 1970). Soils are generally acidic with a pH of 4.5 to 5.0 and drainage varies from well-drained Lordstown soils to poorly-drained Volusia and Mardin soils. Soil profile development has been limited by extensive wind throw disturbance as witnessed by pit and mound microtopography (about 700 mounds/ha; Daugherty and Hanna 1972).

The Arnot Forest is part of the Allegheny northern hardwood forest (Stout and Nyland 1986) which extends across much of New York State's southern tier. Prior to the arrival of Europeans in the area, Native Americans had only limited and localized impacts on the forest (Odell et al. 1980). Europeans settled the study area in the early 19th century, with farms on the better lands. From 1873–1887 the area was logged extensively for hemlock and hardwoods (Beatty 1929). Two major fires in the early 20th century burned much of the cut-over area of the Arnot Forest (Wilm 1932). However, the present study was conducted in unburned areas. Since 1927, the forest has been managed by Cornell University.

Methods. ESTABLISHMENT AND REMEASUREMENT OF PERMANENT PLOTS. During 1934 and the spring of 1935, 51 permanent study plots were established throughout the Forest. The objective was to "study the amounts of timber cut and left in relation to stand improvement measures, and to record the data to be used in comparison with the subsequent records to be taken" (Van Order 1937). Thus, timber stand improvements were carried out throughout most of the study area at this time. The criteria for selection of plot locations was not specified. The plots were positioned along existing lot lines, probably for ease of surveying. Except as noted below, the permanent plots were 2 chains (1 chain = 66 ft) by 5 chains, or 1 acre (0.405 ha), in size. In 1935, all trees over 5 cm diameter at breast height (dbh, 1.3 m) were identified and tabulated into 1 inch (2.5 cm) dbh classes. Height was estimated to the nearest 5 feet (1.5 m) for each stem. Trees were not permanently marked. Plot descriptions also included site information (slope, angle, aspect and soil descriptions), a qualitative assessment of ground cover, observations on disease and insect damage, and a description of previous treatment history of the plot. For nine of the plots a complete census was included of the trees removed in the silvicultural thinning operations.

Using the information contained in the site description, 22 of the plots were relocated in 1985 for resurvey. Plot locations were verified by the presence of original chestnut stakes at one or more of the corners. The remaining 29 plots were excluded from this study because either (1) they had been disturbed by cutting, planting, or road construction since 1935; (2) they were originally conifer plantations or were located in areas designated in the original surveys as burned over ground; or (3) plot corners could not be relocated. Each plot was subdivided into ten 0.04 ha quadrats. We measured dbh (to ± 1 mm) and estimated height (to ± 1.5 m using a clinometer) of all stems larger than 5 cm dbh on a quadrat-by-quadrat basis in summer 1985.

DATA ANALYSIS. The criteria for locating plots in the 1935 survey were not described; thus, patterns of change in forest composition and structure could not be generalized across the entire Arnot Forest on the basis of statistical analysis. To verify the non-quantitative classification of Howard (1936), the 1935 data for the 22 plots were classified into forest types based on woody vegetation (≥ 5 cm dbh) using TWINSPAN (Hill 1979). We calculated importance values for the TWINSPAN analysis from transformed data: the diameter of each tree in the plots was raised to 1.3 power and summed by species. This transformation may provide a better representation of overall species importance than the sum of relative density and relative dominance because it takes into account the usual exponential survivorship curves exhibited across smaller size classes (H. G. Gauch, Cornell Univ., pers. comm.). The 1985 data were similarly classified with TWINSPAN.

Linear correlations were calculated for plot-wide data between all combinations of three parameters: basal area, density and quadratic mean diameter ($QMD = (\Sigma_i^n d_i^2/n)^{1/2}$, where d is dbh and n is number of trees ≥ 5 cm dbh) in 1935 and 1985. QMD is the dbh of the tree that has average basal area and is a useful index of the stage of development in forest stands. Changes in the variance of plot basal areas between 1935 and 1985 were analyzed with a two-tailed F statistic. A t-test was used to compare basal area of plots with greater and lesser amounts of hemlock.

Results. CHANGES IN FOREST COMPOSITION AND STRUCTURE. Following timber stand improvement (TSI) operations in 1935, the Arnot Forest plots were dominated by six tree species (Table 2): American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), red maple (*Acer rubrum* L.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), and white ash (*Fraxinus americana* L.). Twenty tree species were measured on the plots. Mean stem density (stems ≥ 5 cm dbh) was 974 stems/ha, mean basal area was 16.9 m^2/ha, and quadratic mean diameter (QMD) averaged 15.9 cm (Table 1). Ring counts on stems har-

Table 1. Summary of characteristics for twenty-two permanent plots in the Arnot Forest, New York.

Forest type[1] and plot #	Topography[2]	Predominate soil drainage class[3]	Treatment	Stem density[4] (stems/ha)			Basal area[4] (m^2/ha)			Quadratic mean diameter[4] (cm)			Canopy height[5] (m)	
				1935—precut	1935—postcut	1985	1935—precut	1935—postcut	1985	1935—precut	1935—postcut	1985	1935	1985
Second-Growth Hardwoods														
1	14–16%, M, S.E.	S	Improvement Cut	1064	831	1040	31.6	23.5	31.2	19.9	19.0	19.6	20.1	24.7
2	12–16%, M, S.E.	M	Improvement Cut	1013	736	1087	20.3	12.6	31.7	17.3	15.8	19.3	18.2	25.9
3	12–16%, M, S.E.	S	Improvement Cut	966	734	1740	23.7	14.9	30.3	17.6	16.1	14.9	17.2	19.0
4	12–16%, M, S.E.	S	Improvement Cut	766	598	1878	22.5	15.8	36.1	19.2	18.4	15.6	17.6	20.4
5A	12–18%, M, S.W.	P	Improvement Cut	1589	1421	1127	23.4	15.8	27.2	14.2	11.9	19.2	18.3	22.6
5B	12–18%, M, S.W.	S	Control, No Cut	1779	1779	1120	21.8	21.8	29.8	12.6	12.6	17.4	18.1	20.4
6A	15–20%, M, S.W.	M	Improvement Cut	na	1641	1161	na	16.2	35.6	na	11.2	19.7	18.0	20.3
6B	15–20%, M, S.W.	M	Control, No Cut	1952	1952	1102	19.6	19.6	35.1	11.3	11.3	20.1	18.3	21.2
11	30–40%, M, S.E.-E.	W	Improvement Cut	na	1147	1275	na	13.5	30.5	na	12.2	17.4	15.1	22.7
12	12–20%, US, S.E.	W	Improvement Cut	na	1223	1512	na	11.8	30.1	na	11.1	15.9	13.4	21.0
14	10–30%, LS, N.E.	S	Improvement Cut	na	581	783	na	17.0	31.3	na	19.3	22.6	19.1	18.7
Hemlock Hardwoods														
15[6]	20–35%, MS, N.E.	W	Improvement Cut	na	798	796	na	22.3	29.5	na	18.9	21.7	20.3	19.8
16	15–25%, MS, E.	W	Hemlock Cut	na	813	1290	na	17.9	32.5	na	16.8	17.9	17.7	20.0
17	15–25%, MS, E.	W	Hemlock Cut	na	534	1065	na	17.4	27.9	na	20.4	18.2	18.0	19.9
18	5–35%, US, E.	M	Hemlock Cut	na	437	702	na	25.1	30.0	na	27.0	23.3	20.2	20.0
19	5–35%, US, E.	M	Hemlock Cut	na	499	709	na	22.6	27.5	na	24.0	22.2	18.6	20.0
20	18–20%, US, E.	W	Hemlock Cut	na	736	544	na	25.1	33.8	na	20.8	28.1	17.4	25.3
Second-Growth Hardwoods														
24	10–18%, LS, E.	P	Improvement Cut	1206	1129	1161	16.6	13.2	28.1	13.2	12.2	17.5	19.3	19.6
25	12–16%, MS, S.	P	Improvement Cut	1144	1016	1344	17.7	12.4	24.6	14.0	12.4	15.2	18.8	17.8
35	12–16%, MS, S.	W	Improvement Cut	na	818	749	na	14.7	34.3	na	15.1	24.1	20.8	17.4
Hemlock Hardwoods														
36	12–24%, MS, S.	W	Improvement Cut	1562	1320	1600	15.1	11.1	36.3	11.1	10.4	17.0	16.6	15.9
42	20–25%, MS, S.W.	M	Improvement Cut	1099	689	1619	19.0	7.5	39.7	14.8	11.8	17.7	17.8	18.2
AVERAGE VALUES (standard deviations in parenthesis)					974 (91)	1155 (77)		16.9 (1.04)	31.5 (0.77)		15.9 (1.0)	19.3 (0.7)	18.1 (1.7)	20.5 (4.7)

[1] Forest type classes in 1935 as described by Howard (1936).
[2] Slope angle (%), slope position (U = upper-slope; M = mid-slope; L = lower-slope), slope aspect (cardinal directons).
[3] After Van Order (1937) (W = well drained; M = moderately well drained; S = somewhat-poorly drained; P = poorly drained).
[4] Statistics for all stems ≥5 cm DBH.
[5] Mean height of tallest 15% of stems.
[6] Re-classified on basis of TWINSPAN analysis of 1935 data.

Table 2. Density (all stems >5 cm DBH), basal area and quadratic mean diameter for trees in the Arnot Forest, New York in 1935 (post-thinning) and 1985.

	Density (stems/ha)		Basal area (m^2/ha)		Quadratic mean diameter (cm)	
Species	1935	1985	1935	1985	1935	1985
Acer pensylvanicum	0	<1	0	<0.01	—	7.6
A. rubrum	136	91	1.65	3.65	12.4	22.6
A. saccharum	219	335	2.93	8.90	12.8	18.4
Amelanchier spp.	2	<1	<0.01	<0.01	7.5	6.2
Betula lenta	74	37	0.86	0.88	13.6	17.4
B. alleghaniensis	27	6	0.33	0.15	12.5	17.9
B. papyrifera	<1	<1	<0.01	<0.01	18.0	19.0
Carpinus caroliniana	5	16	0.03	0.05	9.7	6.1
Carya cordiformis	0	<1	0	<0.01	—	11.0
C. ovata	<1	<1	<0.01	0.03	16.8	18.3
Castanea dentata	<1	<1	<0.01	<0.01	7.4	7.0
Fagus grandifolia	169	334	3.94	6.97	16.3	16.3
Fraxinus americana	79	70	1.38	3.55	14.6	25.3
Hammamelis virginiana	0	2	0	<0.01	—	5.3
Magnolia acuminata	<1	<1	0.02	0.03	23.4	29.6
Ostrya virginiana	5	63	0.03	0.38	8.3	8.2
Pinus strobus	0	<1	0	<0.01	—	14.0
Populus grandidentata	42	7	0.93	0.57	18.0	31.2
P. tremuloides	<1	<1	0.29	0.09	27.6	23.9
Prunus serotina	5	2	0.18	0.14	23.4	27.3
Quercus alba	9	<1	0.11	0.03	12.9	38.2
Q. palustris	0	<1	0	0.13	—	51.0
Q. rubra	11	12	0.53	1.31	24.3	36.8
Q. velutina	0	<1	0	0.02	—	35.2
Tilia americana	96	48	2.11	2.45	19.2	25.5
Tsuga canadensis	22	134	1.56	2.34	27.0	14.9

vested in the stand improvement operations indicated that most of the trees originated following extensive logging in the late 19th century (Van Order 1937). However, the age and size distributions of trees on the plots were variable, as illustrated by the large range in density, basal area and QMD; thus, the logging activity was not uniform across the entire Arnot Forest.

In 1985, the same six species dominated the overstory as in 1935. Twenty-six species were measured in the plots, including all the original species plus six additional ones (Table 2). For all plots density averaged 1155 stems/ha. Among the individual plots density increased on 15, decreased on six, and remained essentially constant on one. Although increases in density probably resulted in part from the effects of the TSI in 1935, on six of the nine plots with pre-treatment data, density increased above the pre-treatment levels (Table 1). Most of the density increase was associated with four species: sugar maple, beech, hemlock and hop hornbeam (*Ostrya virginiana* [Mill.] K. Koch). Overall decreases in stem density were observed for basswood, red maple, black birch (*Betula lenta* L.), big-toothed aspen (*Populus grandidentata* Michx.), and yellow birch (*Betula alleghaniensis* Britton).

Mean basal area nearly doubled on the plots during the 50 years, increasing from 16.9 to 31.5 m^2/ha (Table 1). Much of the basal area increase was attributed to sugar maple (from 2.9 to 8.9 m^2/ha), with smaller increases observed for beech, hemlock, red maple, white ash, and hop hornbeam (Table 2). Among the dominant species only big-toothed aspen exhibited a large basal area decline.

As a consequence of the variable stand disturbance histories and the TSI operations, high between-plot variation in basal area was observed in 1935 (coefficient of variation = 29%) and this variation declined by 1985 (CV = 11%); the decline in variance was highly significant ($P < 0.01$) based upon a two-tailed F test. Thus, basal area in the study plots converged on about 32 m^2/ha in 1985 from disparate values in 1935. Not surprisingly, the basal area increase among plots was inversely correlated with the 1935 (post-TSI) basal area ($r = -0.85$, $P < 0.01$).

Quadratic mean diameter increased on 17 of the 22 plots, with the overall average value increasing from 15.9 to 19.3 cm (Table 1). In 1935, QMD was highly correlated with plot basal area ($r = 0.70$, $P < 0.01$), whereas in 1985 this correlation was very weak ($r = 0.10$, $P > 0.05$). A strong inverse correlation observed between QMD in 1935 and basal area change ($r = -0.70$, $P < 0.01$) reflected the relationships between initial basal area and change in basal area, noted earlier.

Changes in stand structure occurred during the 50 years of stand development (Fig. 2). The 1985 diameter distributions illustrated the increases in stem density noted earlier; however, an overall decline in density in the 10–15 cm size class occurred during the interval. Most of the changes in stand structure were associated with the two dominant species, sugar maple and beech. The dbh distributions of both species in both 1935 and 1985 were steeply descending, monotonic curves typical of tolerant species (Fig. 2).

Size-class distributions of hemlock changed between 1935 and 1985. In 1935, hemlock was uncommon in most of the forest, a condition created in part by the selective removal of this species during the silvicultural treatments (Table 1). By 1985, abundant recruitment was exhibited in the size classes below 25 cm, an indication of the ability of this species to become established and grow beneath a closed canopy. The decline of hemlock in the larger size classes indicates high mortality in the overstory between 1935 and 1985. Observations of Adams (1953) suggest that severe windstorms in the early 1950's caused extensive damage to hemlock in the Arnot Forest.

The three principal mid-tolerant species (Burns and Honkala 1990) (red maple, basswood, and white ash) all exhibited a reduction in density in the smaller size classes (Fig. 2). These reductions can be explained by mortality of suppressed individuals and the inability of these species to reproduce under a closed canopy. In 1985, the diameter distributions of all the mid-tolerant species either approached a normal distribution or were broad and irregular. Increases in QMD were observed for all these species (Table 2). The abundance of the principal shade intolerant species, big-toothed aspen, declined markedly between 1935 and 1985.

FOREST CLASSIFICATION. Howard (1936) classified the forest types in the Arnot Forest on the basis of non-quantitative criteria. The plots used in the present study were classified into two forest types, second-growth hardwoods and hemlock hardwoods. We confirmed this earlier classification by cluster analysis using TWINSPAN (Hill 1979) on the 1935 data (Table 3). The first, highly significant division in the dendrograph distinguished two forest types that corresponded very closely to those of Howard (1936). Only one plot (#15, Table 1) appeared to be mis-classified in the earlier study. The principal differential species in the TWINSPAN analysis were hemlock and beech (much more abundant in hemlock hardwoods) and white ash and basswood (much more abundant in second-growth hardwoods). Other species for which abundance was significantly different ($P < 0.05$) between the two forest types included sugar maple and white ash (both more abundant in second-growth hardwoods).

The differences in composition between the two forest types were influenced by both environmental variation and disturbance history. For example, 8 of the 14 second-growth hardwood plots were located on poorly or somewhat-poorly drained soils, whereas all the hemlock hardwood plots were on moderate to well-drained sites (Table 1). Three of the hemlock hardwood plots (#18, 19, 20) included many older trees in 1935 and quadratic mean diameter values were the highest among all the plots (Table 1). Apparently the previous logging was less intense on these three plots than for the others.

The permanent plots also were classified with the 1985 data using TWINSPAN, and no changes in plot classifications were observed. Most of the compositional differences between the two forest types were retained after 50 years of stand development (Table 3).

The relative abundance of sugar maple increased on every plot in both forest types between 1935 and 1985; thus, throughout most of the Arnot Forest, irrespective of spatial variation in environment and previous disturbance history, sugar maple is a dominant species and is increasing in relative importance. Other differences in the 50-year changes in forest structure and composition reflected in a simple way the initial differences noted above. For example, white ash grew rapidly after 1935 (Volk and Fahey 1994), and its contribution to total basal area increased on 8 of the 12 second-growth hardwood plots but only 2 of the 8 hemlock hardwood plots. Variation in the 50-yr changes in stem density, plot basal area and QMD was not related in any simple way to forest type, in part because of the wide variation among plots in stand struc-

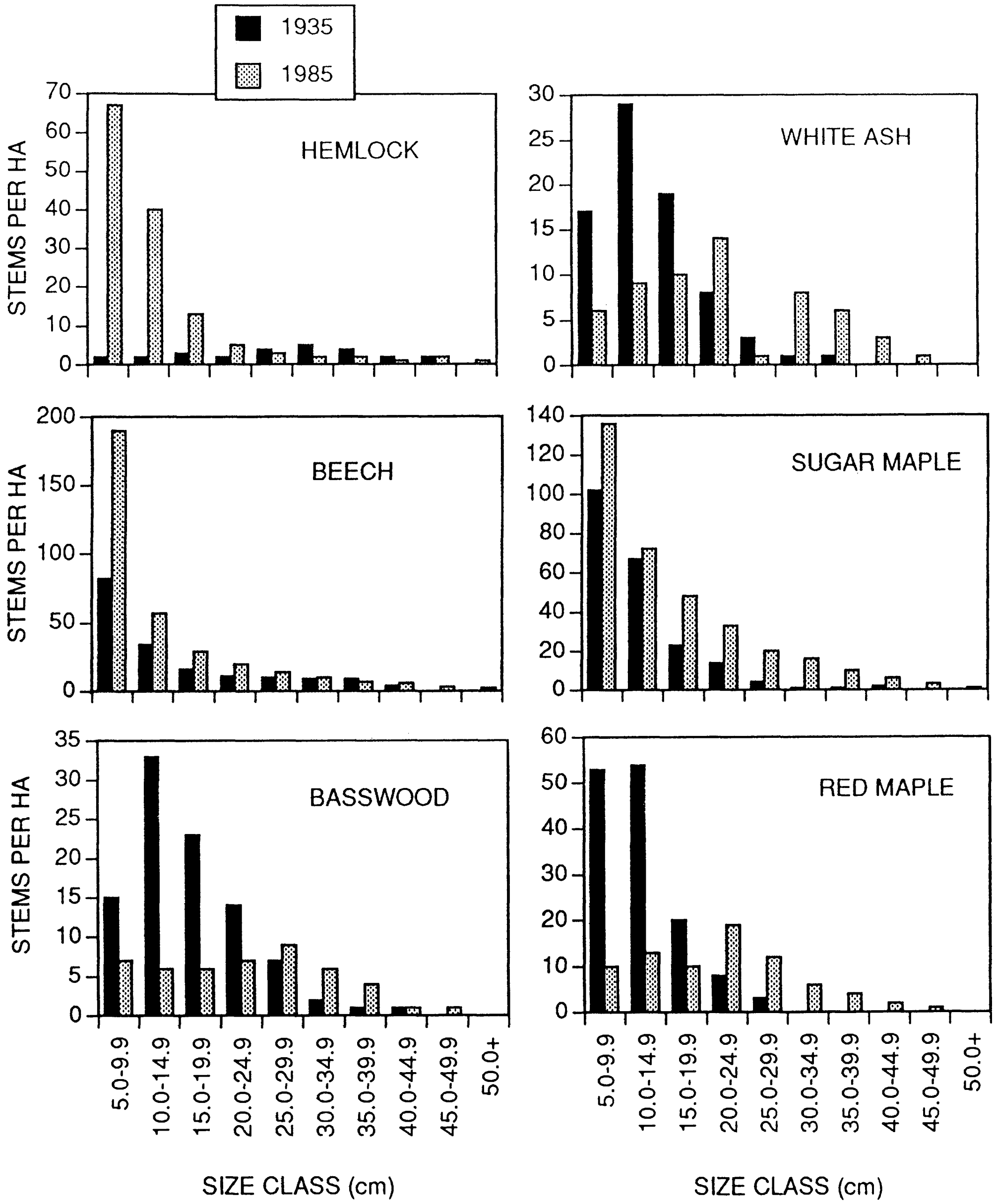

Fig. 2. Diameter distributions of the number of stems/ha (stems >5.0 cm dbh) for six individual tree species in 1934–1935 and 1984–1985 on 22 study plots in the Arnot Forest, central New York: hemlock (*Tsuga canadensis*), white ash (*Fraxinus americana*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), basswood (*Tilia americana*), red maple (*Acer rubrum*).

ture following the TSI operations (Table 1). However, the basal area of the plots in 1985 did vary with the abundance of hemlock. In seven of the 22 plots hemlock comprised over 10% of stand basal area, and a *t*-test showed that the total basal area of these plots (33.5 m^2/ha) was significantly higher ($P < 0.05$) than those with less hemlock (30.9 m^2/ha).

Discussion. At the time of the original census and silvicultural treatments in 1935, the Arnot Forest was a mixture of stands recovering from different intensities of disturbance by logging in the late 19th century. Despite this disturbance history, the composition of the Arnot Forest appeared to be qualitatively similar in 1985 to the pre-disturbance regional forest, as revealed by surveyors' notes (Marks and Gardescu 1992). Prior to timber stand improvement (TSI) operations, eleven plots with records showed about a two-fold range of basal area (15.1 to 31.6 m^2/ha) and density (776 to 1562 stems/ha; Table 1). The range in stand structure across the plots was further accentuated by the TSI (Table 1), and the legacy of these disturbances remained in the size structure of the plots in 1985 (Fig. 2). However, the variation among plots in total basal area declined significantly over the 50-year period and the average basal area in 1985 was 32 m^2/ha.

The basal area of several other eastern deciduous forests has been observed to converge on values similar to those noted at the Arnot Forest. Held and Winsted (1975) reported that the maximum basal area of seven climax stands on mesic sites in the central region of the eastern deciduous forest ranged from 25.8 to 32.2 m^2/ha with an average of 29.9 m^2/ha. In mesic, undisturbed forests of New York, studied by Harcombe and Dixon (1984), 30 m^2/ha was given as the characteristic maximum basal area.

In the Arnot Forest, plots composed of >10% hemlock had significantly higher basal area than those with lower hemlock abundance. This result confirms patterns observed previously. In central New Hampshire, Leak (1987) measured average basal area of 38.3 m^2/ha in northern hardwood stands with >15% conifer component while those with <15% conifers averaged 27.8 m^2/ha. Kelty (1989) observed a similar pattern for stands composed primarily of hardwoods and adjacent hemlock-hardwood stands in southern New England.

Because of the long lifespan of most of the tree species, no major changes in forest composition occurred during the 50-year interval. No species was lost entirely from all the plots and six additional species were recruited into the >5 cm DBH classes. Perhaps most notable was the general increase in abundance across all size classes and most plots of sugar maple, a result that matches long-term observations in other eastern deciduous forests (Parker et al. 1985; Schlesinger 1989). Other overall patterns of change included: (1) very little increase in the abundance of large beech trees, as a result of widespread mortality from beech bark disease (Runkle 1990; Krasny and Whitmore 1992); (2) continued recruitment of the shade-tolerant species—sugar maple, beech, hemlock and hop hornbeam—leading to monotonic, descending size-structure curves; (3) limited recruitment of mid-tolerant species—white ash, red maple, basswood, black birch—accompanied by large basal area increases, at least for

Table 3. Relative dominance (percentage of total basal area for stems ≥5 cm dbh) of principal trees in two forest types in the Arnot Forest, south-central New York in 1935 and 1985. Asterisks indicate significant differences between forest types for each year of measurement ($P < 0.05$).

Species	1935 Second-growth hardwoods	1935 Hemlock hardwoods	1985 Second-growth hardwoods	1985 Hemlock hardwoods
Acer rubrum	8.9	13.1	6.7*	16.3
A. saccharum	21.6*	12.2	34.0	26.1
Betula lenta	3.6	6.8	2.5	3.0
Fagus grandifolia	14.8*	33.0	15.9*	30.1
Fraxinus americana	13.4*	2.0	16.3*	2.3
Populus spp.	11.8	3.2	2.5	0.8
Quercus rubra	4.0	2.9	3.4	5.4
Tilia americana	15.2	6.7	8.9	5.0
Tsuga canadensis	2.8*	17.6	4.9*	10.5
Others	3.9	2.5	4.9	0.5

white ash and red maple (Table 2), as a result of rapid growth of canopy trees (Volk and Fahey 1994). Basal area of basswood increased only slightly (Table 2) as a result of both declining growth rates and high mortality (Volk and Fahey 1994). The causes of the basswood decline at the Arnot Forest and the future role of this species in the regional forests deserve further study.

Although two forest types (hemlock hardwoods and second-growth hardwoods) were readily distinguished within the study area, any differences in overall patterns of stand development (i.e., changes in basal area, density, QMD) between these two types were masked by the initially high variation in forest structure that resulted from different disturbance histories. The principal compositional differences between the two forest types were retained through 50 years of stand development: beech, hemlock and red maple were more abundant in hemlock-hardwoods and basswood and ash in second-growth hardwoods. In the continuing absence of large-scale disturbance the composition of these forest types is likely to converge somewhat because the differences between the types in the relative dominance of beech, sugar maple and hemlock became smaller over the 50 years of forest development (Table 3).

The silvicultural operation in 1935 reduced basal area in the study area by about one-third (21.1 m^2/ha to 14.1 m^2/ha, based on nine plots with TSI records; Table 1). This treatment was not sufficient to allow the recruitment of significant numbers of either intolerant or mid-tolerant species into the forest (Volk and Fahey 1994). Selection cutting in northern hardwoods gave a similar result (Leak and Wilson 1958). The maintenance of mid-tolerant species, particularly basswood and ash, in large amounts in the pre-Columbian forest of the region (Marks and Gardescu 1992) probably required a disturbance regime that resulted in overstory gaps larger than those provided by light thinning, selective cutting, and even the windstorms of 1950 and 1954. In the future, the composition and structure of unmanaged, upland forests in this region will be influenced primarily by continuing mortality of overstory beech and basswood and vegetative reproduction of the former; establishment and recruitment of sugar maple and hemlock, possibly influenced by high population densities of white-tailed deer (Marquis 1981); and unpredictable, larger-scale disturbance events such as severe ice and wind storms that could result in successful recruitment of mid-tolerant species.

Literature Cited

ADAMS, H. P. 1953. A summer survey of deer and grouse in the Arnot area. M.S. Thesis, Cornell University, Ithaca, NY. 56 p.

BEATTY, S. P. 1929. The Arnot Forest: Its foundation for management. M.F. Thesis, Cornell University, Ithaca, NY.

BURNS, R. M. AND B. H. HONKALA [eds.]. 1990. Silvics of North America: 2. Hardwoods. Agriculture Handbook 654. UDSA, For. Serv. Washington D.C., Vol. 2. 887 p.

CANHAM, C. D. AND D. L. LOUCKS. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65: 803–809.

CHRISTENSEN, N. L. AND R. K. PEET. 1981. Secondary forest succession on the North Carolina Piedmont, pp. 230–245. In D. C. West, H. H. Shugart and D. B. Botkin [eds.], Forest succession: Concepts and application. Springer-Verlag, New York.

CLINE, M. G. 1970. Soils and soil associations of New York. Extension Bulletin 930, New York State College of Agriculture, Cornell University, Ithaca, NY.

DAUGHERTY, L. A. AND W. E. HANNA. 1972. Landscape evolution of a glaciated upland valley in south central New York. M.S. Thesis, Cornell University, Ithaca, NY.

DELLA-BIANCA, L. 1983. Sixty years of stand development in a southern Appalachian cove-hardwood stand. For. Ecol. Manage. 5: 229–241.

DIEBOLD, C. H. 1938. Interrelationships between water tables, soil characteristics, silvics, reforestation, and flood control in south central New York. Ecology 19: 463–479.

HARCOMBE, P. A. AND P. M. DIXON. 1984. Air pollution-tree growth relationships in New York State: Assessment using forest survey data. Ecosystem Research Center, Cornell University, Ithaca, NY.

HELD, M. E. AND J. E. WINSTEAD. 1975. Basal area and climax status in mesic forest systems. Ann. Bot. 39: 1147–1148.

HENRY, J. D. AND J. M. A. SWAN. 1974. Reconstructing forest history from live and dead plant material—An approach to the study of forest succession in southwest New Hampshire. Ecology 55: 772–783.

HIBBS, D. E. 1983. Forty years of forest succession in central New England. Ecology, 64: 1394–1401.

HILL, M. O. 1979. TWINSPAN: A fortran program for arranging multivariate data in an ordered 2-way table by classification of the individuals and attributes. Cornell Ecology Programs, Cornell University, Ithaca, NY.

HOUGH, A. F. AND R. F. TAYLOR. 1946. Response of Allegheny hardwoods to partial cutting. J. For. 44: 30–38.

HOWARD, R. F. 1936. A stock inventory of the Arnot Forest. M.F. Thesis, Cornell University, Ithaca, NY.

KELTY, M. J. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage. 28: 237–258.

KRASNY, M. E. AND M. C. WHITMORE. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. Can. J. For. Res. 22: 139–143.

LEAK, W. B. 1987. Fifty years of compositional change in deciduous and coniferous forest types in New Hampshire. Can. J. For. Res. 17: 388–393.

——— AND D. S. SOLOMON. 1977. Influence of density and stand structure on growth of northern hardwoods in New England. USDA For. Ser. Sta. Pap. NE-362.

——— AND R. J. WILSON. 1958. Regeneration after cutting of old-growth northern hardwoods in New Hampshire. UDSA N.E. For. Exp. Sta. Pap. No. 103.

MARKS, P. L. AND S. GARDESCU. 1992. Vegetation of the central Finger Lakes Region of New York in the 1790s. Bull. No. 484, New York State Museum, Biological Survey, Albany, NY. 35 p.

MARQUIS, D. A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. U.S.D.A. Forest Service, Northeastern Forest Experiment Station, Research Paper NE-475.

ODELL, A. L., J. P. LASSOIE AND R. R. MORROW. 1980. A history of Cornell University's Arnot Forest. Nat. Res. Research and Extension Series No. 14. Dept. of Natural Resources, Cornell University, Ithaca, NY.

OLIVER, C. D. 1978. The development of northern red oak in mixed stands in central New England. Yale University: School of Forestry and Environmental Studies. Bull. No. 91. 63 p.

——— AND STEPHENS, E. P. 1977. Reconstruction of a mixed species forest in central New England. Ecology 58: 562–572.

PARKER, G. R., D. J. LEOPOLD AND J. K. EICHENBERGER. 1985. Tree dynamics in an old-growth, deciduous forest. For. Ecol. Manage. 11: 31–57.

RUNKLE, J. R. 1990. Eight years change in an old *Tsuga canadensis* woods affected by beech bark disease. Bull. Torrey Bot. Club 117: 409–419.

SCHLESINGER, R. C. 1989. Dynamics of the sugar maple component of a white oak-yellow poplar community, pp. 262–266. *In* USDA For. Serv. Gen. Tech. Rep. NC-132, North Central For. Exp. Sta., St. Paul, MN.

STEARNS, F. S. 1949. Ninety years of change in a northern hardwood forest in Wisconsin. Ecology 30: 350–358.

STEPHENS, G. R. AND J. S. WARD. 1992. Sixty years of natural change in unmanaged mixed hardwood forests. Bull. 902, Conn. Agri. Exp. Sta., New Haven, CT. 63 p.

STOUT, S. L. AND R. D. NYLAND. 1986. The role of species composition in relative density measurement in Allegheny hardwoods. Can. J. For. Res. 16: 564–571.

THOMPSON, J. E. 1966. Geography of New York State. Syracuse University Press, Syracuse, NY.

VAN ORDER, R. A. 1937. An analysis of the growing stock in permanent sample plots at the Arnot Forest. M.F. Thesis, Cornell University, Ithaca, NY. 30 p.

VOLK, T. A. AND T. J. FAHEY. 1994. Fifty-three years of change in an upland forest in south-central New York: Growth, mortality and recruitment. Bull. Torrey Bot. Club 121: 140–147.

WHITNEY, G. G. 1986. Relation of Michigan's presettlement pine forest to substrate and disturbance history. Ecology 67: 1548–1559.

WILSON, R. W. 1953. How second growth northern hardwoods develop after thinning. USDA For. Ser. N.E. Exp. Sta. Pap. No. 62.

WILM, H. G. 1932. The relation of successional development to the silviculture of forest burn communities in southern New York. Ph.D. Thesis, Cornell University, Ithaca, NY. 74 p.