Bulletin of the Torrey Botanical Club 116(1), 1989, pp. 52–64

TORREYA

Forty-eight years of canopy change in a hardwood-hemlock forest in New York City[1]

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ABSTRACT

RUDNICKY, J. L. AND M. J. MCDONNELL (Institute of Ecosystem Studies, The New York Botanical Garden, The Mary Flagler Cary Arboretum, Box AB, Millbrook, NY 12545). Forty-eight years of canopy change in a hardwood-hemlock forest in New York City. Bull. Torrey Bot. Club 116: 52–64. 1989.—In the mid-1930's, all trees (≥15 cm dbh) in a 16-ha forest on the grounds of The New York Botanical Garden, Bronx, New York, were identified, measured and mapped. In 1985 the forest was resampled and the change in canopy structure and composition determined. Clustering and ordination techniques indicate that approximately 70% of the forest in the 1930's was composed of two vegetation types: a Hemlock Type and an Oak Type. In 1985 these two cover types comprised about one-third of the forest. Although *Tsuga canadensis* (L.) Carr. and *Quercus borealis* Michx. are still the most important species in the forest, a Maple/Birch/Cherry Type covers the greatest area. Several lines of evidence suggest that hurricanes, arson, human trampling and vandalism have contributed to these changes in canopy composition.

Key words: *Tsuga canadensis, Quercus, Prunus serotina,* urban natural areas, forest change, New York City.

Remnant patches of natural forests within urban areas provide excellent opportunities to examine the effect of urbanization on plant and animal communities (Numata 1977). Fortunately, in some highly urbanized areas, even New York City, patches of the original forest have remained relatively intact within city parks. The structure and composition of such forests has been studied (Bagnall 1979; Hoehne 1981; Dorney *et al.* 1984; Cwikowa *et al.* 1984; Airola and Buchholz 1984; Kunick 1987), but there have been only a few attempts to study long-term vegetation dynamics of natural areas in urban environments.

Using colonial surveyors' records, Greller (1972) determined that the present composition of remnant and regenerated forests in Queens County, New York are similar to the forests originally encountered (except for *Castanea dentata* (Marsh.) Borkh., eliminated by chestnut blight). Airola and Buchholz (1982) compared 1949 and 1980 vegetation data for the Greenbrook Sanctuary, Hoboken, New Jersey and found that the major plant communities (oak, hemlock-hardwood and swamp-hardwood) were spatially and compositionally similar in both years, but the 1980 canopy was more homogeneous in species composition than in 1949. The authors concluded that the forest was recovering from an earlier disturbance and becoming more uniform. Stalter (1981) surveyed Alley Pond Park, Queens County, New York and, using Works Project Administration (WPA) maps of tree stems in the 1930's, contrasted the vegetation composition over nearly 40 years. Although *Quercus* spp. dominated the overstory during the entire time span, there were few *Quercus* spp. seedlings and saplings in the current forest; *Prunus serotina* Ehrh. was the most abundantly regenerating species. Loeb (1982) compared the WPA maps made for Seton Falls Park, Bronx, New York with

[1] Contribution to the program of the Institute of Ecosystem Studies, The New York Botanical Garden. This project was supported by a grant from the DeWitt Wallace-Reader's Digest Fund.

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[3] We would like to thank William Bunch for his help in recording data from the WPA maps and A. Wayne Cahilly, Matthew Hayes, William Nieder, and Elissa Wolfson for their assistance in field sampling. We are grateful to M. Kelty, S. T. A. Pickett, R. Pouyat, E. Russell, and two anonymous reviewers for valuable comments and suggestions on the manuscript.

Received for publication April 9, 1988 and in revised form October 12, 1988.

two recent surveys (1979, 1981) of the vegetation and found that *P. serotina* had gained in dominance over that time and that total tree density had increased between 1936 and 1979.

These urban studies have documented vegetation change over time, but have not elaborated on the patterns of development, as has been done in rural forests. In the Harvard Forest (central Massachusetts), large canopy openings created by hurricanes have led to a change in age class distribution and allowed *Quercus borealis* to assume a canopy position (Oliver and Stephens 1977). The predominant canopy change over time following the creation of large openings has been the replacement of the faster growing shade tolerant species that formed the original canopy with shade intolerant species (Kelty 1986). On the other hand, smaller openings prompted growth of shade tolerant species already established in the understory (Hibbs 1982, 1983). Differences in height growth rates determined which species would grow into the gap. The size of the gap is important since trees surrounding the opening grew laterally to fill in the hole. The composition of Harvard Forest stands is shifting to more shade tolerant species such as hemlock (*Tsuga canadensis* (L.) Carr.). The development of two forests in northwestern Pennsylvania also exhibit change in species composition with the trend favoring more shade tolerant species; however, over-grazing by deer has created an open understory and a gap in the diameter size class distribution (Hough 1965; Whitney 1984). Grazing removed the smaller diameter hemlock and apparently stimulated the regeneration of shade intolerant species by allowing more light to reach the forest floor. However, the change in composition to a shade tolerant overstory and the reduction of shade intolerant species was predicted in one forest (Whitney 1984).

The purpose of the present study was to document 48 years of change in the tree stratum of one of the last remnants of the original forest once covering New York City, The New York Botanical Garden (NYBG) Forest. Due to the long-term ownership of the property by the Lorillard family (1792–1880) and its subsequent purchase in the 1880's by New York City for the development of Bronx Park, the forest was never cleared or altered by the growth of the surrounding city (Britton 1906). During the 1930's the WPA mapped the location of tree stems in the forest. The specific objectives of our study were (1) to determine the composition and structure of the tree stratum of the forest in the 1930's using the WPA maps made for the forest, (2) to determine the present-day composition and structure of the tree stratum, and (3) compare the change in the canopy that has occurred over 48 years with changes found in rural forests of similar species composition.

Study Site. The NYBG Forest (40°50′N, 73°50′W) is a 16-ha forest located on the grounds of The New York Botanical Garden, Bronx (Fig. 1). The predominant canopy tree species listed in order of importance are *Tsuga canadensis, Quercus borealis* Michx., *Acer rubrum* L., *Fagus grandifolia* Ehrh., *Liquidambar styraciflua* L. and *P. serotina.* Maps made during the late 1800's show the eastern half of the forest as a hemlock forest and the western half as hardwoods. Records indicate that from 1895 to the present no live trees have been removed from the forest by NYBG staff. Some dead trees have been removed for public safety and other trees have been killed by vandalism (e.g., trees cut down, snapped off or girdled). Unfortunately, no records about specific removals or vandalism-related mortality exist. Britton (1906) in a lecture before the Bronx Society of Arts and Science, requests that the practice of raking the leaves in the forest be stopped. How long the forest had been raked or its effect on the growth of seedlings will never be known. Because Britton was then Director of The New York Botanical Garden, it is reasonable to assume that this practice was discontinued in the early 1900's. There are no additional references to this practice following this date.

The climate of the area is characterized by warm, humid summers and cold winters. Climatological data were obtained from the Central Park Observatory, approximately 16 km (10 miles) south of the forest. The average annual air temperature is 12.5°C with a January average of 0.6°C and a July average of 25°C (Pack 1974). Average annual precipitation is 107.6 cm, evenly distributed throughout the year (Pack 1974).

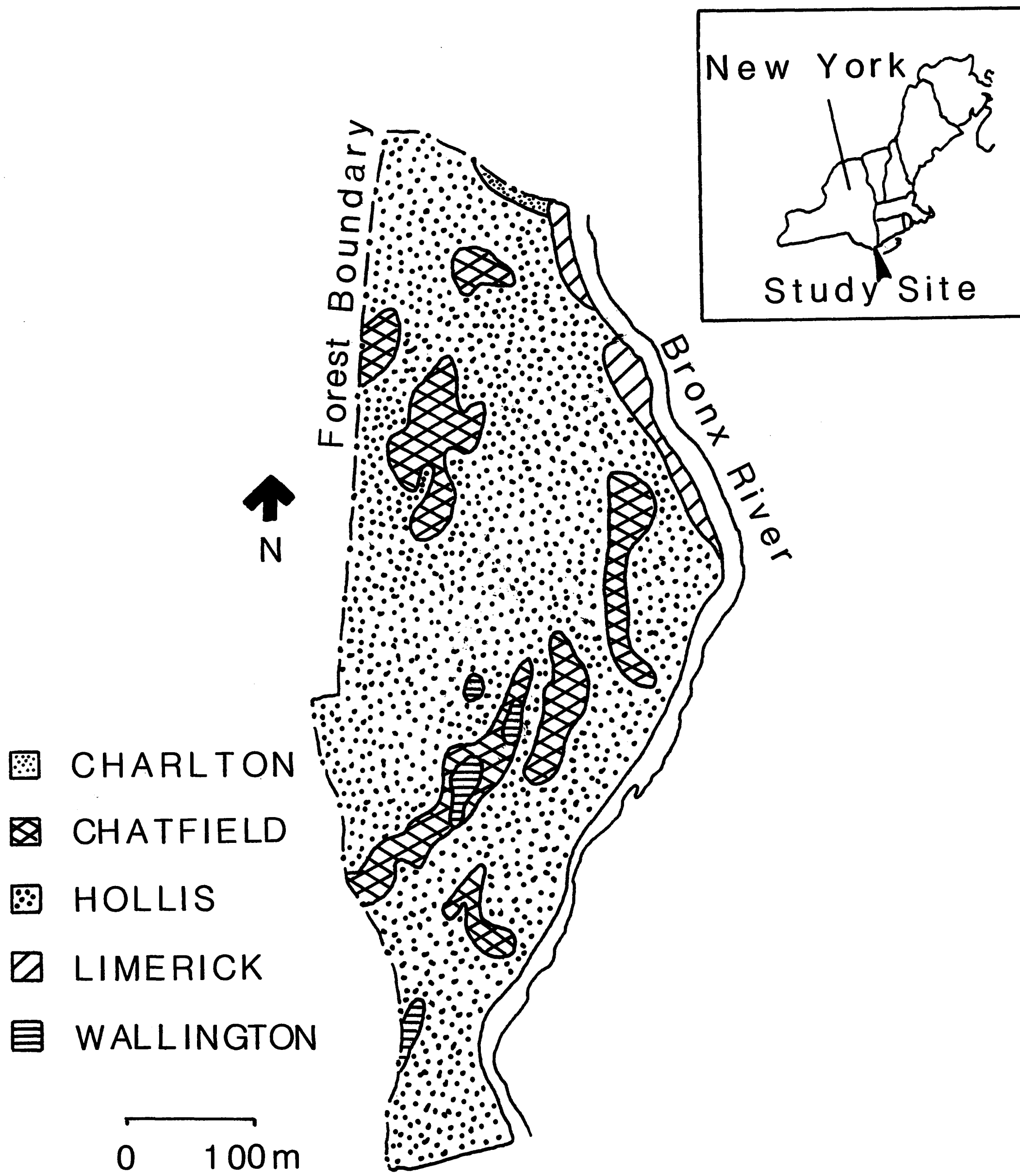

Fig. 1. Map of The New York Botanical Garden Forest showing the forest's boundary and soil series. Inset is a map of the eastern United States showing the location of the study site.

The Bronx River borders the eastern edge of the forest. A few small ephemeral streams and old drainage ditches are also present. Trails and rock outcrops are numerous. Bedrock is composed of Fordham gneiss and Manhattan schist (Schuberth 1968). The soils belong to the Hollis, Chatfield, Charlton, Limerick and Wallington series (Tornes 1974) (Fig. 1). The soils are mostly Entic Lithic Haplorthods (Hollis) and Entic Haplorthods (Charlton and Chatfield), with a few small pockets of Aeric Fragiaquepts (Wallington) and a narrow zone of Typic Fluvaquents (Limerick) along the river. Additional soil information is given in White and McDonnell (1988).

Methods. HISTORIC RECORDS. During the 1930's the WPA mapped the location, identity to genus (some to species), and diameter at breast height (dbh) to the nearest inch (2.54 cm), of all stems in New York City parks. A set of these maps for the NYBG was obtained and analyzed to determine the structure and composition of the canopy at the time the maps were drawn (circa 1937). The validity of this study depends upon the reliability of the WPA maps, which has been questioned by Loeb (1982). He suggested errors were made in identification and dbh measurements on maps of other New York City parks. In a preliminary survey of the forest, we compared the stems present with those mapped in 1937 and found few misidentifications. Some individual *Betula* spp. and *Ulmus* spp. were misidentified, but the number was small (<1% of all trees) and did not affect the accuracy of the maps in determining changes in canopy composition. Thus, we are confident in using the maps made for the NYBG Forest to identify overstory composition using stems ≥15 cm dbh. The usefulness of the maps would have been better had the *Quercus* stems been identified to the species level. Due to logistical problems, including the fact that younger trees have grown up during the last 48 years in close proximity to the original stems, it was impossible to relocate exactly every tree mapped in the 1930's to identify it to species. In addition, because of the high mortality rates (>60%) of the larger trees found with the preliminary survey, it would still be impossible to identify to species those trees that died over the last 48 years. Thus, to obtain the most accurate description of the forest in the 1930's, species composition data were taken directly from the maps. On the maps, the NYBG Forest was divided into 447 plots, each 400 m^2 in area. Each plot was subdivided into four 100-m^2 quadrants and the identity and dbh of all stems in each quadrant were recorded. Not all the stems with a dbh <15 cm were mapped by the WPA workers (McQuigan personal communication), thus, only stems ≥15 cm dbh were used in this study. Importance values (IV) based upon the sum of the relative values of basal area, density and frequency (using the number of quadrants within a plot that a species/genus occurred on) were computed for each plot, and for each species/genus for the whole forest.

An indirect ordination of the plots was made using detrended correspondence analysis (DCA) (Hill 1979; Hill and Gauch 1980) on the IV of species that occurred on ≥3% of the 447 plots (a total of 20 species). Additional information readily obtained from the maps such as aspect, slope, maximum and minimum elevation, and distance from the river was recorded for each plot. These data and the species IV's for each plot were compared to plot DCA axes scores using Pearson's product-moment correlation analysis (SAS Institute Inc. 1982). The plots were then clustered with a SAS algorithm (SAS Institute Inc. 1982), using the IV of only those species used in the DCA. The clusters were used to delineate vegetation types. IV's for all species were recalculated by vegetation type. (The frequency used in the calculations was now the number of plots within a cluster.) Nomenclature follows Gleason and Cronquist (1963).

VEGETATION SURVEY IN 1985. In 1985 the forest was surveyed as part of a larger more intensive study to document its current vegetation structure and composition (McDonnell and Rudnicky in preparation). Thus, due to the broader objectives of this study, the exact sampling methods used in the 1930's sample could not be matched. The sampling technique described below provides data on the structure and composition of the forest canopy as it appeared in 1985. Although these data do not allow for an account of the dynamics of each tree mapped in 1930, vegetation types can be identified using clustering and ordination techniques, and the spatial extent and composition of these vegetation types can be compared to the 1930's data.

In 1985, 10-m-wide belt transects oriented east-west, with transects spaced 30 m apart were established. Using a stratified random design, 243 10 × 10 m plots, representing 15% of the forest, were sampled along the transects. The identity and dbh of all stems ≥15 cm were recorded. Aspect, slope, minimum and maximum elevation and rock and trail cover were also measured.

Table 1. Diameter at breast height, density, basal area, frequency and importance values for trees ≥15 cm dbh in the NYBG Forest in 1937 and 1985. The 1937 calculations are based on 447 plots (100% sample of forest). The 1985 calculations are based on 227 plots (15% of the forest).

Genera	Mean dbh (cm)	Density (no./ha)	Basal area (m^2/ha)	Frequency (%)	Importance value
1937 Survey					
Tsuga	38	52	6.7	62	76
Quercus	47	34	7.2	63	68
Betula	33	28	2.7	55	43
Cornus	19	6	0.2	46	17
Carya	30	9	0.7	23	15
Liriodendron	54	6	1.5	15	14
Liquidambar	45	6	1.1	13	12
Fagus	38	6	0.8	15	10
21 Others	35	23	1.9		45
Total	38	170	22.8		300
1985 Survey					
Tsuga canadensis	33	47	4.6	29	47
Quercus borealis	38	31	4.5	27	40
Acer rubrum	24	27	1.5	21	24
Betula lenta	30	19	1.6	23	22
Fagus grandifolia	30	19	1.6	17	20
Liquidambar styraciflua	34	16	1.7	16	19
Prunus serotina	24	14	0.6	30	18
Liriodendron tulipifera	60	9	2.7	8	17
Fraxinus americana	25	16	0.9	19	16
28 Others	24	57	4.9		77
Total	32	255	24.6		300

For each plot a species IV based upon the sum of relative basal area and relative density were computed for species that occurred on ≥3% of the plots (a total of 20 species). Because the plots were 10 × 10 m it was not appropriate to calculate the frequency of canopy trees on a plot basis. To determine the status of each species of tree, IV's were also calculated for the forest as a whole, with a relative value of frequency (the number of plots a species occurred in throughout the forest) added to the calculations. The analyses conducted on the 1985 data were the same as those used on the 1937 data.

Results. 1930'S CANOPY COMPOSITION AND STRUCTURE. In the mid-1930's, the canopy of the NYBG Forest was dominated by *Tsuga canadensis, Quercus* spp. and *Betula lenta* L. (Table 1). Total density for all species with a dbh ≥15 cm was 170 stems/ha and total basal area was 22.8 m^2/ha. The diameter size class distribution of all species reveals a distribution with the highest density of stems falling into the 15 to 45 cm diameter classes (Fig. 2). The dominant species also have diameter distributions skewed toward the smaller classes (Fig. 2). The first two axes from the DCA represent 59% of the summed eigen scores for axes 1–4 and were used in the correlation analyses. The axes scores for the 1937 plots correlated weakly with the environmental data (best correlation was 0.26, $P = 0.0001$, between axis 1 and plot distance from the Bronx River). Stronger correlations were obtained with the species IV calculated for each plot. *T. canadensis* IV had the best correlation (−0.81, $P = 0.0006$) with axis 1.

The cluster analysis grouped the 1937 plots into ten clusters. Four of the clusters each had less than 1% of the plots and represented unusual groupings. These were eliminated from further analyses, leaving six groups or vegetation types to describe the overstory in 1937 (Table 2). Over two-thirds of the 1937 plots were grouped in the Hemlock and Oak Types (Table 3). The Hemlock Type plots occurred mostly in the eastern half of the forest, consistent with an early description of the forest's composition (Britton 1906). The Tulip Poplar/Birch/Elm Type and the Birch Type were the next most

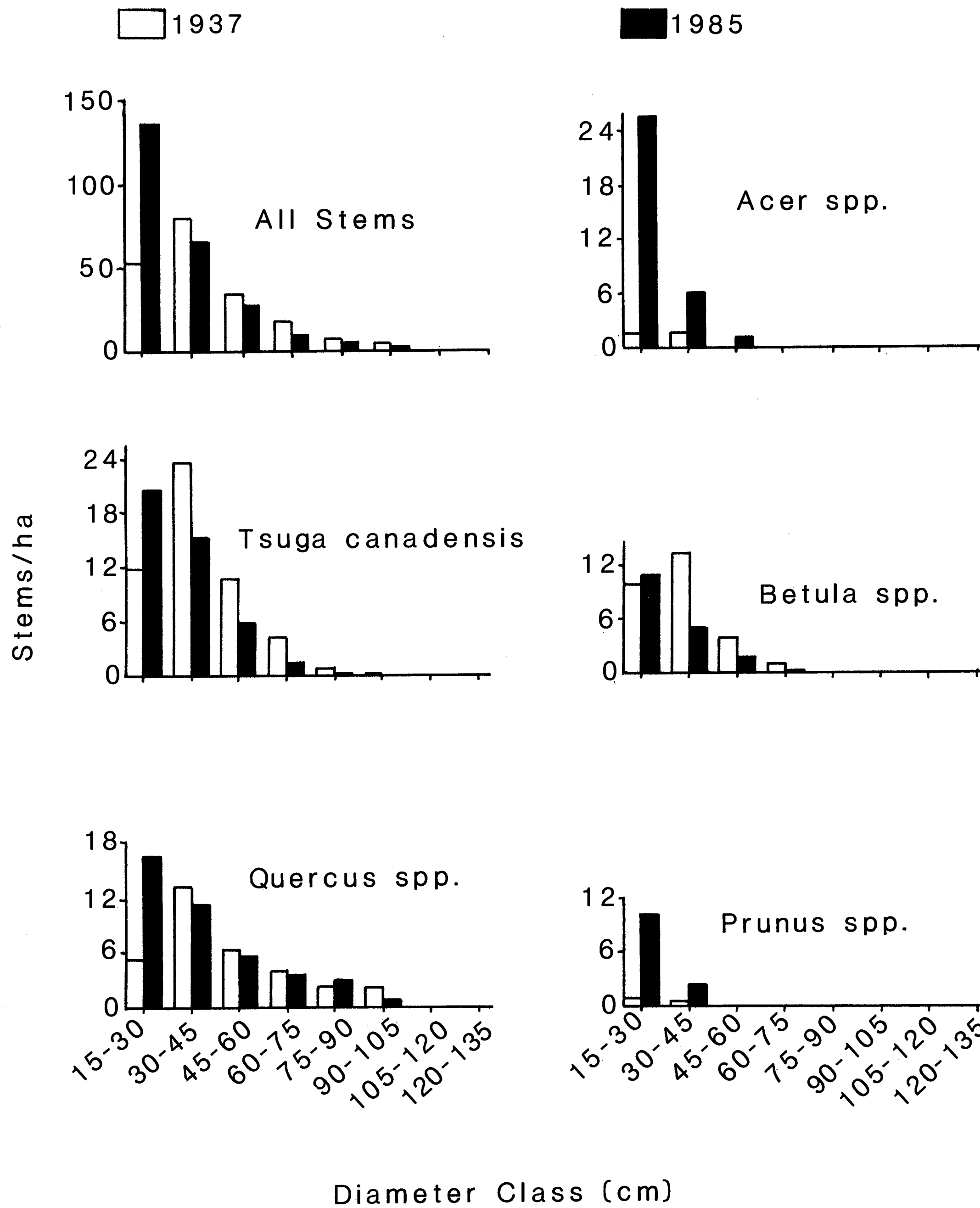

Fig. 2. Size class distribution of trees in The New York Botanical Garden Forest for 1937 and 1985.

widespread in the forest. A Sweet Gum Type and a Beech Type occurred in small areas in the southern half of the forest. These areas of the forest have poorly drained soils which have a hard pan within a meter of the surface (Tornes 1974). The Beech Type had the lowest density whereas the Birch Type had the highest. The Beech Type also had the lowest total basal area and the Hemlock Type had the highest.

1985 CANOPY COMPOSITION AND STRUCTURE. In 1985 the NYBG Forest canopy was still dominated by *Tsuga can-*

Table 2. The five most important species within each of the 1937 and 1985 cluster types.

Type name	Species (importance value)[a]
1937 Survey	
Hemlock	TSCA (150), QUSP (41), BESP (40), COSP (11), FAGR (9)
Oak	QUSP (138), TSCA (36), BESP (29), COSP (19), CASP (19)
Tulip Poplar/Birch/Elm	LITU (43), BESP (38), ULSP (35), TSCA (27), QUSP (26)
Birch	BESP (119), QUSP (35), TSCA (34), CASP (26), LITU (18)
Sweet Gum	LIST (132), QUSP (36), BESP (30), TSCA (27), COSP (25)
Beech	FAGR (146), QUSP (34), LIST (27), CASP (24), CACA (22)
1985 Survey	
Maple/Birch/Cherry	ACRU (55), BELE (47), PRSE (35), QUVE (23), TSCA (18)
Red Oak	QUBO (191), TSCA (17), LIST (15), PHAM (12), BELE (9)
Hemlock	TSCA (192), BELE (25), ACRU (19), PHAM (9), PRSE (8)
Beech	FAGR (196), ACRU (20), BELE (14), QUBO (13), PHAM (11)
Sweet Gum	LIST (166), FRAM (24), PRSE (20), ACRU (18), FAGR (17)
White Oak	QUAL (144), QUVE (30), PRSE (20), ACSA (13), PHAM (12)
Tulip Poplar	LITU (144), TSCA (19), FRAM (18), PRSE (17), ACRU (16)
White Ash	FRAM (136), TSCA (41), BELE (16), PRSE (16), ASCA (12)

[a] Species code: ACRU = *Acer rubrum*; ACSA = *Acer saccharum*; BELE = *Betula lenta*; BESP = *Betula* spp.; CACA = *Carpinus caroliniana*; CASP = *Carya* spp.; COSP = *Cornus* spp.; FAGR = *Fagus grandifolia*; FRAM = *Fraxinus americana*; LIST = *Liquidambar styraciflua*; LITU = *Liriodendron tulipifera*; PHAM = *Phellodendron amurense*; PRSE = *Prunus serotina*; QUAL = *Quercus alba*; QUBO = *Quercus borealis*; QUSP = *Quercus* spp.; QUVE = *Quercus velutina*; TSCA = *Tsuga canadensis*; ULSP = *Ulmus* spp. Maximum importance value is 300, only stems ≥15 cm dbh used in calculations.

adensis and *Quercus* spp., but their size and density were lower than in the 1930's (Table 1). Unlike the 1930's forest which had a small number of clearly dominant species (Table 1), in 1985 there was a relatively large group of additional species which were only slightly less important than the dominants. These species were *A. rubrum, B. lenta, F. grandifolia, L. styraciflua, P. serotina, Liriodendron tulipifera* L., and *Fraxinus americana* L. All species combined (dbh ≥15 cm) had a density of 255 stems/ha and a basal area of 24.6 m^2/ha. The diameter size class distribution has a reverse J-curve with the highest density of stems falling in the 15- to 45-cm size classes (Fig. 2). The large increase of stems in the 15- to 30-cm size class from 1937 to 1985 for all stems and dominant species (Fig. 2) is notable.

The first two axes of the DCA analysis represented 60% of the cumulative eigen scores for axes 1–4 and were used in the correlation analyses. The DCA axes scores for the 1985 plots also had weak correlations with the environmental data (best correlation was 0.33, $P = 0.0001$, between axis 1 and maximum plot elevation). Analysis with the species IV's for each plot showed axis 1 to be most highly correlated with *F. grandifolia* (-0.62, $P = 0.0001$) and axis 2 with *P. serotina* (-0.58, $P = 0.0001$).

The 1985 plots were grouped into nine clusters, with one cluster being composed of only one plot, leaving eight clusters to describe the present overstory (Table 2). The most widespread type is a Maple/Birch/Cherry Type (Table 3). Hemlock and Red Oak Types are the next most widespread. Beech and Sweet Gum Types are still present in the southern half of the forest. White Oak Type, a Tulip Poplar Type and a White Ash Type were limited in extent. The White Oak Type had the lowest density and the Hemlock Type had the highest. The Maple/Birch/Cherry Type had the lowest basal area and the Tulip Poplar Type had the highest.

Discussion. The composition of the canopy trees in the NYBG Forest has undergone subtle, yet important change. The 1937 forest can be characterized as an old-growth hemlock-oak forest, consistent with earlier observations (Britton 1906). Tree ring analysis of *T. canadensis* and *Quercus* spp. stems revealed some trees to be over 250 years old (Shepard and Cook personal communication) and the diameter distributions show that the forest had very large stems in the 1930's. Because the Bronx was not heavily urbanized before 1870 (New York City Planning Commission 1969) and many of the trees present in 1937 became established before this time, we believe that these data support the contentions that this forest is one of the last remnants of the original forest which once covered the New York City area (Britton 1906; Moore 1923). Thus, any changes in the canopy composition would not be an artifact from previous development of the land.

Tsuga canadensis and *Quercus* spp. were the most important species in the forest in both 1937 and 1985 (Table 1). This is not simply a result of the survival of trees present in 1937, for the data clearly indicate that the number of stems of *T. canadensis* and *Quercus* spp. in the 15- to 30-cm size class has increased over the past 48 years (Fig. 2). The NYBG Archives, first hand recollections (T. H. Everett personal communication), and tree core analysis indicate that the persistence of *T. canadensis* in the canopy is the result, at least in part, of plantings made from the 1920's through the early 1940's by Garden personnel (Britton and Moore 1927). With the apparent lack of *T. canadensis* reproduction, the decision was made to plant young trees to maintain the forest in its former state (Britton 1926). We have found few naturally regenerated *T. canadensis* under 30 cm dbh within the forest. There is no information to suggest that *Quercus* spp. were planted in the forest, thus its continued importance is the result of the survival of large trees and the successful recruitment of trees <15 cm dbh into the canopy. The increased importance of *A. rubrum* and *P. serotina* is another notable change (Table 1). Both of these species were nearly absent from the 1930 survey and now occur predominantly in the 15- to 30-cm size class. A more subtle change is the virtual elimination of *Castanea dentata* and *Cornus florida* L. from the forest. Both species were present after the turn of the century (Britton 1906). *Castanea dentata* was decimated by the chestnut blight and only a few stems were present in 1937 and 1985. The abundance of *C. florida* in the understory of the NYBG Forest was notable (New York City Department of Parks 1902) and it occurred on nearly half of the plots in 1937 (Table 1). By 1985 most of the stems had succumbed to the dogwood decline.

For all species combined, the forest had a higher stem density in 1985, however, in 1937 the trees were generally larger (Fig. 2).

Table 3. Total density and basal area (stems ≥15 cm dbh) for the 1937 and 1985 cluster types and the percentage of the plots for each year that were grouped into the type.

Year	Type name	Density (no./ha)	Basal area (m^2/ha)	Percent of sample
1937	Hemlock	181	25.1	36
	Oak	158	22.9	33
	Tulip Poplar/ Birch/Elm	192	23.2	14
	Birch	201	19.8	9
	Sweet Gum	138	24.1	3
	Beech	107	13.9	2
1985	Maple/Birch/ Cherry	246	16.3	32
	Red Oak	231	28.8	17
	Hemlock	303	27.2	17
	Beech	240	18.3	9
	Sweet Gum	263	26.6	7
	White Oak	215	33.6	6
	Tulip Poplar	279	49.9	6
	White Ash	273	20.3	5

This pattern also characterizes *T. canadensis, Quercus* spp. and *Betula* spp. (Fig. 2). The density of trees ≥15 cm dbh for the NYBG Forest is considerably lower than the densities reported for rural forests of similar species composition in southern New England.

Kelty (1984) presented data on hemlock-hardwood and hardwood stands (primarily *Quercus* spp., *Acer* spp. and *Betula* spp.) in the Harvard Forest, Massachusetts, and Great Mountain Forest, Connecticut. The latter stand was on the same soil type as the NYBG Forest. The stands in the Harvard Forest (HF) were 44 years old and those in the Great Mountain Forest (GMF) were 87 years old. Density for stems >15 cm dbh in the hemlock-hardwood stands were 1350 (HF) and 950 (GMF) stems/ha and in the hardwood stands 760 (HF) and 484 (GMF) stems/ha. Total basal areas were 44 (HF) and 48 (GMF) m^2/ha in the hemlock-hardwoods and 27 (HF) and 34 (GMF) m^2/ha in the hardwoods. The densities of these stands are higher than the NYBG Forest in the 1930's and 1985. Kelty's stands were younger and even-aged so the higher densities are not unusual. However, such a large difference illustrates that there are fewer stems in the NYBG Forest than would be expected in natural forests. Basal areas are closer to Kelty's hardwood stands, but are generally lower.

The increase in the number of stems in the 15- to 30-cm class and decrease in the larger size classes over the last 48 years indicates that the canopy structure of the NYBG Forest has changed and now has a greater number of smaller trees. Tree ring analysis indicating periods of release after major recent hurricanes, especially 1938, 1944 and 1950, and a description of the storm damage on the NYBG grounds following the 1944 hurricane (Graves 1944) indicate that hurricanes have blown over trees in the forest. The pit-and-mound topography in the forest suggests blow-downs in the past. Some of the trees present in 1937 have filled openings created by hurricanes and grown into the canopy. However, mortality has exceeded replacement in the larger size classes and this has moved the diameter distribution toward the smaller size classes. This combination of the removal of the larger trees and low stem density resulted in the NYBG Forest having a smaller basal area than Kelty's stands.

Hurricanes are recognized to influence forests throughout the northeast by forming gaps in the canopy (Oliver and Stephens 1977; Bormann and Likens 1979; Hibbs 1983; Foster 1988). However, changes in canopy structure and composition of the NYBG Forest following hurricanes have been unusual compared to other northeastern forests. In the Harvard Forest, large multi-tree gaps have helped the regeneration of *Quercus borealis, Acer rubrum* and *Betula lenta* (Oliver and Stephens 1977; Hibbs 1982, 1983). In the NYBG Forest *Acer rubrum* and *B. lenta,* however, have increased without the formation of large gaps. Small single tree gaps in the Harvard Forest resulted in an increase in height growth of shade tolerant species such as *T. canadensis,* which was also found to regenerate up to 10 years after a disturbance (Hibbs 1983). Early reports mention *T. canadensis* reproduction in areas of the NYBG Forest where canopy openings existed (Lloyd 1900; Britton 1906; Robinson 1909). However, by 1985 naturally regenerated *T. canadensis* were virtually absent in the understory. The result of the increase on the shade intolerant species in the NYBG Forest is being expressed throughout the forest. The spatial extent of the Hemlock and Oak Types has been reduced by half and replaced by the early successional Maple/Birch/Cherry Type (Fig. 3). This conversion is in contrast to rural forests of similar species composition which are becoming dominated by more shade tolerant, late successional species (Oliver and Stephens 1977; Hibbs 1983; Whitney 1984; Parker *et al.* 1985; Kelty 1986).

As early as 1898, there was concern over the persistence of the forest (Lloyd 1900; Gager 1907). Because of its uniqueness and the possible problems caused by the urban surroundings, an extensive study was undertaken by the NYBG staff on the climate and soils of the NYBG Forest as compared to similar forests in New York and Connecticut (Moore *et al.* 1924; Gleason 1924). This study found relatively small differences in the measured parameters both within sites and among distant sites (Moore *et al.* 1924; Gleason 1924). Robinson (1909) found the *T. canadensis* in the forest produced viable seeds and noted the presence of seedlings, but they apparently did not survive long. We have also observed abundant first-year seedlings in the forest; however, all the seedlings we observed died within a year. The inability of *T. canadensis* to grow beyond the seedling stage may be related to the surrounding urban environment because *T. canadensis* is reproducing in other forests (Charney 1980; Airola and Buchholz 1982; Hemond *et al.* 1983; Hibbs 1983; Whitney 1984).

There are many possible reasons for the poor rate of survival of young trees in the NYBG Forest. In the past, dead trees were removed for public safety, which also removed potential seedbeds (i.e., rotten logs) for *T. canadensis* (Fowells 1965). Trampling of vegetation and arson are chronic problems that were noted early in the Garden's history (Britton 1906). Because *T. canadensis* grows slowly in the understory (Fowells 1965), it is especially susceptible to trampling. The shallow root system, thin bark and small needles of *T. canadensis* make it easily damaged by fires and it grows better in protected areas (Brown 1960; Hemond *et al.* 1983). During 1985 and 1986, there were at least 12 fires set in the NYBG Forest. The majority of the burns appear to

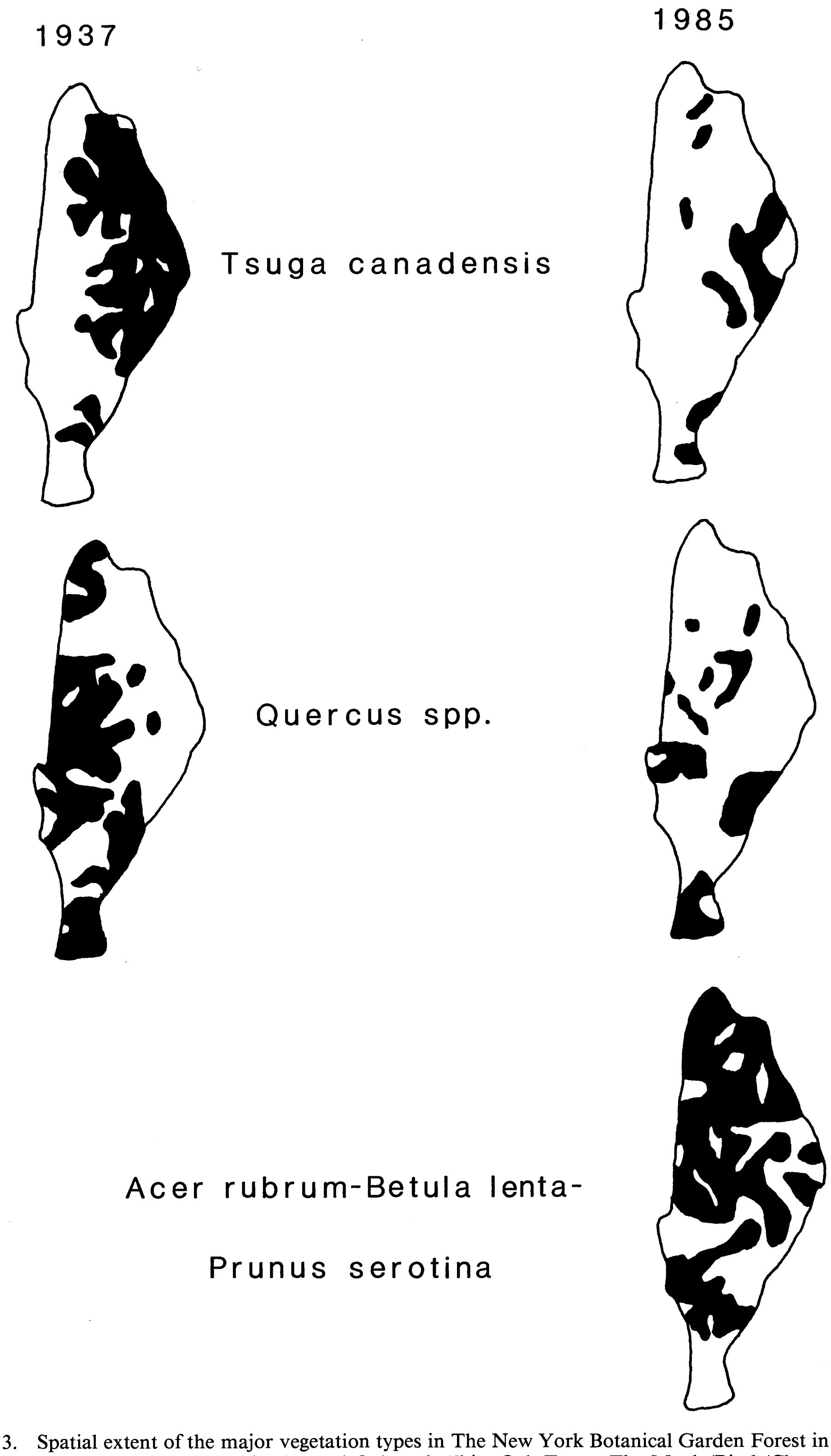

Fig. 3. Spatial extent of the major vegetation types in The New York Botanical Garden Forest in 1937 and 1985. The 1985 Oaks Type includes the Red Oak and White Oak Types. The Maple/Birch/Cherry Type did not exist in 1937.

be surface fires of limited extent and were not hot enough to remove the organic layer. However, fire-scarred trees and charcoal deposits are common throughout the forest.

The survival of seedlings and seeds in the NYBG Forest must be related to the dense small mammal population (e.g., 45–50 grey squirrels/ha vs. 6–10/ha in rural environments, Honkala and McAninch 1981). The density of grey squirrels (*Sciuris carolinensis*) were the same in 1985 (McAninch unpublished). Browsed stems are common throughout the forest. A lack of natural predators and an additional food source from visitors have allowed high numbers of rodents to exist in and around the forest.

Pollution may also be influencing tree growth and canopy development. White and McDonnell (1988) have found that the soils in the NYBG Forest have lower nitrification potentials than a rural *T. canadensis* forest 120 km to the north and speculated that this may be caused by exogenous factors retained in the soils. They also noted that the soils exhibited hydrophobic tendencies and had elevated concentrations (2 to 10 times higher than rural levels) of lead, nickel and copper.

The urbanization of the area surrounding the NYBG Forest has been accompanied with an increase in the frequency of disturbance in the understory and this appears to have favored the spread of *P. serotina* and other shade intolerant species. *Prunus serotina* is an opportunistic species well adapted to invading fragmented forests (Auclair and Cottam 1971) and has become established in other forests throughout New York City (Stalter 1981; Loeb 1982) as well as in Europe (Eijsackers and Oldenkamp 1976). It produces abundant seeds which are widely dispersed and can quickly colonize disturbed areas. Seedlings and saplings of *P. serotina* can also sprout readily. *A. rubrum* and *B. lenta* may also be numerous in the NYBG Forest due to their sprouting and colonization abilities. An important feature of the forest that may help in the establishment of all these shade intolerant species is the amount of edge and open areas created around rock outcrops in the forest. In 1985, nearly 20% of the forest floor was measured as a rock outcrop or trail. The majority of the trails were not present before 1900, which may, in part, explain the small number of *P. serotina* trees in the NYBG Forest in the 1930's. These features allow sunlight to penetrate to the ground and aid in the establishment of these species. Also, the reduction of *Castanea dentata* and *Cornus florida* stems within the forest would also increase the amount of light reaching the forest floor.

Conclusions. The NYBG Forest has undergone a change in its overstory composition which is related to the existence of a new disturbance regime. Natural disturbances (e.g., hurricanes) that affect all forests in the Northeast are also important in the development of the overstory of the NYBG Forest. However, urbanization appears to have increased the level of small scale disturbances such as trampling, arson and vandalism by humans. Site conditions that created a *T. canadensis* gradient present in the 1930's, have slowly degraded as disturbances in the understory have increased. The chronic urban stresses plus natural disturbances have shaped the overstory by apparently inhibiting the regeneration of *T. canadensis* and *Quercus* spp. and allowing the growth of opportunistic species which fill openings in the overstory. Tree ring analysis coupled with references in the literature indicate that hurricanes or wind storms have contributed to the loss of large overstory trees, but these storms appeared to remove only scattered trees, not large groups of trees. The ability of *P. serotina, A. rubrum,* and *B. lenta* to fill these small gaps is in contrast to natural areas where small gaps are filled by more shade tolerant species (Oliver and Stephens 1977; Hibbs 1982, 1983). In the NYBG Forest urban stresses have helped to allow more light to reach the forest floor. The open nature of the forest appears to favor the establishment and growth of early successional, shade intolerant species.

Literature Cited

AIROLA, T. M. AND K. BUCHHOLZ. 1982. Forest community relationships of the Greenbrook Sanctuary, New Jersey. Bull. Torrey Bot. Club 109: 205–218.

——— AND ———. 1984. Species structure and soil characteristics of five urban forest sites along the New Jersey palisades. Urban Ecol. 8: 149–164.

AUCLAIR, A. M. AND G. COTTAM. 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in southern Wisconsin oak forests. Ecol. Monogr. 41: 153–177.

BAGNALL, R. G. 1979. A study of human impact on an urban forest remnant: Redwood Bush, Tawa, near Wellington, New Zealand. New Zealand J. Bot. 17: 117–126.

BORMANN, F. H. AND G. E. LIKENS. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York. 253 p.

BRITTON, N. L. 1906. The hemlock grove on the banks of the Bronx River and what it signifies. Trans. Bronx Soc. Arts Sci. 1: 5–13.

———. 1926. An attempt to aid the natural propagation of hemlocks. J. New York Bot. Gard. 27: 6–9.

——— AND B. MOORE. 1927. Planting of young hemlocks in the hemlock grove. J. New York Bot. Gard. 28: 172–173.

BROWN, J. H. 1960. The role of fire in altering the species composition of forests in Rhode Island. Ecology 41: 310–316.

CHARNEY, J. D. 1980. Hemlock-hardwood community relationships in the Highlands of southeastern New York. Bull. Torrey Bot. Club 107: 249–257.

CWIKOWA, A., A. GRABOWSKI, A. J. LESINSKI AND S. MYCZKOWSKI. 1984. Flora and vegetation of the Niepolomice Forest, pp. 1–11. *In* W. Grodzinski, J. Weiner and P. F. Maycock [eds.], Forest ecosystems in industrial regions. Springer-Verlag, New York.

DORNEY, J. R., G. R. GUNTENSPERGEN, J. R. KEOUGH AND F. STEARNS. 1984. Composition and structure of an urban woody plant community. Urban Ecol. 8: 69–90.

EIJSACKERS, H. AND L. OLDENKAMP. 1976. Amerikaanse vogelkers, aanvaarding of beperking? Landbouwkunding Tijds. (1976) 88-12: 365–375.

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

FOWELLS, H. A. (editor). 1965. Silvics of forest trees of the United States. USDA Agric. Handb. No. 271, Washington, DC. 762 p.

GAGER, C. S. 1907. The absence of undergrowth in the hemlock forest. J. New York Bot. Gard. 8: 237–240.

GLEASON, H. A. 1924. Ecological investigation in the hemlock forest. J. New York Bot. Gard. 25: 313–316.

——— AND A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Co., New York.

GRAVES, A. H. 1944. Damage to trees in New York City in the Hurricane of Sept. 4, 1944. Torreya 44: 66–73.

GRELLER, A. M. 1972. Observations on the forests of northern Queens County, Long Island, from colonial times to the present. Bull. Torrey Bot. Club 99: 202–206.

HEMOND, H. F., W. A. NIERING AND R. H. GOODWIN. 1983. Two decades of change in the Connecticut Arboretum Natural Area. Bull. Torrey Bot. Club 110: 184–194.

HIBBS, D. E. 1982. Gap dynamics in a hemlock-hardwood forest. Canad. J. For. Res. 12: 522–527.

———. 1983. Forty years of forest succession in central New England. Ecology 64: 1394–1401.

HILL, M. O. 1979. DECORANA—A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, NY.

——— AND H. G. GAUCH. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47–58.

HOEHNE, L. A. 1981. The ground layer vegetation of forest islands in an urban-suburban matrix, pp. 41–54. *In* R. L. Burgess and D. M. Sharpe [eds.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

HONKALA, D. A. AND J. B. MCANINCH. 1981. The New York Botanical Garden Hemlock Forest Project, Part II. The New York Botanical Garden, Cary Arboretum, Dept. of Wildlife Resources, Millbrook, NY. Unpubl. report. 80 p.

HOUGH, A. F. 1965. A twenty-year record of understory vegetation change in a virgin Pennsylvania forest. Ecology 46: 370–373.

KELTY, M. J. 1984. The development and productivity of hemlock-hardwood forests in southern New England. Ph.D. Thesis, Yale University, New Haven, CT.

———. 1986. Development patterns in two hemlock-hardwood stands in southern New England. Canad. J. For. Res. 16: 885–891.

KUNICK, W. 1987. Woody vegetation in settlements. Landscape Planning 14: 57–78.

LLOYD, F. E. 1900. The seeds and seedlings of the hemlock, *Tsuga canadensis.* J. New York Bot. Gard. 1: 97–100.

LOEB, R. E. 1982. Reliability of the New York City Department of Parks and Recreation forest records. Bull. Torrey Bot. Club 109: 537–541.

MOORE, B., H. M. RICHARDS, H. A. GLEASON AND A. B. STOUT. 1924. Hemlock and its environment. Bull. New York Bot. Gard. 45: 325–350.

———. 1923. Investigation of the hemlock forest. J. New York Bot. Gard. 24: 163–165.

NEW YORK CITY DEPARTMENT OF PARKS. 1902. Report 1902. Pp. 103–113.

NEW YORK CITY PLANNING COMMISSION. 1969. Plan for New York City. 2. The Bronx. MIT Press, Cambridge, MA. 154 p.

NUMATA, M. 1977. The impact of urbanization on vegetation in Japan, pp. 161–171. *In* A. Miyawaki and R. Tuxen [eds.], Vegetation science and environmental protection. Maruzen, Tokyo.

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

PACK, A. B. 1972. The climate of New York, pp. 257–280. *In* Climates of the States. Eastern States plus Puerto Rico and the U.S. Virgin Islands, Vol. 1. Water Information Center, Port Washington, NY.

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

ROBINSON, W. 1909. Experiments on the effect of the soil of the hemlock grove of the New York Botanical Garden upon seedlings. J. New York Bot. Gard. 10: 81–87.

SAS INSTITUTE INC. 1982. SAS user's guide: Statistics, 1982 ed. SAS Institute Inc., Cary, NC. 584 p.

SCHUBERTH, C. J. 1968. The geology of New York City and environs. Natural History Press, New York.

STALTER, R. 1981. A thirty-nine year history of the arborescent vegetation of Alley Park, Queens County, New York. Bull. Torrey Bot. Club 108: 485–487.

TORNES, L. A. 1974. Soil survey of the hemlock forest at The New York Botanical Garden, Bronx, New York. USDA Soil Conservation Service. Unpubl. report. 23 p.

WHITE, C. S. AND M. J. MCDONNELL. 1988. Soil characteristics and nitrogen transformation processes in a mixed hardwood-hemlock forest in New York City. Biogeochemistry 5: 243–262.

WHITNEY, G. G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock-white pine-northern hardwoods stand. Ecology 65: 403–408.