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FORESTS OF THE CATSKILL MOUNTAINS, NEW YORK¹

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TABLE OF CONTENTS

ABSTRACT	143	Leading dominants	147
INTRODUCTION	143	Selected stands	149
GEOLOGY AND SOILS	143	Diversity	151
CLIMATE	144	Interspecific correlation	152
HISTORY AND VEGETATION	144	Ordination	152
METHODS	145	DISCUSSION	153
RESULTS	146	ACKNOWLEDGMENTS	159
Tree composition	146	LITERATURE CITED	159

ABSTRACT

The modern forest of the Catskill Mountain region, New York, particularly the area within the New York State Forest Preserve, was studied and compared with the presettlement forest as determined from surveyors' records. The most notable changes were a marked drop in the proportion of beech (*Fagus grandiflora*) and hemlock (*Tsuga canadensis*) and increases in sugar maple (*Acer saccharum*), red oak (*Quercus borealis*), and chestnut oak (*Quercus prinus*). Reproduction and size-class data suggest that in old-growth hemlock stands hemlock is replaced by hardwoods and is not a part of a homogeneous climax forest in spite of its prominence in the presettlement forest. Beech does not give evidence, in the dynamics of the modern forest, of returning to its presettlement dominance. Some pioneer stands are as rich in species and as diverse as are those usually thought of as climax. The comparison of presettlement and recent forests is related to recent discussion of climax concept.

INTRODUCTION

The Catskill Mountains of New York State, although celebrated in the stories of Washington Irving, the natural history writings of John Burroughs, and paintings of the Hudson River School, notably Thomas Cole, have never been the subject of intensive botanical or ecological investigation, and little has been published about the ecology of this region. Most of the forest vegetation has been disturbed since settlement, but much of the Catskill Mountains is still forested (ca. 80%), and extensive areas, approximately 235,000 acres (95,104 ha), are now included in the Catskill Forest Preserve of New York State. The Forest Preserve lands, by provision of the New York State constitution, are to remain undisturbed, which gives maximum assurance that the area will be free from future cutting or management. Four areas within the Catskill Forest Preserve have been proposed as wilderness areas (Stout 1961).

The Catskill Mountains are difficult to bound precisely, except on the north and east, and the area included in the present study is more restricted than the broadest interpretation of the extent of the Catskills. The area included, approximately 500 square miles (1,295 km²), parallels the steep east-facing escarpment from North Mountain south to the

Roundout Reservoir, west from there to the East Branch of the Delaware River, northeast along the East Branch to the Schoharie Reservoir, and southeast along the Blackhead Mountains to North Mountain. An arbitrary lower altitude was set at 1,000 ft (305 m). The majority of the sample areas are located in Ulster and Greene Counties, New York, in the region of the higher Catskill peaks which are more heavily forested than the peripheral areas which were, and still are, more heavily farmed and used as resort and recreation areas.

This study considers primarily the deciduous hardwood and hemlock forests of the Catskills. The spruce-fir forests were discussed earlier by McIntosh and Hurley (1964). Quantitative samples, secured from diverse sites with different histories of disturbance, are used to clarify present patterns of forest relations and succession and to provide a basis for future studies of vegetational change in the Catskills.

GEOLOGY AND SOILS

The Catskill Mountains were formed by the uplift of an ancient delta and stand at the northeast end of the Allegheny Plateau of which they are a part. The higher peaks rise 2,000 ft (610 m) above the surrounding plateau, a remnant of a peneplain at a level of 2,000 ft (Guyot 1880). The summits of the higher

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peaks, some of which exceed 4,000 ft (1,220 m), are capped with a hard conglomerate, which accounts for their superior elevation. The conglomerate overlies shales and sandstones which are more easily eroded. The strata lie nearly flat with a slight dip to the west and southwest. The mountaintops are mostly flat ridges, some of considerable extent, rather than abrupt peaks. To the north, northeast, and east the mountains drop off in a series of precipitous step-like ledges to the level of the Allegheny Plateau to the north and northeast and to the Hudson River Lowlands to the east. To the south and west they descend gradually to the level of the surrounding plateau (Mencher 1939).

The Catskill Mountains are well drained, there being only a few small, natural lakes in the region and little area of lowland swamp. They have been called erosion mountains since the area was uplifted as a high plateau and subsequently dissected by stream action. The mountains are coarsely dissected, and the valleys are few with only narrow strips of level ground bordering the streams. The upper slopes are steep, and the range is marked by several steep-sided gorges, locally called "cloves." The Catskills may be considered as three areas of high mountains and plateaus divided by narrow valleys. The Northern Catskills extend from the northeastern escarpment to the Schoharie Creek; the Central Catskills lie between the Schoharie Creek and the Esopus Creek; and the Southern Catskills, including the highest peak (Slide Mountain, 4,180 ft, 1,274 m), lie south of the Esopus Creek and merge with the Allegheny plateau.

The entire Catskill region was covered by Pleistocene glaciers (Rich 1935). The northern portion of the mountains was more heavily scoured by the ice than the central and southern areas, and it is likely that the later ice sheets did not extend to the southern portions of the range. Principal effects of the glaciers are seen in deep deposits of gravel in the valleys, and most of the Catskill area is covered with very stony glacial till.

The greater part of the region and most of the sample areas are on the slopes where the soil is simply rocky with little profile development. Except for the conglomerate areas at higher altitudes, where the forests are spruce-fir or stands of scrubby hardwoods, the soil materials are derived from red shales and sandstones, and what mineral material accumulates is brown to dark red. On the lower slopes the soils are deeper but still derived from the red shale and sandstone or the glacial till. These soils are acid and podzolized with a hardpan (Sweet and Secor 1940). In some cases areas which were once cleared and eroded are now covered with forest. Diverse soils of the limited areas of level stream valleys are commonly in farm or resort lands and are nonforested or

very recently disturbed, so no account of them is given.

CLIMATE

Climatic data for the Catskill Mountains are limited and most are from lower altitudes. At Roxbury (elevation 1,494 ft, 453 m) in the western Catskills, mean annual temperature is 44.2°F (6.6°C), lowest temperature of record is -28°F (-33.3°C), and the record maximum is 100°F (37.7°C). Average annual precipitation, evenly distributed throughout the year, is 43.14 inches (109.6 cm). Mean annual snowfall is 84.4 inches (214.4 cm) (U.S. Weather Bureau). Records of the New York City Board of Water Supply, from several stations, show an average annual precipitation of 49.2 inches (125 cm) in the eastern Catskills (Esopus Watershed) and somewhat less, 42.6 inches (108 cm), in the western Catskills (Schoharie Watershed). Temperature, precipitation, and snowfall are, no doubt, much different at the higher altitudes. Annual precipitation at Slide Mountain (2,650 ft, 808 m), the highest station, exceeds 50 inches (127 cm). The growing season ranges from 105 to 134 days (Mordoff 1949) and may exceed this in the lower altitudes. The area is occasionally subject to high winds and unusually heavy rains from hurricanes.

HISTORY AND VEGETATION

The postglacial history of southeastern New York is reported by Cox (1959). Pollen profiles are similar to those previously reported for eastern North America. An early period of spruce (*Picea*), fir (*Abies*), and pine (*Pinus*) was followed by a period of pine dominance replaced by hemlock (*Tsuga*)-hardwoods, which continues to the present. There is no evidence of substantial Indian occupancy of the Catskill Mountains (Parker 1920, Ritchie 1965); and it was not until 1800 that extensive settlement and disturbance by Europeans began, although the adjacent Hudson River Valley had been settled early in the 17th century (McIntosh 1962). The forest at the time of settlement, according to surveyors' records (ca. 1800), was largely hardwoods and hemlock (*Tsuga canadensis*). Beech (*Fagus grandifolia*) constituted nearly half (49.5%) of the tree density, hemlock, 20.3%, and sugar maple (*Acer saccharum*), 12.8% (McIntosh 1962). Following these early land surveys, extensive exploitation of the Catskills forest began. In the early 19th century the Catskills were the center of a tanning industry which used the hemlock for tanbark. Later the young sprout hardwoods were cut for barrel staves and hoops and other wood products. Extensive cutting was also done in certain areas at lower altitudes for the kilns of glass factories (Clearwater 1907, Haring 1931, Evers 1958). Since the early 19th century the Catskills have

been famous as a resort and recreation area. Except for inaccessible higher slopes and ridgetops it is probable that all of the Catskill forest has been cut one or more times. Chestnut (*Castanea dentata*) was present, at least at lower altitudes, in the southern Catskills; but the chestnut blight appeared about 1910 and mature chestnut was eliminated from the forest (Stevens 1931).

Botanical references to the vegetation of the Catskill Mountains are scarce (House 1942). Braun (1950) commented, "Literature on the vegetation of the Catskill Mountains is scant." Harshberger (1905) recognized seven plant "formations" in the Catskills: deciduous forest; coniferous forest; hemlock, white pine (*Pinus strobus*), and balsam fir (*Abies balsamea*) forests; rocky ledge; and lake and marsh. The deciduous forest, he said, covered the mountain slopes to about 3,500 ft (1,066 m). Recknagel (1915, 1923) recognized five forest types: hardwood ridge, hardwood slope (N and S), bottomlands, and spruce ridge. His tally (Recknagel 1915) for slope type shows beech dominant (38.35% density) followed by birch [sic], probably mostly yellow birch (*Betula lutea*) (30.24%), and maple [sic], probably mostly sugar maple (*Acer saccharum*) (17.08%). The ridge type is dominated by birch (49.56%) followed by beech (17.78%), hemlock (15.82%), and maple [sic] (12.62%), either sugar maple or red maple (*Acer rubrum*).

Braun (1950) includes the Catskills in the Allegheny section of the Hemlock-White Pine-Northern Hardwoods Region, noting the presence of red spruce (*Picea rubens*) as a distinctive aspect. According to Braun, the lower altitudes, to 1,200 ft (366 m), are oak-chestnut forest. Above that the dominants are sugar maple, beech, yellow birch, and hemlock to 3,500 ft (1,066 m). Spruce and fir enter at about 2,000 ft (610 m) and may become dominant above 3,700 ft (1,127 m). Ferree and Davis (1954) place 72% of the forest area of the Catskills in the Northern Hardwood forest type (mixtures of beech, sugar maple, and yellow birch) and 14% in the Oak type. They report smaller areas of coniferous types: 4.7% White Pine-Hardwood, 5% Hemlock-Hardwood, 0.9% White Pine, and 0.4% Hemlock. Smith (1954) reviews various descriptions of eastern forests that include some reference to the Catskills region and includes a map of the "Primeval Forest of New York State."

METHODS

Field surveys were conducted during the summers of 1960-63. Sample data for trees were collected by the point-quarter method of Cottam and Curtis (1956). One-meter-square samples were located at each point, and presence of tree seedlings and herbaceous species was determined in these areas. On

slopes, the lines were run on the contour usually 20 or 30 paces between successive points. A sample of 20 points or 80 trees constituted a stand. Commonly two or three parallel lines of points were made, the lines separated by 20-30 paces. Stands were on uniform slope exposure and geological substrate and were widely distributed geographically and altitudinally (Table 1) throughout the mountain area, although it was not feasible to randomize them. Most of the sites were selected arbitrarily in the almost continuous forest, although some attempt was made to locate areas which, because of their limited extent, were not readily encountered, e.g., stands of hemlock, pine, or pine-hardwoods mixtures. Stand data were tested for homogeneity of major dominants by a chi-squared test (Curtis and McIntosh 1951). Four stands were eliminated from subsequent analysis because one or more tree species were significantly nonrandomly distributed. Indications of past disturbance in an area were noted, but stands were not selected on the basis of a putative undisturbed condition. Areas subject to obvious and recent cutting or fire were not sampled.

TABLE 1. Distribution of stands by altitude

Elevation (ft)	All stands	Stands ^a dominated by spruce or fir
1,000-1,500	26	0
1,500-2,000	31	2
2,000-2,500	24	3
2,500-3,000	20	2
3,000-3,500	9	4
3,500-4,000	10	7
Total	120	18

Three soil samples were taken in some stands from the A₂ layer and combined into a composite sample. The soil samples were air-dried and passed through a 2-mm screen. Soil analyses were made at the Soil Laboratory, Department of Agronomy, Cornell University. Moisture-holding capacity was determined with Hilgard cups (Maycock and Curtis 1960), and pH was measured with a Beckman portable pH meter. Plant specimens not identifiable in the field were collected for later determination. Nomenclature follows Gleason (1952).

Quantitative procedures and calculations, except as noted below, follow methods outlined in earlier studies (Curtis and McIntosh 1951, Maycock and Curtis 1960). Importance value is the sum of relative frequency, relative density, and relative dominance for a species, the maximum possible value being 300. Similarity indices are the familiar index ($2w/(a+b)$) (Maycock and Curtis 1960), where w is the amount of any measure (e.g., density) two stands

TABLE 2. Percentage presence, number of stands as leading dominant, mean density (%) in stands of occurrence, and maximum density (%) of trees over 4 inches dbh in a single stand

Species	Presence (%)	Number of stands as leading dominant	Mean density (%)	Maximum density (%)
<i>Abies balsamea</i> (balsam fir)	20	3	22	96
<i>Acer pensylvanicum</i> (striped maple)	40	0	5	25
<i>A. rubrum</i> (red maple)	61	5	11	41
<i>A. saccharum</i> (sugar maple)	81	27	26	92
<i>A. spicatum</i> (mountain maple)	8	0	2	4
<i>Amelanchier</i> sp. (juneberry)	11	0	2	7
<i>Betula cordifolia</i> (round-leaved white birch)	12	1	10	32
<i>B. lenta</i> (black birch)	36	1	7	46
<i>B. lutea</i> (yellow birch)	67	9	10	80
<i>B. papyrifera</i> (white birch)	26	4	15	73
<i>Carpinus caroliniana</i> (blue beech)	2	0	1	1
<i>Carya glabra</i> (pignut hickory)	13	0	5	11
<i>C. ovata</i> (shagbark hickory)	2	0	7	11
<i>Fagus grandifolia</i> (beech)	70	16	19	57
<i>Fraxinus americana</i> (American ash)	61	0	8	17
<i>Juglans cinerea</i> (butternut)	6	0	2	4
<i>Liriodendron tulipifera</i> (tulip tree)	1	0	1	1
<i>Nyssa sylvatica</i> (black gum)	1	0	2	2
<i>Ostrya virginiana</i> (ironwood)	29	0	4	14
<i>Picea rubens</i> (red spruce)	25	15	47	97
<i>Pinus resinosa</i> (red pine)	1	0	15	5
<i>P. rigida</i> (pitch pine)	1	0	19	19
<i>P. strobus</i> (white pine)	18	0	5	16
<i>Populus grandidentata</i> (large-toothed aspen)	16	0	5	14
<i>P. tremuloides</i> (trembling aspen)	3	0	7	10
<i>Prunus serotina</i> (black cherry)	29	2	6	38
<i>Quercus alba</i> (white oak)	1	0	2	2
<i>Q. prinus</i> (chestnut oak)	38	7	22	67
<i>Q. borealis</i> (red oak)	55	18	24	87
<i>Sorbus americana</i> (mountain ash)	8	0	1	2
<i>Tilia americana</i> (basswood)	25	0	3	15
<i>Tsuga canadensis</i> (hemlock)	54	12	19	89
<i>Ulmus rubra</i> (slippery elm)	9	0	2	7

have in common, and a and b are the measurements for stands a and b .

RESULTS

Tree composition

Thirty-three tree species (> 4 inches dbh) were encountered in 120 stands (Table 2). Stands dominated by spruce or fir are not considered further in this paper. Only 12 species were found as the leading dominant species in any one of the remaining stands, and only eight species were leading dominants in at least four stands. A few additional tree species were found as seedlings or saplings, e.g., sassafras (*Sassafras albidum*), chestnut (*Castanea dentata*), and flowering dogwood (*Cornus florida*). Common shrub and herb species are given in Table 3.

Tree-species distributions in relation to altitude are shown in Fig. 1. Mixed stands of chestnut oak (*Quercus prinus*) and red oak (*Quercus borealis*) are most common in the areas of heavily disturbed forest below 2,000 ft (610 m), although red oak reaches its maximum mean density percentage above 2,500 ft (761 m). These mixed-oak stands are generally open, many trees have multiple trunks, and there is an understory of shrubs, particularly *Vaccini-*

um sp. The herbaceous flora in these stands is limited. Hemlock reaches its maximum density below 1,500 ft (457 m) and is uncommon above 3,000 ft (914 m). It is a much smaller proportion of the forest than it was prior to the year 1800. Stands dominated by either beech or sugar maple, or mixtures of these with other hardwoods, are prominent to 3,500 ft (1,066 m). Old-growth hardwoods-spruce mixtures are characteristic on steep slopes and shoulders between 3,000 and 3,500 ft. Yellow birch becomes increasingly prominent above 2,500 ft (762 m), and most of the stands dominated by yellow birch are above 2,900 ft (883 m), one being over 4,000 ft (1,220 m).

Black cherry (*Prunus serotina*) is also most prominent at higher altitudes, above 3,000 ft (914 m); both of the stands dominated by black cherry are above 3,500 ft (1,066 m). Spruce-fir stands are most characteristic above 3,500 ft, and nearly pure stands of balsam occur above 3,700 ft (1,127 m) on several peaks. Much of the mountain area above 3,500 ft is, however, covered with mixtures of scrubby hardwoods with fern understory, indicative of disturbance or deterioration of spruce-fir forest, e.g., red maple (*Acer rubrum*), mountain maple (*Acer spicatum*),

TABLE 3. Presence percentage and maximum frequency percentage of common shrub and herb species in a single stand

Species	Presence (%)	Maximum frequency (%)
Shrubs		
<i>Hamamelis virginiana</i>	16	30
<i>Kalmia latifolia</i>	18	70
<i>Rhododendron roseum</i>	12	80
<i>Rubus</i> sp.	31	55
<i>Vaccinium</i> sp.	17	100
<i>Viburnum acerifolium</i>	34	55
<i>V. alnifolium</i>	30	60
Herbs		
<i>Aralia nudicaulis</i>	54	70
<i>Arisaema triphyllum</i>	25	60
<i>Aster acuminatus</i>	20	70
<i>A. macrophyllum</i>	23	85
<i>Clintonia borealis</i>	21	90
<i>Coptis trifolia</i>	8	55
<i>Dennstaedtia punctilobula</i>	6	25
<i>Dryopteris austriaca</i>	45	95
<i>D. marginalis</i>	22	30
<i>Eupatorium rugosum</i>	17	75
<i>Galium triflorum</i>	14	45
<i>Gaultheria procumbens</i>	15	45
<i>Hydrophyllum virginianum</i>	12	60
<i>Laportea canadensis</i>	18	100
<i>Lycopodium complanatum</i>	8	35
<i>L. lucidulum</i>	24	75
<i>Maianthemum canadense</i>	52	95
<i>Oxalis acetosella</i>	32	100
<i>Polystichum acrostichoides</i>	17	30
<i>Smilacina racemosa</i>	17	25
<i>Solidago flexicaulis</i>	16	25
<i>Streptopus roseus</i>	9	50
<i>Tiarella cordifolia</i>	21	45
<i>Trientalis borealis</i>	41	85
<i>Uvularia sessilifolia</i>	34	45
<i>Viola canadensis</i>	13	50

round-leaved white birch (*Betula cordifolia*), fire cherry (*Prunus pensylvanica*), and black cherry. Spruce stands may be found as low as 1,800 ft (548 m) along stream sides and at 2,000 ft (610 m) on upland areas, particularly in the northern Catskills (McIntosh and Hurley 1964).

Leading dominants

The interrelations of the tree species may be examined in a general way by the method of leading dominants (Curtis and McIntosh 1951). Table 4 gives the relative densities of common tree species in stands in which a given species is the leading dominant, and Table 5 shows the reproduction of each tree species in these stands. It is notable that sugar maple, beech, yellow birch, and hemlock are each dominant in the sapling class in those stands in which they are the leading dominant. Stands dominated by red oak and white birch (*Betula papyrifera*) both have maximum sapling and seedling reproduction of sugar maple followed by red maple, whereas stands dominated by chestnut oak have considerable red maple and hemlock in the reproductive classes.

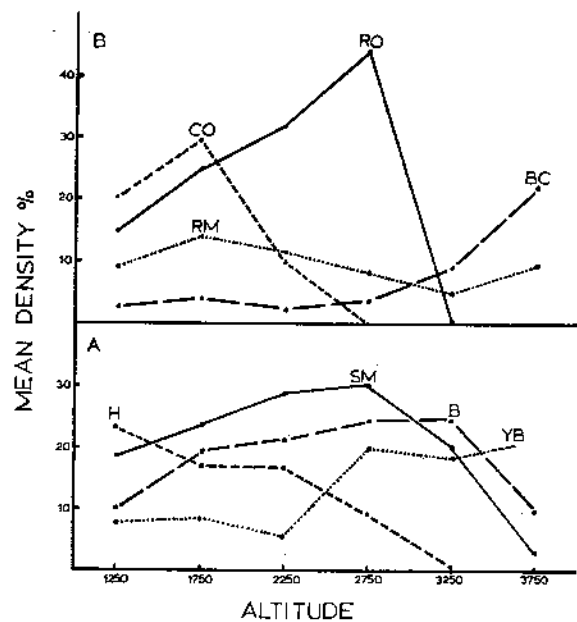


FIG. 1. Mean density (%) of common tree species by altitude. CO, chestnut oak; RM, red maple; RO, red oak; BC, black cherry; H, hemlock; SM, sugar maple; B, beech; YB, yellow birch.

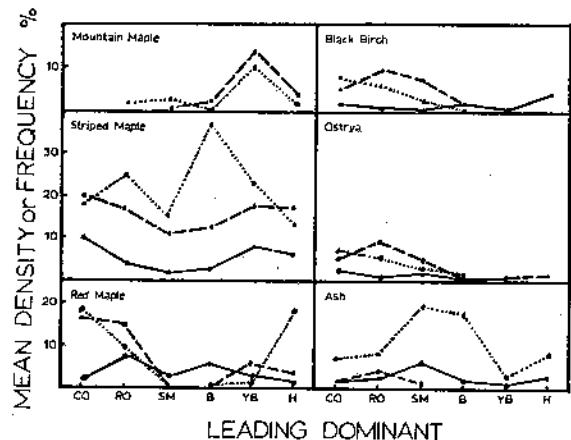


FIG. 2. Mean density (%) of subdominant trees and saplings and mean frequency (%) of seedlings in stands grouped by leading dominant. CO, chestnut oak; RO, red oak; SM, sugar maple; B, beech; YB, yellow birch; H, hemlock. Solid line, trees over 4 inches dbh; long-dash line, saplings; dotted line, seedlings.

Striped maple (*Acer pensylvanicum*) is prominent in the sapling and seedling classes of stands dominated by all species and, although it does not become a canopy species, may materially affect the success of reproduction of other species. Mountain maple (*Acer spicatum*), also a small tree, is prominent in stands in which yellow birch is the leading dominant but not elsewhere (Fig. 2).

Age structure and reproduction are commonly taken as an indication of the future trends of forest succession (Goff 1968). The interrelations of beech,

TABLE 4. Mean density (%) of major tree species in stands in which a species is the leading dominant (number of stands in parentheses)

Species	Leading dominant							
	Sugar maple (27)	Beech (16)	Hemlock (12)	Yellow birch (9)	Red oak (18)	Chestnut oak (7)	Red maple (5)	White birch (4)
Sugar maple	53.1	20.1	6.9	7.0	6.6	0.4	9.2	6.7
Beech	12.8	40.5	5.9	11.1	0.9	0.1	17.4	2.7
Hemlock	1.8	8.9	49.1	0.2	0.6	5.2	0.6	0.0
Yellow birch	5.7	9.8	7.1	45.7	0.4	0.7	6.4	0.5
Red oak	5.5	2.1	2.2	0.5	50.6	22.5	5.4	1.5
Chestnut oak	0.7	0.1	2.6	0.0	13.2	47.1	0.0	0.0
Red maple	2.8	6.3	1.5	3.1	8.7	2.0	38.4	10.0
White birch	1.4	0.6	0.5	0.1	1.3	0.2	13.3	61.0
American ash	6.2	2.4	2.7	1.0	3.4	1.8	2.2	2.7
Basswood	2.1	0.6	1.0	0.2	0.6	0.0	0.0	0.0

TABLE 5. Mean reproduction (saplings as mean density (%), seedlings as mean frequency (%)) in stands in which a species is the leading dominant (number of stands in parentheses)

Reproduction		Leading dominant							
		Sugar maple (25)	Beech (16)	Hemlock (12)	Yellow birch (6)	Red oak (18)	Chestnut oak (5)	Red maple (5)	White birch (3)
Sugar maple	Saplings	37 ^a	20	8	10	25 ^a	7	15	18 ^a
	Seedlings	43	40	15	7	16	3	34	43
Beech	Saplings	29	49	12	18 ^a	8	<1	48	9
	Seedlings	12	36	7	7	1	1	16	10
Hemlock	Saplings	3	7	37 ^a	2	2	9	4	0
	Seedlings	0	2	21	1	1	9	0	0
Yellow birch	Saplings	3	2	5	14	2	<1	5	4
	Seedlings	5	10	9	7	3	0	13	7
Red oak	Saplings	<1	<1	1	0	5	3	1	4
	Seedlings	1	0	<1	0	13	34	7	5
Chestnut oak	Saplings	<1	0	0	0	1	6	0	0
	Seedlings	0	2	<1	0	4	17	0	0
Red maple	Saplings	<1	1	6	4	15	17	15	17
	Seedlings	3	6	19	2	10	18	18	40
White birch	Saplings	0	0	<1	0	<1	0	4	5
	Seedlings	<1	0	0	2	0	0	2	3
American ash	Saplings	1	0	<1	<1	4	2	1	7
	Seedlings	20	18	9	3	9	7	26	26
Basswood	Saplings	<1	0	0	0	<1	0	0	0
	Seedlings	1	0	0	0	1	0	0	0

^aHighest species in both saplings and seedlings.

sugar maple, and hemlock are of particular interest in this respect since a beech-maple climax, with or without hemlock, is commonly considered a stable end point of forest succession in many areas. Beech and sugar maple are, reciprocally, the second most important species in stands dominated by either species (Table 4). But mean values do not make clear that beech is, in some instances, absent from stands, particularly young stands, dominated by sugar maple.

Beech and sugar maple both reproduce best in stands in which they are dominant (Table 5). The relative reproduction of these species in stands in which either is at least 25% of the tree density or, if less, is the leading dominant is shown in Table 6. Beech is heavily overrepresented in the saplings of stands in which it clearly exceeds sugar maple (2x) and is slightly overrepresented as saplings even in stands where sugar maple predominates. It is likely that

TABLE 6. Mean reproduction of beech (B) and sugar maple (SM) in mixed stands in which either species is the leading dominant or, if not, in which either is at least 25% of the density of mature trees (number of stands in parentheses)

Ratio of density of mature trees	Ratio of density of saplings	Ratio of frequency of seedlings
<2B:1SM (9)	4.6B:1SM	0.8B:1SM
1-2B:1SM (8)	2.0B:1SM	1.1B:1SM
0.5-1B:1SM (7)	1.1B:1SM	0.3B:1SM
0.25-0.5B:1SM (9)	0.6B:1SM	0.3B:1SM
0.125-0.25B:1SM (7)	0.4B:1SM	0.2B:1SM
0B:1SM (5)	0.2B:1SM	0.2B:1SM

most of the beech saplings and most seedlings are root sprouts, for all of those examined were. In contrast to the overrepresentation of beech in the sapling class it is underrepresented in the seedling class in stands where the canopy is predominantly beech or about an equal mixture of beech and sugar maple. In stands where sugar maple exceeds beech in the tree class, although there is considerable variation, beech is proportionately represented or slightly underrepresented in the seedling class. In stands in which beech exceeds sugar maple (when either one is at least 25% of the total density) there is also a greater mean density of hemlock (21.2% to 5.4%) in the canopy, and a greater mean density of hemlock saplings (7.5% to 0%), as compared to stands where sugar maple exceeds beech.

Selected stands

Even a cursory examination of the data of stands arranged by the leading dominant method makes clear that some things are masked by this method. A species may have quite different species as secondary species in stands in which it is the leading dominant. Sugar maple (27 stands), for example, characteristically has beech (12 stands) as the second most important species, but in five stands red oak is the second species, three stands each red maple, and yellow birch, two American ash (*Fraxinus americana*), and one each ironwood (*Ostrya virginiana*) and white birch.

Stands with the same leading dominant may differ greatly in age, composition, and structure. To identify groups of stands of maximum similarity, a matrix of similarity index values was constructed for all combinations of stands based on all tree species plus 31 prominent shrub and herb species (essentially those listed in Tables 2 and 3). From this matrix, groups of three stands were selected which had a common leading dominant and which had maximum similarity values as measured by the similarity index. Stands selected by leading dominants in the case of two species, hemlock and sugar maple, were very

different. In these instances two separate groups of three stands were identified as above, one of younger trees (designated young sugar maple or young hemlock, respectively) and the other groups including clearly old-growth stands dominated by large hemlock or sugar maples along with other large trees.

The mean similarity values within each group of three stands were compared with the mean similarity values between the groups of stands (Table 7). The highest values were, of course, within groups, although the difference among the within-group values was considerable. The maximum similarity value between any pair of stands was 68.7. Bray and Curtis (1957) found that replicate samples in the same stand of a Wisconsin forest gave mean similarity values of 80. Beech (60.0) and old-growth hemlock (59.5) stands are the most homogeneous (similar) groups of three stands and white birch (39.6) and red oak (35.0) stands the least homogeneous. Old-growth hemlock stands are more similar to beech stands than to young hemlock stands, and old-growth sugar maple stands are more similar to either beech or old-growth hemlock stands than they are to young sugar maple stands. The groups dominated by red oak and chestnut oak are least similar to any of the groups, e.g., beech, old-growth sugar maple, or old-growth hemlock which might be most representative of the presumed climax of the region. Among the groups, that in which yellow birch is the leading dominant has, as might be expected, the highest similarity value (19.7) to a group of old-growth spruce stands not included in this study. Tree-size and density characteristics of these stands are given in Table 8.

These groups of three stands of maximum similarity were further examined, to assess their successional status, by treating each group as a unit and dividing the trees into 3-inch diameter classes. The relative density values in each size class suggest the general pattern of change in composition within each group of stands (Goff 1968). Density percentage was calculated for each diameter class, and distribution of sapling reproduction in these classes was compared (Fig. 3).

Stands dominated by beech had proportionately less beech in the smaller size classes and saplings, whereas sugar maple and hemlock increase in the smaller size classes and saplings. This suggests that sugar maple and hemlock are invading the beech stands. The drop of beech in the 23-inch size class is due to a substantial representation (28%) of yellow birch in that class.

Old-growth sugar maple stands show an increase in the proportion of yellow birch in the larger size classes and an increase in the proportion of beech in the medium size classes, which suggests an inverse relation between beech and sugar maple. Stands

TABLE 7. Matrix of mean values of similarity index within and between groups of three stands of maximum similarity

	Beech	Old-growth hemlock	Old-growth sugar maple	Young sugar maple	Yellow birch	Red maple	White birch	Young hemlock	Red oak	Chestnut oak
Beech	60.0	53.1	40.2	30.9	30.1	26.0	25.6	18.1	8.4	10.8
Old-growth hemlock		59.5	36.5	29.7	36.6	23.8	22.9	30.9	11.2	10.6
Old-growth sugar maple			40.5	37.9	30.5	17.9	19.4	8.1	12.9	7.9
Young sugar maple				55.6	12.3	19.3	23.2	10.3	9.5	11.2
Yellow birch					54.5	13.8	12.4	14.5	9.5	6.5
Red maple						43.6	25.6	15.5	14.2	17.5
White birch							39.6	18.5	21.6	24.7
Young hemlock								48.9	10.6	11.1
Red oak									35.0	28.8
Chestnut oak										53.7

TABLE 8. Altitude in hundreds of feet, total basal area in square feet per acre, number of trees per acre, and mean basal area per tree (square inches) in selected groups of similar stands in which the species named is the leading dominant

Group	Stand number	Altitude	Total basal area	Number of trees per acre	Mean basal area per tree
Old-growth sugar maple	38	27	210	232	130
	48	26	317	291	157
	78	34	304	284	154
Young sugar maple	39	28	163	395	59
	90	25	183	273	96
	100	26	178	371	69
Beech	63	25	266	324	118
	104	27	309	367	121
	106	23	199	329	87
Old-growth hemlock	37	21	303	270	162
	61	28	328	252	187
	81	22	293	247	171
Young hemlock	15	19	301	482	90
	43	15	424	460	133
	59	10	280	466	86
Yellow birch	40	33	141	297	69
	80	29	274	415	95
	101	30	362	279	187
Red oak	25	17	193	324	86
	45	26	196	409	69
	79	23	366	614	86
Chestnut oak	41	14	193	378	73
	55	19	263	643	59
	74	16	192	338	82
Red maple	92	24	170	336	73
	66	13	159	521	44
	105	19	250	492	73
White birch	70	18	93	293	45
	82	23	208	521	57
	86	23	267	734	52

dominated by young sugar maple, often almost pure stands, have small amounts of beech in the smaller size classes, but exhibit no clear trend.

Old-growth hemlock stands show hemlock drop-

ping out of the smaller size classes and being replaced by beech and sugar maple. Young hemlock stands, however, have high proportions of hemlock in all size classes, including saplings, but beech and sugar

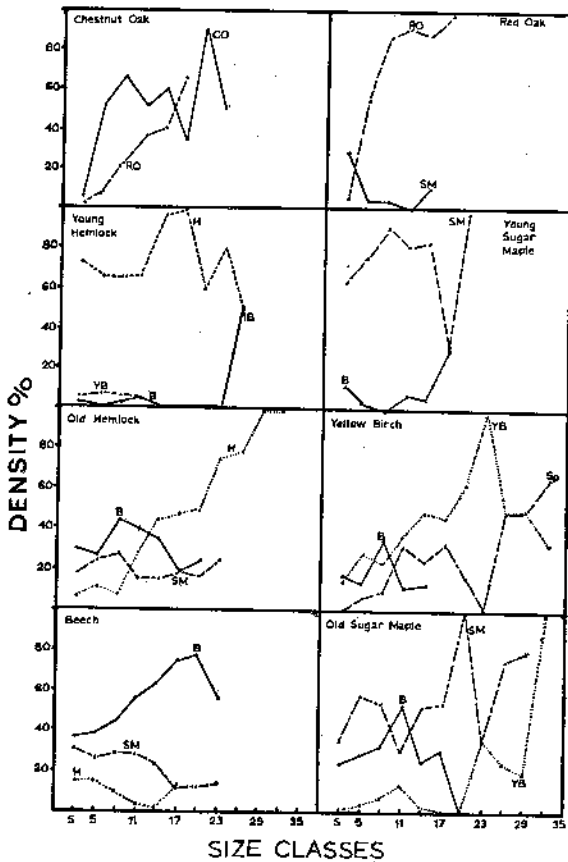


FIG. 3. Mean density (%) of saplings and 3-inch dbh size classes of selected tree species in selected groups of stands of maximum similarity. CO, chestnut oak; RO, red oak; SM, sugar maple; H, hemlock; YB, yellow birch; B, beech; SP, spruce.

maple also appear in the smaller size classes. In stands dominated by yellow birch, yellow birch is dropping out of the smaller size classes and being replaced by beech. Sugar maple also appears in the smaller size classes. Stands dominated by chestnut oak have fewer chestnut oak trees in the smaller size classes. Sugar and red maples appear and increase in

the smaller size classes. In stands in which red oak is the leading dominant, red oak decreases in the smaller size classes and sugar maple increases.

Stands dominated by red maple (not illustrated) have less red maple in the smaller size classes and a marked increase of beech with lesser amounts of sugar maple. Those dominated by white birch have lesser amounts of white birch in the smaller size classes with an increase of red and sugar maples along with lesser amounts of beech and hemlock in the smaller size classes.

Diversity

Diversity in the same selected groups of stands was calculated using the diversity index described by McIntosh (1967a) (Table 9). This index expresses the observed diversity as a proportion of the maximum possible diversity:

$$\frac{N - \sqrt{\sum_i n_i^2}}{N - \sqrt{N}}$$

where N equals the number of individuals, n_i equals the number of individuals in the i th species, and S equals the number of species. The index ranges from zero, if there is only one species, to a maximum of 1 if the species have equal numbers of individuals. The indices in individual stands ranged from a minimum (0.08) in a young sugar maple stand to a maximum (0.74) in a stand dominated by yellow birch. The group of three young sugar maple stands was least diverse (0.15), and the old-growth hemlock stands and yellow birch stands were most diverse (0.54). However, the latter were not more diverse than obviously pioneer stands dominated by red maple. The mean number of tree species per group varied from 5.3 to 7.6. The least diverse stands, as measured by the diversity index, had as many species as the most diverse stands; hence, the variation in diversity is primarily due to the equitability component (the concentration of density in one or a few

TABLE 9. Mean indices of diversity of trees and saplings, mean density (%) of the leading dominant, the second dominant as a percentage of the first, and mean number of species in each group of three stands

Group	Mean index of diversity		Mean density (%) of leading dominant	Second dominant as percentage of first	Mean number of species
	Trees	Saplings			
Young sugar maple	0.15	0.33	86	5	6.6
Red oak	0.20	0.39	75	17	5.6
Young hemlock	0.29	0.38	72	11	7.6
White birch	0.30	0.68	62	24	7.3
Old-growth sugar maple	0.39	0.46	56	50	5.3
Chestnut oak	0.41	0.67	59	37	7.0
Beech	0.44	0.52	52	50	6.3
Red maple	0.53	0.29	39	79	6.3
Yellow birch	0.54	0.65	45	67	6.3
Old-growth hemlock	0.54	0.54	34	76	7.0

species) rather than richness in species. This is apparent in the proportionate levels of dominance of the first and second leading tree dominant (Table 9).

In general, diversity values calculated for saplings were higher than those for trees. This is notably so in pioneer stands of white birch and chestnut oak. Red maple stands, however, show just the reverse. Old-growth stands of sugar maple, hemlock, and beech had less markedly increased diversity in the sapling class.

Interspecific correlation

Correlation coefficients (r) were calculated for each combination of tree species in all stands. These complement the data from the leading dominant method and, in general, suggest the same pattern of relations. Species characteristic of higher altitudes, balsam fir, mountain ash, and round-leaved white birch, are linked with mountain maple and black cherry by significant positive correlations (Fig. 4, group 1). Sugar maple, basswood (*Tilia americana*), and ironwood form a cluster of highly significant (> 0.01) positive correlations with American ash, and there are significant (> 0.05) positive correlations between some of these species and beech, slippery elm, and red oak (Fig. 4, group 3). Another apparent cluster of significant (> 0.05) positive correlations including yellow birch and hemlock, black birch, red maple, and striped maple (Fig. 4, group 2) is interesting in that there are no significant positive correlations between these species and any of those associated in the first two clusters suggested by the pattern of positive correlation coefficients. Yellow birch and hemlock are significantly positively

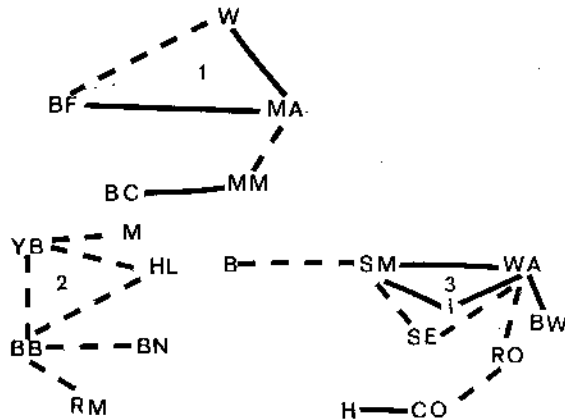


FIG. 4. Diagram showing significant positive correlation coefficients of tree species. Species connected by a solid line have a correlation coefficient (r) greater than 0.01; by a dashed line, greater than 0.05. W, round-leaved white birch; BF, balsam fir; MA, mountain ash; MM, mountain maple; BC, black cherry; M, striped maple; YB, yellow birch; HL, hemlock; BB, black birch; BN, butternut; RM, red maple; B, beech; SM, sugar maple; WA, American ash; SE, slippery elm; BW, basswood; RO, red oak; CO, chestnut oak; H, pignut hickory.

correlated in spite of the difference in altitudinal distribution (Fig. 1). Neither species is significantly positively correlated with beech or sugar maple with which they are commonly linked as climax associates.

Ordination

The deciduous hardwood-hemlock forests were ordinated by the principal components method based on density of trees per acre and a correlation coefficient matrix between tree species. The distribution of stands by leading dominants on the first two principal component axes is shown in Fig. 5. The pioneer chestnut oak stands are on the upper left and the species usually considered climax—sugar maple, beech, yellow birch, and hemlock—are in a line on the right. The overlap of these species in the ordination space is considerable, but when densities of the major species are plotted, each species has its own center of maximum density (Fig. 6). The uppermost hemlock and lowermost sugar maple stands include those designated above as young hemlock and sugar maple, being strongly dominated by those species (Table 9) and not markedly similar (Table 7) to the central stands which include the old-growth hemlock and sugar maple stands and the beech stands.

The deciduous hardwood-hemlock tree-density data were also used to ordinate species by the principal components technique (Fig. 7). The high altitude species—balsam fir, mountain ash (*Sorbus americana*), round-leaved white birch (*Betula cordifolia*), and red spruce—are on the lower left. The pioneer

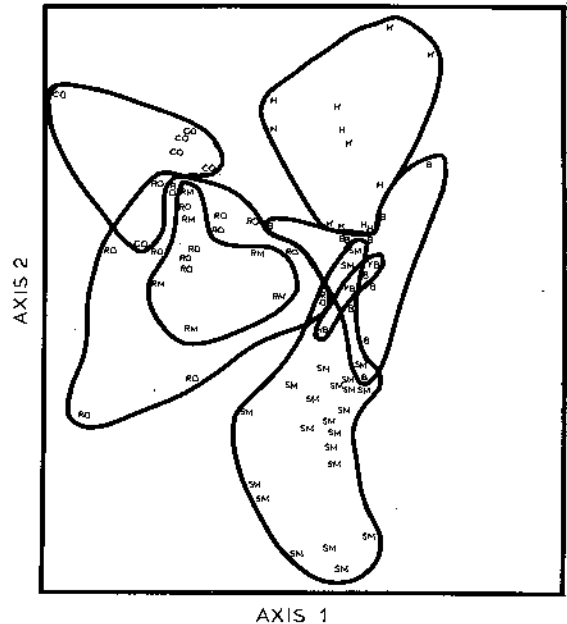


FIG. 5. Distribution of stands by leading dominant of the common trees on the first two principal component axes. CO, chestnut oak; RO, red oak; RM, red maple; H, hemlock; B, beech; YB, yellow birch; SM, sugar maple.

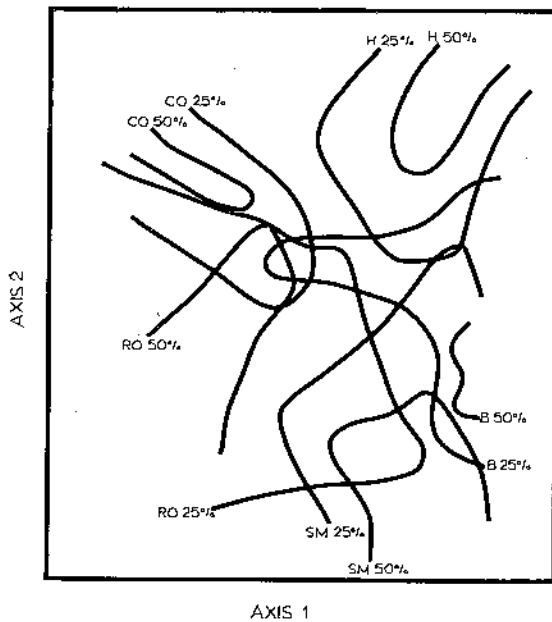


FIG. 6. Distribution of major tree dominants on the first two axes of Fig. 6 in stands in which they are over 25% density and over 50% density. CO, chestnut oak; RO, red oak; H, hemlock; B, beech; SM, sugar maple.

species—chestnut oak, white pine, and large-toothed aspen (*Populus grandidentata*)—are grouped on the upper left, and the shade-tolerant climax species, e.g., sugar maple, American ash, beech, and basswood (*Tilia americana*), are on the upper right. Since the first three dimensions necessarily distort the multidimensional relations among the several species, dotted lines are drawn connecting species pairs which are not nearest neighbors in the three dimensional representation, but one of which has its maximum correlation coefficient with the other. The arrow directed toward a species indicates that a species has its maximum correlation coefficient with that species. If a line has two arrows it indicates that the species are reciprocally maximally correlated with each other. The principal components method produces a spatial arrangement of species on the first three axes in which the pattern of species groups suggested in Fig. 4 is evident.

Recent papers by Swan (1970), Austin and Noy-Meir (1971), and LaFrance (1972) emphasize the distortions which are inherent in ordination representations in that these attempt to reduce nonlinear species responses to linear mathematical models. Although published ordination diagrams are commonly suggestive of the main lineaments of phytosociological relations, it is clear that they cannot be readily interpreted as the main gradients of vegetational or environmental variation. If different ordination methods lead to different interpretations, there is no authoritative way to select the correct one. Such diffi-

culties and limitations are not absent from other phytosociological techniques, but a better understanding of the distortions produced by specific ordination techniques is needed.

DISCUSSION

A familiar and dramatic effect of human disturbance in a forested area is a gross change in the forest cover either by deforestation or marked change in composition (Curtis 1956). Although a very large proportion (80%) of the Catskill Mountain region remains forested today, the composition has changed greatly in the past two centuries. Reconstruction of an original forest for comparison with modern forests is not easy or wholly accurate, particularly on specific sites; but surveyors' records, made about 1800, suggest a relatively homogeneous forest throughout extensive areas of the middle altitudes (1,000–3,000 ft, 305–914 m) of the Catskills. The forests of the lower altitudes in the late 18th century were mixtures of hardwoods and hemlock; nearly half (49.5%) of the trees recorded by the surveyors were beech (McIntosh 1962). The preponderance of beech, as estimated by density, recorded by early surveys of the presettlement forest was also noted in southwestern New York (Gordon 1940), adjacent Pennsylvania (Lutz 1930), and Vermont (Siccama 1971). In the Catskills, hemlock was the second major tree species (20.3%) followed by sugar maple (12.8%) and birch (probably mostly yellow birch, 7.3%). This order of importance was quite consistent in surveys throughout the region, although the percentages varied and there was more beech (63.0%) and less hemlock (8.0%) in the western Catskills than in the eastern areas. The consistency of the forest cover is further suggested by the fact that, in only one of twenty-two different surveyors' records was a tree species other than beech the leading dominant. In only six records was hemlock not the second leading dominant tree, being replaced in these cases by sugar maple which is, in all of the other records, the third leading dominant. These quantitative records were confirmed by the descriptive statements of the surveyors, 96% of which listed beech as the first tree. Combinations of tree species were suggested in their written descriptions, 42% being recorded as beech-maple-hemlock, 20% beech-birch-maple-hemlock, 9% beech-maple, and 5% beech-birch-maple. Hemlock was mentioned first in only 2% of the verbal descriptions. Several tree species, such as red maple (1.1%), black cherry (0.9%), chestnut oak (0.1%), and red oak (0.1%), were rarely recorded by the surveyors as witness trees, and only infrequently mentioned, although they are widespread and common in the modern forest (McIntosh 1962).

If, as Parker (1920) asserted, there was little In-

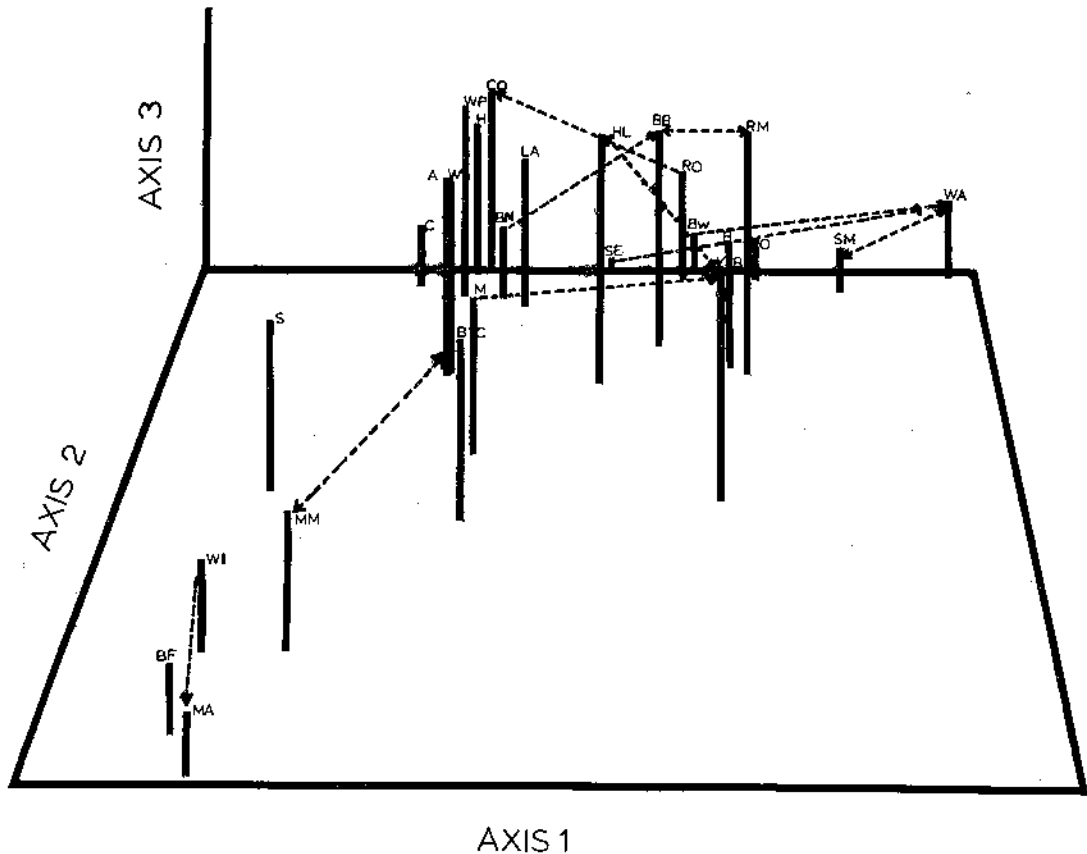


FIG. 7. Principal components ordination of tree species using density per acre of trees and the correlation coefficient. A, *Amelanchier*; B, beech; BB, black birch; BC, black cherry; BF, balsam fir; BN, butternut; BW, basswood; C, blue beech; CO, chestnut oak; H, pignut hickory; HL, hemlock; LA, large-toothed aspen; M, striped maple; MA, mountain ash; MM, mountain maple; O, ironwood; RM, red maple; RO, red oak; S, spruce; SE, slippery elm; SM, sugar maple; W, white birch; WI, round-leaved white birch; WA, American ash; WP, white pine; YB, yellow birch.

dian occupancy of the Catskills before European settlement, the presettlement forest was relatively undisturbed. Ritchie (1965), in a more recent study of the archeology of New York State, records no Indian artifacts from the Catskills. Day (1953) noted the widespread impact of the Indian on the supposed primeval forest. He specifically referred to the well-known extensive settlements and agricultural activity in the Hudson River Valley. Limited surveyors' records and historical descriptions show that the forests of the Hudson River Valley were very different from the Catskill forests. The three leading dominants in the valley surveys were white oak (*Quercus alba*, 15%), black oak (*Quercus velutina*, 14%), and rock or chestnut oak (13%). Hemlock (8%), sugar maple (5.6%), and beech (3.3%) were relatively minor components of these forests (McIntosh 1962). These forests were in an area very much disturbed by Indian settlement and agriculture; and since beech-maple and hemlock forests are found in the Hudson Valley, it may well be that this area differs from the

Catskills more because of a longer history of intensive disturbance than anything else. It seems reasonable to infer that in the 18th century extensive areas of the Catskill Mountains below 3,500 ft (1,066 m) supported a mixed hardwood-hemlock forest of varying proportions of beech, sugar maple, yellow birch, and hemlock with smaller proportions of American ash, ironwood, and basswood. Above 3,500 ft, and lower in some areas, red spruce was mixed with the hardwoods largely as older trees. The deciduous forests of the Catskills may be described as an altitudinal continuum, or gradient merging with the spruce-fir forest as suggested by Bormann and Buell (1964) in the Green Mountains of Vermont and by Siccama's (1971) study of presettlement forests of Vermont, which parallels the deciduous-boreal forest transition described by Maycock and Curtis (1960) in the Lake States' forests.

The present-day forest must be assessed as a very much modified version of that of 200 years ago. Adequate pursuit of historical records may allow

more detailed analysis of the impact of European settlement and activities, and particularly fire, on specific sites, but at present these are just becoming available (Kudish 1971). Much of the area was never cleared for agriculture, and the upper slopes have been continuously in forest but subjected to varying kinds and intensities of disturbance. Extensive areas at lower altitudes are cleared for pasture (but not plowed) in the 19th century and were abandoned following the peak of exploitation of the region.

The history of the Catskills includes a major period of exploitation (ca. 1820–70) of hemlock for tanbark which greatly depleted the original hemlocks. The hardwoods, principally sugar maple and yellow birch, were used for a limited furniture industry, the young sprout-hardwood trees were extensively used (ca. 1850–90) for barrel hoops, and other hardwoods were used locally as fuel for a short-lived glass industry in the early and mid-19th century. Extensive cutting continued until large-scale incorporation of lands into the New York State Forest Preserve in the early part of this century. Cutting, an indeterminate history of fire, and occasional wind storms combined to create the conditions in which the modern forests are found.

The most notable change in the forest since 1800 is the decline in the proportion of beech. Unless the surveyors' records seriously overrepresent it, beech has drastically declined in spite of the fact that it was not, like hemlock, or, to a lesser extent, sugar maple, a prime commercial species. If the hardwoods-hemlock stands of the present study (7,000 trees) are treated as a composite, beech constitutes only 12.8% of the trees as compared to 49.5% of the surveyors' records. Neither sample is random or entirely adequate, but the figures do illustrate the gross change in proportion. Siccama (1971), comparing the presettlement (18th century) and current forests of Chittenden County in northwestern Vermont, found similarly that beech made up over 40% of the trees in the presettlement forest as compared to 3–5% in 1962; in the midelevations (1,000–2,000 ft, 305–610 m) beech was nearly one-half the total tree density in the surveyors' records. In the Vermont forests sugar maple was the second leading dominant (16–18%) below 2,000 ft and hemlock third at altitudes below 1,500 ft. Beech in the Catskills has been severely affected by *Nectria*-scale disease (Zabel, Silverborg, and Fowler 1958, Zabel 1961), which may account in part for its failure to maintain itself.

There is no clear evidence that beech in the Catskills represents the three varieties of Camp (1951) as found by Whittaker (1956) in the Great Smoky Mountains. Although Camp annotated specimens in the New York State Herbarium at Albany, it was not apparent how these were recognized, nor did Camp ever publish the criteria by which they could

be distinguished. Some rather scrubby, nearly pure, beech stands were seen at higher altitudes, but there was no altitudinal separation of beech stands as noted by Whittaker.

Hemlock has also declined in the modern forest (20.3% to 9.5%) most likely because of the extensive cutting for tanbark and its failure to reproduce effectively in the secondary hardwoods forests particularly in sugar maple stands. It is probable that 9.5% overestimates the proportion of hemlock in the modern Catskills forest since the more unusual stands were selected to include hemlock. Of the presettlement dominants only sugar maple has increased substantially (12.8% to 23.2%), and, in general, it is now the most ubiquitous species in the forest. It also increased in the Vermont forest (Siccama 1971). If, as surmised, the trees described by the surveyors simply as "birch" were largely yellow birch, then the present forest has essentially the same proportion (7.3% to 7.1%) of yellow birch. Black birch (*Betula lenta*) is not specifically mentioned in the surveyors' records, but comprises 3.6% of the individuals in the current forest sample.

Other distinctive changes in composition are the great increases in the incidence of red maple (1.2% to 7.0%), American ash (0.4% to 3.7%), and particularly red oak (0.1% to 12.3%) and chestnut oak (0.1% to 5.2%). Unlike much of New England, there are no extensive secondary forests of white pine (*Pinus strobus*), which is only sparsely represented in the present forest. The extensive areas of chestnut oak and red oak forest between 1,000 and 2,500 ft (305–761 m) are essentially due to extension of the chestnut oak into the mountains from the lower valley forests, although its companion oaks there, white oak and black oak, seem not to have moved into the higher altitudes following disturbance.

The closest approximation to undisturbed, old-growth forest is seen in the groups of stands designated as old-growth hemlock and beech, which are also most similar to one another (Table 7). If these two groups are considered as a unit, 41% of the trees are beech, 21% hemlock, 21% sugar maple, and 11% yellow birch. These stands are, along with the old-growth sugar maple stands, clearly the oldest and least disturbed among those sampled. Limited numbers of stump counts of trees of comparable size indicate that the larger trees in these stands are over 200 years old. Hemlock stumps over 600 square inches basal area were over 200 years old, and stumps 400–600 square inches basal area ranged from 120 to 300 years. Sugar maple stumps of comparable size were generally younger, but stumps as large as 600 square inches basal area approximated 200 years. Only two beech stumps were encountered (120 square inches basal area, 135 years; 250 square inches basal area, 260 years). Standing beech trees

were not found as large as standing hemlock or sugar maple trees. The largest trees in these old-growth stands, which give them their character, are hemlock, sugar maple, or occasionally yellow birch.

The relation of beech, sugar maple, hemlock, and yellow birch is clearly central to the interpretation of the forest of the Catskills. Although they occur together in a wide range of proportions, there is little suggestion that they constitute a homogeneous climax mixture throughout the Catskills. Each species has a different curve of distribution on an altitudinal gradient (Fig. 1). Seedling and sapling reproduction of each species is maximum in the stands in which they are the leading dominants (Table 5).

The relations of beech and sugar maple are somewhat equivocal. Beech was clearly the dominant in the presettlement forest, but sugar maple has increased since settlement. In the modern forest each is reciprocally the second most important species in stands dominated by the other (Table 4). Beech saplings are low in density, but are proportionately overrepresented in stands dominated by sugar maple (Table 6), and age-class relations of beech and sugar maple in old-growth sugar maple and beech stands are inverse to each other (Fig. 3). Young sugar maple stands have little or no beech. Beech stands contain more hemlock (Table 4, Fig. 3) and are more similar to old-growth hemlock stands than sugar maple stands (Table 7). Beech occurs more frequently in pioneer stands of red maple than sugar maple does, whereas sugar maple occurs more frequently in pioneer stands of white birch (Table 4). Sugar maple has significant positive associations with a number of other hardwood species not shared by beech. Although they clearly occur together in the Catskills they do not appear to be ecological equivalents, and recent conditions favor sugar maple. Beech has not been able to take advantage of disturbance conditions since settlement, whereas sugar maple has been able to produce nearly pure stands following disturbance as well as grow successfully in the shade of established forests.

The age structure of the old hemlock stands indicates clearly that hemlock in these stands is being replaced by beech and sugar maple (Fig. 3). Hemlock has long been a problem species in the interpretation of succession and climax in the eastern deciduous forest. From the early Clementsian theory which called for a common life form of dominant in the climax, thus excluding hemlock, to the thesis of Martin (1959), that hemlock is the climax dominant over extensive areas of the northeast, opinions have differed widely. Hemlock does have a capacity to persist for a long time and dense stands do resist encroachment by other species for extended periods, but, except where favored by local site conditions, it does not persist and is not a component of a self-

perpetuating, homogeneous climax forest. Curtis (1959) comments that in Wisconsin it does best in moist sites such as valley bottoms, and Hough (1936) says that hemlock in Pennsylvania is favored by cool and moist sites with lower summer air temperature. Adams and Loucks (1971) found that photosynthesis in hemlock increased on cooler slopes. Ohmann and Buell (1968) also comment that hemlock segregates from the other species on steep slopes and ravines. Martin (1959) quotes Marshall as saying that hemlock does not have a correlation between age and size because of the ability of suppressed individuals to survive for long periods and then grow rapidly when released, but Morey (1936a) found a high correlation between age and diameter at breast height of hemlock. Martin further comments that hemlock is capable of growing up into the canopy of sugar maple and replacing it and that its seedlings can persist in the shade to take over when an opening in the canopy occurs. Hemlock reproduction in the Catskills is very low in stands dominated by beech (Table 5, Fig. 3). In the Catskills, at least, there is little suggestion that hemlock can persist in, or successfully invade, sugar maple stands, although young hemlock may persist in old beech stands. Egler (1940) notes that, in the Berkshire Plateau, even clear cutting of everything except hemlock will not change the composition of the subsequent forest with respect to hemlock. Hough (1936) and Morey (1936b) found, in mixtures of beech and hemlock in Pennsylvania, that hemlock was dominant in the larger size classes and beech in the smaller size classes. In the Catskills hemlock has positive significant correlation coefficients with yellow birch and black birch (*Betula nigra*), but not with beech and sugar maple (Fig. 4). Ohmann and Buell (1968) found that it had no significant correlations with any other tree species.

Ordinations of hemlock-hardwood stands (Fig. 5-6) suggest that there is a core of old-growth stands as shown in Table 7. Those dominated by sugar maple or beech tend to perpetuate themselves while the old-growth stands dominated by hemlock do not (Fig. 3), but become increasingly dominated by hardwoods. The ordinations also show that stands of younger and relatively pure sugar maple and hemlock are distributed peripherally in the ordination space as are stands dominated by chestnut oak, red oak, and red maple, all clearly pioneer species on disturbed sites. Sugar maple and hemlock have been more effective than beech in occupying or remaining on sites disturbed in the 200-year history of extensive activity in the Catskills. Hough and Forbes (1943) commented that hemlock in Pennsylvania became established in peak numbers following fire and tornado. Miles and Smith (1960) make the same point about hemlock in southwestern

Nova Scotia. Hemlock seems, similarly, in the Catskills to get started as nearly pure stands which slowly become mixed as hardwoods encroach on them. Their long life span perpetuates these trees for extended periods, but in this they are analogous to pine-hardwood stands. It seems improbable that "... climax forests of hemlock eventually break up and deteriorate, only to return once more, gradually as the dominant form of vegetation" as Langford and Buell (1969), interpreting Hough and Forbes (1943), suggest, except as the result of periodic disturbance. Contrary to this view and to Martin's (1959) assertion that hemlock is the climatic climax species and encroaches on hardwood forests, hemlock is not climax in the Catskills and gives no evidence of spreading effectively into hardwood forests at any altitude.

Yellow birch is most common at altitudes above 2,500 ft and hemlock below 2,500 ft. Yellow birch, like hemlock, persists in mixed stands at lower altitudes in the larger size classes, but it is poorly represented in smaller size classes and reproduction (Fig. 3). In stands in which yellow birch is the leading dominant, it is less common in smaller size classes. It behaves more like black birch as a pioneer or disturbance species. Yellow birch is positively correlated with hemlock, in spite of their different responses to altitude, probably because both appear in moist sites on lower slopes and along streams.

Yew (*Taxus canadensis*), which is a common understory shrub in some areas of northern hardwood forests, is not prevalent in the Catskills, although there are dense mats of it on north slopes of Twin and Hunter Mountains. A favorite deer food, it may be much reduced as it is in similar forests in Wisconsin (Stearns 1951). The effect of deer on the Catskill forest is not clear, although since the 1930's, the herd has been large and a favorite deer food like hobblebush (*Viburnum alnifolium*) is almost universally browsed.

The net result of extensive disturbance of the Catskill Mountain forests is a much more heterogeneous mixture of forest communities than recorded by the surveyors about 1800. The regional dominance of beech and hemlock has decreased. The lower altitudes and more xeric slopes and ridges to 2,500 ft have extensive stands of mixtures of chestnut and red oak and of red maple. Large areas between 1,000 and 3,000 ft are covered by young stands of sugar maple, which is the only one of the major presettlement dominants to increase following settlement. The number of tree species, or richness, is not markedly different in pioneer stands dominated by white birch or red maple than in old-growth stands of beech, yellow birch, or hemlock (Table 9). In fact, the smallest mean number of species was found in old-growth sugar maple stands. Stands dominated by red maple have as high a diversity index,

which incorporates equitability of species, as do the old-growth stands of yellow birch and hemlock. Stands of young sugar maple, red oak, and hemlock have minimum diversity or maximum concentration of dominance. Whittaker's (1964) demonstration that species richness is not related to climax or stability is borne out in the Catskills.

The surveyors' records and descriptions of the Catskills forest between 1,000 and 3,000 ft (305-914 m) suggest a relatively homogeneous presettlement forest dominated by mixtures of beech, hemlock, and sugar maple. This is reminiscent of the classical climax forest of Clements (1936) and other descriptions of a unit northern hardwoods forest. The similarity noted to the presettlement forests of Vermont and Pennsylvania also suggests a widespread convergence of forest under comparatively undisturbed conditions. This raises the traditional dilemma of the climax and with it the nature of the plant association. Langford and Buell (1969) have recently reviewed the controversy concerning the nature of the plant association and revived a modernized version of Clements's (1936) climax association. They set their view opposite that of Gleason's (1939) individualistic concept and the continuum concept (Curtis and McIntosh 1951, Whittaker 1951, Curtis 1959, McIntosh 1967b). It is not appropriate to attempt here a thorough analysis of the views expressed by Langford and Buell, much less a review of the tangled web of climax concepts. Langford and Buell comment, "The climax association in the sense in which we have discussed and defended it, is now largely an abstraction of a historical phenomenon, albeit an interesting one, but the processes that shaped it are operative today in existing aggregations of species." Consideration of the presettlement Catskill forest, abstracted from surveyors' records, and the assessment of existing forest aggregations by current methods of analysis afford an opportunity to consider some aspects of the controversy they note between the association concept of Clements and the concept of vegetation as a continuum while, hopefully, avoiding the scholasticism of earlier polemics on the subject.

Langford and Buell (1969) consider the plant association as an area of definite, but not uniform, composition distinct from adjacent associations. They reject Clements's analogy of the community with an organism, his idea of the climate as the rigidly controlling factor leading to the monoclimate, and ignore his terminology. This leaves us, as they note, with Tansley's (1939) emendation of Clements's (1936) climatic climax. Tansley recognized as climax, and applied the word association to, "... areas characterized by discrete life form, habitat factors remain unchanged, and the only way in which they differ from the climatic climax vegetation is that in addi-

tion to the climatic factors there are edaphic or biotic factors, not depending or only partly and indirectly depending on climate, permanently at work to stabilize the community." In short, a polyclimax.

The vegetation of the Catskills, as reconstructed from the surveyors' records, was indeed an extensive area, relatively undisturbed by man, in which a limited number of tree species such as beech, hemlock, and sugar maple were, in varying proportions, the dominants. That beech had achieved a position of dominance over extensive areas of the eastern United States prior to European settlement is clear from the several studies of presettlement forest noted earlier. Langford and Buell suggest that sugar maple, ". . . would achieve the number one position over a very wide area of the deciduous forests as mapped by Weaver and Clements (1929)," and cite numerous studies suggesting this potentiality. The present-day forests of the Catskills and of portions of Vermont (Siccama 1971) suggest rather that sugar maple has increased following disturbance, and its present relative success in these areas is not so much due to its inherent properties as a dominant but to its ability to persist and spread following disturbance. It is clear that, in many areas, sugar maple or beech, or both, encroach on pioneer hardwood or conifer forest. If one wishes to recognize either beech or sugar maple or combinations thereof with admixtures of other species as climax over an extensive area subject to fluctuating environmental conditions which now favor one against the other and at times favor *Tilia americana* or *Betula lutea* without changing the fundamental nature of the forest greatly, it is entirely in keeping with the Clementsian tradition to do so. Clements's (1936) "faciation" and "lociation," as the concrete subdivisions of the association, allow considerable room for shifts in species composition and proportions of species.

It should, however, be clear that recognition of this varying complex of species each with its own regional, altitudinal, and local response to fluctuating environmental conditions as relatively stable does not, as Langford and Buell suggest, vitiate the utility of the gradient or continuum approach. Such a climax, as Langford and Buell (1969) assert, "leaves room for variability and recognizes gradual change in any association." The assessment of this variability and gradual change is one advantage of the gradient approach as against recognizing a unit potential "climax area" which will then have to be subdivided to account for the obvious variations. Much of the putative "climax" or "climax area," in Langford and Buell's usage, will not actually be covered by climax vegetation, but will only have the potential of being so covered. They do not infer, as Clements did, that all of the area will eventually be capable of developing to the climax, but only that it will be

capable of doing so on "well-developed soil of a depth sufficient to support the climax association." This is reminiscent of a definition of climax as the vegetation which can develop in intermediate sites.

It does not follow, as Langford and Buell (1969) assert, that the continuum concept of vegetation, as developed in the Wisconsin studies (Curtis 1959), is largely a consequence of considering only seral stages nor, as they and Daubenmire (1966) (cf. Cottam and McIntosh 1966) assert, that these studies ignored changes in composition or developmental trends. In the early statement of Curtis and McIntosh (1951) it was clear that the forests constituted a cline from pioneer species to climax species and that successional processes were involved in the series. Curtis (1959) specifically noted the stabilizing influence of sugar maple in southern Wisconsin forests and commented that such a forest was the closest approach to the climax. Curtis also stated, "This likeness of the most mesic members of all the deciduous forest types is largely responsible for the concept of Clements and other early American plant ecologists that the plant formation may be described and delimited solely in terms of its mesophytic or climax community and that all other communities may be related in one way or another to this climax type. If the relations be considered as possible trends rather than as positive eventualities, then the concept certainly receives much support from the available evidence from the mesic forest." A similar point is made by Whittaker (1951) who notes, as previously stated by Weaver and Clements (1929), that succession from initial stage to climax is usually continuous; but then Whittaker comments, "The conclusion, however, that all series in an area converge ultimately on a climatic climax is as much subject to doubt as is the association. We can observe that a tendency toward convergence exists, but we cannot therefore assume that this convergence can be extrapolated to a climatic climax."

The climax as a potential steady state at the end point of a succession may be the state towards which successional processes in the forest tend. If one accepts the view of climax as stated by Tansley (1939) and reaffirmed by Langford and Buell (1969), the process may stop short of the end point for local microclimatic or edaphic reasons which differ from place to place. Since there is no demonstration that the process will stop only at certain places in the seral sequence, these local "climax" areas may be viewed as elements of a continuum as are the seral stages which may be in process towards another end point. It is, of course, necessary to distinguish between areas which are seral and those which have stabilized under local control, which introduces difficulties of its own. Vegetational gradients or continua do not only express differences in successional status

but express, in a quantitative way, differences in vegetation corresponding to changes in the environment which may not be, and commonly are not, successional related.

Langford and Buell (1969) comment that their view of the climax does not envision the succession to the climax of flat peatlands in southern Québec or northern Michigan, hence such areas are not seral to the climax. Curtis and Maycock (1960) incorporate in their forest continuum the gradient from the peatlands in that area to mesic sugar maple stands as well as the gradient from dry, upland pine sites to maple stands. The latter is recognized by Langford and Buell as seral, the other not; thus in the same continuum gradient are included a successional series and an equally continuous series which is not successional. Curtis (1959) recognized prairie continua within an area which Langford and Buell would incorporate in a maple-basswood association. According to Curtis, there was no indication of successional relations between stands on this prairie gradient, and Whittaker (1951, 1956) notes that there is no necessary successional relationship between the elements of the climax pattern discernible in his ordinations of the vegetation of the Great Smoky Mountains.

The diagrams offered by Langford and Buell (1969) showing the general tendency of stand continuum index values to increase in the sapling class, as compared to the mature trees, support their contention that the upland forests of New Jersey converge on a more mesophytic forest dominated by sugar maple. Goff and Zedler (1972), in a similar procedure, construct "succession vectors" illustrating the direction of change of species association values with age by calculating the association indices of tree species by size class in a wide range of conifer-hardwoods forests in central Wisconsin. In the upland forests on good soils they find that the succession vectors of many species (e.g., *Pinus strobus*, *Quercus borealis*, *Acer rubrum*) are directed toward the sugar maple and basswood forest. In this their observations agree with those of Langford and Buell. However, the succession vectors of hemlock and yellow birch move toward sugar maple and basswood but then stop (in the larger size classes), suggesting no tendency of these species to succeed towards sugar maple-basswood forest; and the succession vectors of species of sandy outwash plains (*Pinus banksiana*, *Quercus ellipsoidalis*) also suggest that these species comprise stands which are stable or climax on these sites.

Perhaps the greatest difficulty with the climax association concept as put forward by Langford and Buell and also by Daubenmire (1966) is that it demands recognition, not of the concrete entity on the

ground, but of the potential for it to develop. The assessment of potentiality from primeval remnants is now largely precluded over extensive areas of the earth. Even in Clements's day, when extensive areas of relatively undisturbed vegetation were thought to exist, this was difficult. Now, and in the future, it is difficult to envision any improvement in our ability to reconstruct the primeval state.

Successional tendencies in an area can certainly be inferred, as Langford and Buell (1969) assert, by examination of processes operative in the existing aggregations of organisms. Changes in populations over time can be suggested (with some caveats) by examining the age structure of forests or the changing patterns of association of species in sequential age or size classes. It does not follow that these can be taken as a guide to the unit potential of an entire region. Nothing in the present Catskills forest suggests a tendency to return to the presettlement dominance of beech or the redevelopment of extensive hemlock forest. As the possibility of reconstructing a primeval climax from undisturbed remnants recedes and vanishes we must depend on analyses of current vegetation as it is, not as what it might become.

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