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Drainage, Drought, Defoliation, and Death in Unmanaged Connecticut Forests

G. R. Stephens and D. E. Hill

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Acknowledgements

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Summary

The natural changes during 1959-70 in four Connecticut forests were examined, related to defoliation, drought, and soil drainage, and compared to four other Connecticut woodlands previously studied.

The forests ranged from young to old, moist to dry, and varied in amount of conifers present and in defoliation suffered. Population varied with stand age and disturbance; in 1959 it ranged from 592 to 1119 stems per acre. During 1959-70 population declined about one-tenth in three undisturbed tracts, but increased nearly two-thirds in one disturbed by defoliation and wind. Birth and death of trees were generally unrelated to soil moisture. Birth declined, however, with increasing age in three undisturbed stands. Death, on the other hand, declined with decreasing population.

Basal area, or bulk of the forest, ranged from 76 to 147 square feet per acre in 1959. Stands with many conifers had about 50 percent more basal area than those without. During 1959-70, basal area increased in all tracts. Accretion on persisting trees varied from 17 to 29 percent but showed no clear relation to soil drainage. Mortality varied from 5 to 10 percent of 1959 basal area and was also unrelated to drainage. Since ingrowth was a steady, 1 to 2 percent of persisting basal area, net increase depended chiefly on the balance between accretion and mortality. Considerable differences in growth and loss existed among species.

In total, 24 major and 13 minor species were represented. The four forests were equally diverse in 1959 and their diversity decreased slightly during 1959-70. Composition of the canopy, however, changed little, and the forests looked nearly the same in 1970 as in 1959.

Transitions during 1959-70 among species groups dominating one-eightieth-acre plots were obtained. For forests without conifers the transitions anticipate much maple and birch but little oak in the future. This is much the same as predicted for other hardwood forests observed for 40 years. However, in forests with many conifers, mostly hemlock, the anticipation is many conifers, few maple and birch, and almost no oak. Thus, some markedly different forests are predicted.

Drought appeared to change mortality rate little. Repeated defoliation, however, increased mortality on all but poorly drained soils. Death of major species was 2.3 percent annually in twice-defoliated moderately and well drained sites compared to 1.5 percent in a once-defoliated dry site and 1.3 percent in undefoliated stands. Oak, the prime target of defoliators, lost most: repeated defoliation increased its mortality about half.

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Introduction

Several earlier reports (Collins 1962, Olson 1965, Stephens and Waggoner 1970) described the changes occurring during 30 to 40 years in four unmanaged mixed hardwood woodlands. The relations of population, change, and growth to soil moisture were examined. However, all the tracts lie within 13 miles of one another in central Connecticut and, unfortunately, the division of the sample among moistures classes is irregular. Three of the tracts are in the Meshomasic State Forest (Fig. 1); therefore, we shall refer to all of them as the Meshomasic tracts hereafter.

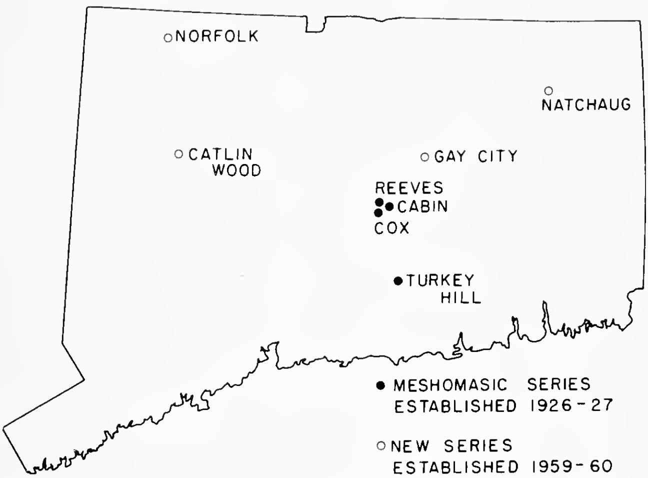

Fig. 1 Locations of the New tracts (open circles) described in this bulletin and the Meshomasic tracts (closed circles) described earlier (Stephens and Waggoner 1970).

During 1959-60 sample transects were established in four widely separated forests on soils common in Connecticut. The new tracts were selected to sample over a greater area of Connecticut, to provide great contrast in age, climate, and drainage and to examine the influence of these factors on change in the forest.

Additionally, the selection afforded contrast of forests with few or many conifers. Further, the trees that grew on the four tracts were subjected to varying degrees of drought and insect defoliation during the last decade. This report will summarize the changes that have occurred during the last decade, relate them to soil drainage, drought, and defoliation and compare them to changes observed during 40 years in the Meshomasic tracts.

The locations of the new tracts are shown in Figure 1 and their characteristics are summarized in Table 1.

Table 1. Characteristics of the new tracts

	Age	Climate	Hardpan	Conifers	Defoliation
Gay City	Young	Driest and warmest	No	None	Most
Natchaug	Young	Dry and warm	Yes	None	None
Norfolk	Older	Wettest and coolest	Yes	Many	None
Catlin Wood	Oldest	Moist and cool	Weak	Many	Some

The Forests

The four tracts all lie in Connecticut's upland region of metamorphic rocks and glaciated soils. Gay City and Natchaug, the relatively young woodlands, are in the eastern highlands; the older woodlands, Norfolk and Catlin Wood, are in the western highlands. The tracts vary in soil, climate, and history.

The Gay City tract, in Gay City State Park, is a mixed hardwood woodland with few conifers. One portion, in Hebron, at an elevation of 550 to 600 feet occupies an east-facing slope that varies from 4 to 11 percent. The soils have formed on friable glacial till derived chiefly from Bolton schist. The well drained Charlton soil occupies the upper slopes; the moderately well drained Sutton occupies the lower slopes, and the poorly drained Leicester occupies the drainage swales. Another portion of the Gay City tract that lies about 0.6 miles to the west in Glastonbury occupies a ridgetop whose crest slopes gently northward. Here, the somewhat excessively drained, shallow Hollis soil dominates the landscape. On all sites the abundance of rocks, the presence of old charcoal hearths and stone walls and the absence of a plow layer suggest that the land was cleared, but never tilled. In 1970 increment borings revealed that the dominant trees on the somewhat excessively drained ridgetop were about 60 to 65 years old and the smaller trees, about 50 to 60 years. Further downslope on the moister sites scattered dominant trees exceeded 70 years and in the poorly drained site some exceeded 100 years. The remaining smaller canopy trees were about 60 years old. This tract is closest, about 10 miles to the northeast, to three of the Meshomasic tracts reported earlier (Stephens and Waggoner, 1970).

The Natchaug tract is in a stand of mixed hardwoods in the Natchaug State Forest in Eastford, about 25 miles northeast of Gay City. Its gently rolling topography ranges in elevation from 700 to 750 feet and its north-facing slope varies from 1 to 7 percent. The soils have formed on compact glacial till derived from Eastford granitic gneiss. A notable characteristic is the presence of hardpan throughout the sample area. The soils include the moderately well drained Woodbridge soil on the upper slopes and the poorly drained Ridgebury soil on the lower slopes. Stone walls indicate that the land was once cleared, but numerous rocks and absence of a plow layer suggest it was never tilled. Increment borings revealed that in 1970 the larger scattered dominant trees were about 70 to 80 years old while many of the smaller canopy trees were 50 to 60 years.

Catlin Wood is a stand of hemlock white pine, and transition hardwoods growing on a nearly flat plain at an elevation of about 900 feet in the White Memorial Foundation, Litchfield. The underlying bedrock is largely Brookfield diorite gneiss. The soils developed on glaciolacustrine sands which thinly mantle the underlying glacial till. On the lower slopes the glacial till forms a weakly developed hardpan at depths of 20 to 30 inches. Slopes range from 1 to 4 percent. On the upper slopes the soils include the well drained Agawam and the moderately well drained Ninigret formed in deep sands, and the moderately well drained Sudbury formed in sand and gravel. The poorly drained Walpole soil occupies a broad drainage swale at the base of the terrace. Catlin Wood, oldest of the four tracts, is about 185 years of age (Smith 1956). Its origin is obscure, but since early 19th century the main disturbance has been cutting or windthrow. Removal or death of chestnut has permitted a second age group of mixed hardwoods and hemlock, 50 to 60 years old, to develop.

The Norfolk tract, in the privately owned Great Mountain Forest, lies about 18 miles north of Catlin Wood in a region of rugged terrain in the Berkshire Hills. Its east-facing slope varies from 1 to 15 percent and lies at elevations between 1400 and 1500 feet. The soils are formed on compact glacial till derived principally from Canaan Mountain schist. Hardpan is present at depths of 20 to 30 inches, restricting downward drainage and creating seepage areas near the base of the slope. The soils include the well drained Paxton on the upper slopes, the moderately well drained Woodbridge soil on the lower slopes and the poorly drained Ridgebury at the base of the slope. Ring counts of recently cut trees adjacent to the transects reveal that the larger white ash and red oak were 80 to 90 years in 1970. Their age, the presence of sprout clumps and charcoal hearths suggest that this area was heavily cut around 1880. Smaller and younger beech, yellow birch, and black cherry, about 60 years, suggest a second disturbance. However, their origin is not clear. Hemlock was not used for charcoal and it may have been removed at a later date. Persistent stumps indicate that chestnut was also present. Therefore, cutting of either hemlock or chestnut could have permitted the younger age groups to become established. The absence of fire scars suggests that this tract was not burned.

Thus, we see that in all tracts older trees comprise a portion of the canopy, but except for Catlin Wood, the remainder of the stand appears younger and even-aged. Clearly, Catlin Wood is oldest, followed by Norfolk. Natchaug and Gay City are of similar age. However, the forest on the dry ridge of Gay City is clearly youngest and, despite the old, scattered dominants on the moister sites, the majority of that forest is likely younger than Natchaug. As we shall see, the older dominants comprise a larger portion of total stems at Natchaug than at Gay City.

The Climate

Climate varies somewhat among tracts. Precipitation data were obtained from stations closest to each tract. At Hartford's Brainard Field, about 10 miles west of Gay City, average annual precipitation was nearly 44 inches during 1949-58. During 1959-69 it decreased to 37 inches. At Mansfield Hollow Dam, 10 miles southwest of Natchaug, precipitation averaged 43 inches during 1953-58 but it decreased to slightly more than 39 inches during 1959-69. At Torrington, about 8 miles northeast of Catlin Wood, annual precipitation averaged 48 inches during 1949-58, but decreased to 42 inches during 1959-69. The weather station 1.5 miles east of the Norfolk tract recorded average precipitation of 55 inches annually during 1949-58. During 1959-69 annual precipitation declined to 48 inches. Thus, Norfolk was the wettest tract followed in turn by Catlin Wood, Natchaug, and Gay City. During 1959-69, annual precipitation was less than the previous average in 8 of 11 years in all tracts. The average reductions were 15 percent at Gay City, 12 at Norfolk and Catlin Wood, and 8 percent at Natchaug.

Temperature data were available only for Gay City, Norfolk, and Natchaug. During 1959-69, Norfolk was coolest; its average annual temperature was slightly less than 44 F. Natchaug was warmer, 47 F, and Gay City warmest, 49 F. Although we have no actual record, because of its location and elevation, average temperature at Catlin Wood was likely between that of Norfolk and Natchaug.

Defoliation

Major defoliation was recorded only for Catlin Wood and Gay City.[1] In 1956, Catlin Wood was more than 50 percent defoliated by the gypsy moth (*Porthetria dispar*). In 1962, several kinds of defoliators attacked Gay City. Most of the tract was more than 50 percent defoliated, but the somewhat excessively drained ridgetop was less than 50 percent defoliated. Again in 1967, all but the dry ridgetop at

[1] Unpublished defoliation maps in the files of the State Entomologist, Connecticut Agricultural Experiment Station, New Haven.

Gay City was more than 75 percent defoliated by the oak leaf tier (*Croesia semipurpurana*) or other closely related insects.

All tracts received less precipitation during the period of observation than before. Hopefully, because of differences in defoliation, we can clearly separate the effects of drought and defoliation.

METHODS

In each tract a base line was established generally perpendicular to the contour and across a series of drainage classes (Fig. 2). Along

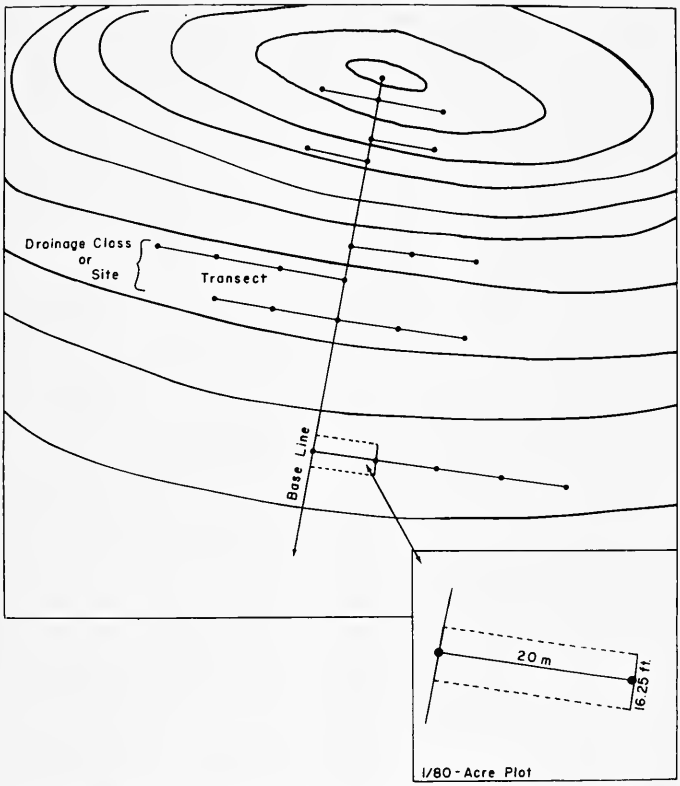

Fig. 2 Schematic representation of baseline, sample transects and 1/80-acre plots in relation to topography and drainage classes (sites). The insert shown the width of a sample transect and the length a rectangular 1/80-acre plot.

the base line the soils were identified according to profile morphology and slope position. Drainage classes, or sites, were identified according to the Soil Survey Manual (1951). Within each drainage class, transects were established parallel to the contour on one or both sides of the base line. The transects were 16.25 feet wide and approximately 66 feet (20 m) to 394 feet (120 m) long. Where possible, approximately equal areas were sampled in each drainage class (Table 2).

Table 2. Sample area (acres) of drainage classes

	Poorly Drained	Moderately Well drained	Well Drained	Somewhat Excess. drained	All
Gay City	.10	.10	.15	.10	.45
Natchaug	.10	.20	—	—	.30
Norfolk	.15	.15	.10	—	.40
Catlin Wood	.10	.22	.12	—	.44
All	.45	.67	.37	.10	1.59

In 1959-1960 all stems larger than 0.5 inch in diameter at 4.5 feet above ground (d.b.h.) were located, identified, and described. There were 24 major tree species and 13 minor species, small trees and shrubs. Compared to earlier surveys (Olson 1965, Stephens and Waggoner 1970) the number of minor species increased from 7 to 13 to include winterberry, spicebush, highbush blueberry, and witchhobble, arrowwood, and witherod viburnums. Description included d.b.h., crown class, and whether or not the stem was in a sprout clump. Crown class is defined in Forest Terminology (Soc. Amer. For., 1950). In 1970, the same information was again recorded for all living stems 0.5 inch d.b.h. or larger. Mortality of stems formerly present and ingrowth of new stems were noted. In sprout clumps, new sprout ranks were assigned where death had removed some stems.

In what follows the tables comparing species represent averages over all tracts. The comparisons among tracts are the averages over all species.

POPULATION

In 1959 the population of stems per acre of major species varied among tracts and drainage classes. The relatively young Gay City had 25 percent more and the old Catlin Wood, 29 percent fewer stems than the average of all tracts. The poorly drained site in Catlin Wood contained less than 400 stems per acre whereas the somewhat excessively drained soil of Gay City supported over 1000 (Table 3).

During 1959-70, the number of major species stems per acre declined on all sites in all tracts except Catlin Wood. Norfolk decreased 4 percent, Natchaug declined 12 percent, and Gay City decreased fully 17 percent. On the other hand, the average stem population at Catlin Wood increased 58 percent. Thus, at Natchaug and Gay City the decline resembled the 12 percent decrease in the Meshomasic tracts during 1957-67 (Stephens and Waggoner 1970), but old Catlin Wood, meanwhile, increased its population markedly.

Table 3. Number of stems per acre

Site	Year	Gay City	Natchaug	Norfolk	Catlin Wood	All
		Major Species				
Poorly Drained	1959	503	734	577	392	554
	1970	402	634	543	493	521
Mod. Well Drained	1959	865	578	765	501	636
	1970	654	518	744	769	672
Well Drained	1959	798		724	426	655
	1970	630		694	821	711
S. Excess. Drained	1959	1046				1046
	1970	996				996
All	1959	802	630	684	456	643
	1970	666	556	656	722	659
		Minor Species				
Poorly Drained	1959	473	382		151	224
	1970	744	312		151	268
Mod. Well Drained	1959	302	302	7	170	192
	1970	201	252	7	376	231
Well Drained	1959	376			64	172
	1970	409			56	182
S. Excess. Drained	1959	91				91
	1970	60				60
All	1959	317	329	3	136	190
	1970	360	272	3	237	219

Minor species also varied among tracts (Table 3). In 1959, they were abundant in Gay City and Natchaug, somewhat below average in Catlin Wood and nearly absent in Norfolk. The reader will recall that we report 13 minor species compared to 7 reported earlier (Olson 1965, Stephens and Waggoner, 1970). However, in 1959, these additional six species comprised only 8 percent of all minor species, a small contribution. Although the number of stems generally decreased with increasing dryness, the well drained soil of Gay City contained more stems than did the moderately well drained. In Catlin Wood moderately well drained soils supported the largest number of minor species stems in 1959.

During 1959-70 the total number of minor species stems increased about 15 percent. This appears to contradict the 25 percent decrease during 1957-67 reported for the Meshomasic tracts. However, the six new species now comprise about 23 percent of total minor species and account for the increase. The original group of seven minor species decreased similarly to the previous report. The largest single gain in the new group of six minor species occurred on the poorly drained site of Gay City. Minor species also increased on the well drained site of Gay City and the moderately well drained of Catlin Wood.

Young stands frequently contain many stems and old stands, few. In 1959, Gay City's number of stems per acre resembled that of the Cox tract, a relatively young stand in 1937 (Table 2, Stephens and Waggoner 1970), and its population was changing at about the same rate. Young Natchaug and older Norfolk resemble the older, less densely populated Turkey Hill tract in 1937. They, too, were changing at about the same rate as Turkey Hill. In 1959 old Catlin Wood had about the same number of stems as 65- to 80-year-old mixed hardwood stands of the Meshomasic tracts. However, the dramatic rise in number of stems during 1959-70 suggests a much younger stand in 1970. Thus, stem number alone is not always a good measure of stand age. We must wait for Distribution of Diameter to see how the stands are structured.

The variation in species composition among tracts reflects their history, age and drainage, but variations among sites result mainly from differences in moisture. In 1959, 10 major and 1 minor species dominated the population (Table 4). In all tracts, red and sugar maples comprised 24 percent; yellow and black birches, 15 percent; oaks, 12 percent; beech, 10 percent; hemlock, 9 percent; witchhazel, 12 percent of all stems. By 1970, the proportion of maples, birches, and witchhazel declined slightly, but oaks decreased by half. Beech increased slightly, while hemlock nearly doubled.

On the poorly drained sites hemlock, red maple, yellow birch, and witchhazel comprised 67 percent of the stems in 1959. In 1970 they contributed 64 percent, but another minor species, spicebush, supplied an additional 15 percent.

On the moderately well drained sites, beech was more common than hemlock and together with red maple, yellow birch, and witchhazel comprised 56 percent of stems in 1959. Sugar maple contributed 7 percent; black birch, 10 percent; and oaks provided 11 percent of all stems. During 1959-70, the proportions of maples and birches decreased slightly and those of beech and witchhazel increased. Hemlock rose three-fold to 12 percent, but oaks decreased to 5 percent.

On the well drained sites beech, red maple, and witchhazel contributed 36 percent initially. Sugar maple provided 12 percent; oaks, 17 percent; but yellow and black birch comprised only 9 percent. By 1970 the maples remained nearly unchanged, beech increased slightly, and the birches decreased slightly. As on the moderately well drained sites, hemlock increased three-fold to 19 percent.

Only Gay City had a somewhat excessively drained soil and little change occurred between 1959 and 1970. Red maple comprised 54 percent; black birch, 15 percent; and oaks, 17 percent of all stems. Only on this site did oaks maintain their proportions of the stand.

The results so far are not surprising. Moist sites support hemlock, yellow birch, witchhazel, and spicebush. As drainage improves, the proportions of beech, black birch, sugar maple, and oaks increase. Excessive drainage eliminates sugar maple and yellow birch, greatly reduces the minor species, but favors oak. Of course, the ubiquitous red maple makes a substantial contribution on all sites. But these are averages over all tracts. Let us examine the differences among tracts.

Conifers, mainly hemlock, occurred only in Norfolk and Catlin Wood and initially comprised 26 and 18 percent of those stands. At cool, moist Norfolk, beech, hemlock, and sugar maple were abundant, 78 percent, but black birch and oaks were rare. Red maple and yellow birch together contributed 15 percent and minor species were nearly absent. A decade left this hemlock-beech-maple-birch forest unchanged in total population and its proportions.

Catlin Wood was also a hemlock-beech-maple-birch forest. In 1959, compared to Norfolk, beech, hemlock, and sugar maple were less abundant, 33 percent, while black birch and oak were more common, 15 percent. Yellow birch and red maple initially contributed 28 percent and witchhazel provided 14 percent. Unlike static Norfolk, the population of Catlin Wood nearly doubled in a decade for both major and minor species. Maples declined by half, birches by a third, and beech slightly. Over all moisture classes, however, hemlock increased 2-fold to 34 percent. This large increase in hemlock was matched by a proportional decline in maple, birch, and beech. In terms of stem number, however, maples decreased 13 percent, but the number of birch actually increased 6 percent, and beech rose fully 53 percent. Although the proportion of witchhazel scarcely changed between 1959 and 1970, its numbers increased 76 percent. Something, possibly disturbance, favored this great increase in population, and we will return to this later.

Gay City and Natchaug had no conifers, hence the proportions of other species will be greater. In 1959, Gay City contained 20 percent red maple, 10 percent yellow birch, and 16 percent oak. Sugar maple comprised 5 percent and black birch, 8. Bluebeech and witchhazel contributed 8 and 9 percent of the proportion of total stems. By 1970 there were only a few major changes in the composition of this

Table 4. Number of stems of major and minor species (percent of total) present in 1959 and 1970 in all tracts

	Poorly Drained		Moderately Well Drained		Well Drained		Somewhat Excessively Drained		All Classes	
	1959	1970	1959	1970	1959	1970	1959	1970	1959	1970
Major Species										
Sugar Maple	.3	.3	6.7	5.4	12.3	11.1			5.7	5.1
Red Maple	19.0	16.7	14.6	13.0	11.0	11.4	54.0	55.2	18.3	16.8
Red Oak	2.6	.8	5.2	3.0	9.1	5.4	8.8	8.6	5.7	3.4
Black Oak					1.0	.0	1.8	1.9	.4	.1
Scarlet Oak			.2	.2			7.1	7.6	.7	.6
White Oak	3.4	2.5	5.9	1.7	6.8	1.5	.9	.0	5.1	1.7
Yellow Birch	12.6	12.7	9.4	7.3	2.6	1.8			7.8	6.8
Black Birch	1.7	2.5	10.1	10.6	6.5	5.7	14.2	16.2	7.4	7.8
Mockernut Hickory					.3	.3			.1	.1
Pignut Hickory	2.0	1.1	1.8	.7	4.5	3.0			2.3	1.3
Shagbark Hickory	.6	.0			1.0	.9			.4	.2
Beech	.6	1.1	16.7	18.0	14.0	17.1			10.4	12.2
White Ash	2.9	1.7	1.8	1.2	1.9	1.2			2.0	1.2
Black Ash	.3	.3							.1	.1
Basswood	.9	.3							.2	.1
American Elm	.6	.6	.2	.2					.2	.2
Bigtooth Aspen							.9	.0	.1	.0
Pepperidge	.3	.6							.1	.1
Black Locust	.3	.0							.1	.0
Black Cherry			.4	.2	1.6	.9	.9	.0	.6	.3
Sassafras	.9	.3	.2	.2			3.5	4.8	.6	.5
White Pine	.3	.6	.0	1.5	.3	.6			.2	.9
Hemlock	21.8	23.8	3.8	11.6	6.2	18.6			8.8	15.5
Redcedar	.3	.0							.1	.0
Stems/Acre	544.3	520.8	636.3	672.0	654.5	710.8	1046.3	996.0	643.1	658.8

Minor Species										
Chestnut	.6	1.4	1.6	4.5	2.3	1.5	8.0	4.8	2.0	3.0
Fl. Dogwood			1.4	1.0	5.5	7.2			1.9	2.1
Bluebeech	8.6	3.1	.7	.2	1.6	2.7			2.9	1.5
Shadbush	1.4	.6	1.3	1.2	.6	0.9			1.1	.9
Hophornbeam	.9	.3	.2	.0					.3	.1
Gray Birch			.4	.0			.0	1.0	.2	.1
Witchhazel	13.5	10.5	15.5	15.8	10.7	8.1			12.5	11.5
Winterberry	2.0	2.0	.7	.0					.8	.5
Spicebush	1.4	14.7							.4	3.7
Blueberry	.3	.6	.7	.8					.4	.5
Witchhobble			.4	1.0					.2	.4
Arrowwood	.0	.8							.0	.2
Witherod			.4	1.2					.2	.5
Stems/Acre	223.5	268.2	192.2	231.0	171.7	182.4	90.5	60.4	189.9	219.4
Total										
Stems/Acre	777.8	789.0	828.5	903.0	826.2	893.2	1136.8	1056.3	833.0	878.2

maple-birch-oak forest. Oaks decreased by half, birches remained unchanged and maples increased about a fifth. Bluebeech was reduced by nearly half, witchhazel decreased slightly, but spicebush increased about 9-fold on the poorly drained site.

Natchaug was also a maple-birch-oak forest. In 1959, red maple comprised 28 percent; oaks, 16 percent; and black birch, 16 percent of the total stems. Witchhazel, however, contributed fully 30 percent of all stems. Unlike Gay City, sugar maple and yellow birch were rare. During 1959-70, only a few changes occurred. Total stems declined about 14 percent; minor slightly more than major species. The proportion of oaks decreased about 35 percent. Red maple increased slightly, but black birch increased more than a third. Witchhazel decreased to 24 percent.

Thus, we see that loss of oak during 1959-70 was the dominant event at Gay City and Natchaug, but the forests still remain essentially maple-birch-oak. In the next section, Diversity, we shall see how these stands differ in population and variety.

DIVERSITY

The verbal descriptions given these tracts, hemlock-beech-maple-birch and maple-birch-oak imply variety. Initially 24 major and 12 minor species were in the sample although not all occurred in each tract or drainage class. In 1959, Gay City boasted 30 species, Natchaug and Catlin Wood each had 15 and Norfolk, only 10. By 1970, bigtooth aspen, black locust, and redcedar had disappeared from the sample, but arrowwood had established itself among the minor species. During the decade the poorly and somewhat excessively drained sites each lost three major but gained one minor species. Since losses exceeded gains, we see decreased variety in 1970.

Several numerical expressions of variety exist, and we have chosen one which considers both variety and population (Pielou 1969, p. 232). Average diversity, H, is expressed:

$$H = \frac{1}{N} \log_2 \frac{N!}{N_1!\,N_2!\,\ldots\,N_s!} \text{ bits/individual}^{2}$$

where N is the total population, and $N_1, N_2, \ldots N_s$ are the numbers of individuals in the first, second, . . . and last of *s* species.

For a given population, H is maximum when all species comprise equal proportions of N. As population decreases or is concentrated in fewer species, H decreases. Although population increased slightly during 1959-70, diversity decreased (Table 5). Loss of species and

[2] Unfortunately, the argument of log was erroneously inverted in Bulletin 707 (Stephens and Waggoner 1970) and should be as it is here.

Table 5. Diversity according to number of species and stems per acre

Site	Year	Gay City	Natchaug	Norfolk	Catlin Wood	All
Poorly Drained	1959	3.3	2.2	1.4	2.5	3.4
	1970	2.8	2.2	1.3	2.3	3.3
Mod. Well Drained	1959	3.5	2.7	2.2	3.1	3.6
	1970	3.1	2.7	2.1	3.1	3.5
Well Drained	1959	3.6		1.7	2.7	3.8
	1970	3.4		1.6	2.1	3.5
S. Excess. Drained	1959	2.2				2.2
	1970	2.1				2.1
All	1959	3.9	2.6	2.4	3.2	3.8
	1970	3.8	2.6	2.3	3.0	3.8

gain of individuals in species already populous caused the decrease. The relatively large values for diversity at Gay City reflect both large population and large number of species. The low diversity of its somewhat excessively drained site results from the relatively few species despite a large population. The relatively low diversity at Norfolk reflects both smaller population and fewer species.

Within any tract, diversity appears unrelated to drainage class. Moreover, the change in diversity during a decade is small. The values reported in Table 5, however, resemble those in other mixed hardwood stands of the Meshomasic series (Stephens and Waggoner 1970).

BIRTH AND DEATH

Periodic enumeration of a population simply reveals net change. We see only that the population rises, falls, or remains constant. Unless we pursue the fate of individuals, we learn nothing of population dynamics. To determine whether replacement or turnover among individuals is slight or great we must examine each stem to determine whether it has been persisted, died, or newly joined the population.

Birth, ingrowth of new individuals into the population, and death are necessary events in the life of a changing forest.[3] Without birth there can be no replacement or opportunity for change. Unless death removes excess trees the persistent have no chance to grow. In young,

[3] We use the terms, birth and death, to denote change among numbers of stems and to distinguish this description from the ingrowth and mortality of the section entitled, Growth.

dense forests death normally outraces birth; the population declines rapidly and permits the persistent to grow. In old or stable forests, birth and death are closely matched; the population changes little and the persistent grow slowly. In the disturbed forest, birth outstrips growth and the population burgeons.

In our discussion of population we noted little change in Norfolk, marked decreases at Gay City and Natchaug, and a large increase in Catlin Wood. By our definitions above, Gay City and Natchaug portray the young forest; Norfolk the stable; and Catlin Wood the disturbed. Let us examine the dynamics of birth and death in these tracts so we may better understand the changes.

Table 6. Death during 1959-70 as percent of stems in 1959

Site	Gay City	Natchaug	Norfolk	Catlin Wood	All
		Major Species			
Poorly Drained	30	26	7	15	18
Mod. Well Drained	34	27	13	19	22
Well Drained	38		15	6	24
S. Excess. Drained	18				18
All	20	27	12	15	22
		All Species			
Poorly Drained	45	30	7	67	28
Mod. Well Drained	39	33	14	18	26
Well Drained	37		15	75	27
S. Excess. Drained	24				24
All	36	32	12	38	27

In what follows, we express death, the number lost, and birth, the number gained, as a proportion of stems alive in 1959. Over all drainage classes, death was moderate (Table 6). By 1970, about a third of the stems of all species present in 1959 died at Gay City, Natchaug, and Catlin Wood. Death in Norfolk was slight, an eighth of the population. Over all tracts average death differed little among drainage classes; during 1959-70 about a fourth of the stems in each drainage class, approximately 2 percent annually, died.

However, the relation of death to drainage differed among tracts. At Gay City, death decreased steadily from 45 percent on the poorly drained to 24 percent on the somewhat excessively drained soils. At Natchaug about a third of the 1959 population died, but there was little difference between the two drainage classes. At Norfolk only a fourteenth of the population died on poorly drained soil, but death doubled on the better drained soils. At Catlin Wood two-thirds of the stems on poorly drained and three-fourths on the well drained soil died, but only a fifth succumbed on the moderately well drained soil. Loss of major species at Gay City and Natchaug was about twice that in Norfolk and Catlin Wood. For any comparable drainage class, Gay City had greater loss than any other tract.

Normally, in crowded stands we expect much, and in sparse stands, little death. We see this clearly for major species (Figure 3). Thus

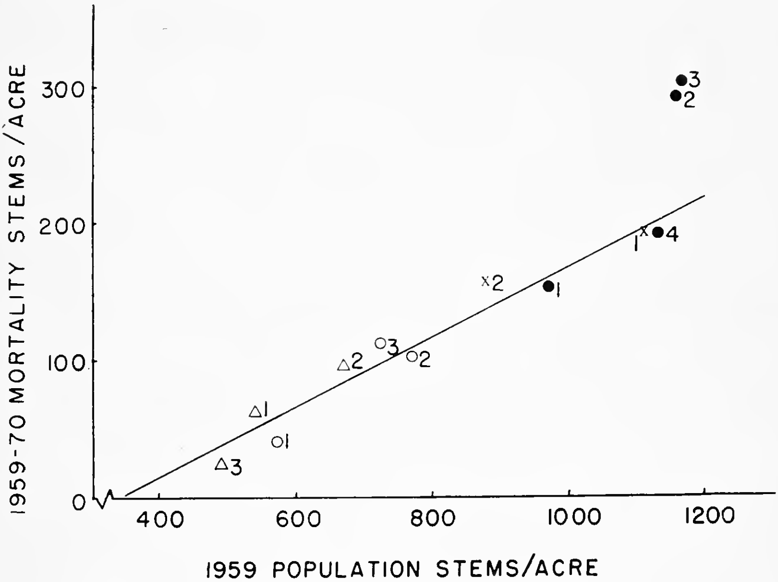

Fig. 3 Mortality of major species during 1959-70 in relation to total population in 1959. The numbers are drainage class: 1, poorly drained; 2, moderately well drained; 3, well drained; 4, somewhat excessively drained. The tracts are Gay City (closed circle), Natchaug (X), Norfolk (open circle), Catlin Wood (open triangle). The line is the trend of mortality in undefoliated Natchaug, Norfolk and Catlin Wood.

loss of major species during 1959-70 was related to total population rather than to drainage class.

Death of minor species was generally about twice that of major, but varied more among drainage classes. Although minor species aid in maintaining diversity, the major species really determine the character of the forest.

In the discussion of diversity we learned that three species, bigtooth aspen, black locust, and redcedar, were eliminated from the sample. However, on individual tracts additional species disappeared and were not replaced by birth. At Gay City, black cherry and shadbush, never numerous, succumbed. In Natchaug, hophornbeam and gray birch were eliminated. The proportion of trees dying was great for some species and the average over all tracts is in Table 8. However, among major species with a great proportion dying, only white oak and pignut hickory were numerous. Bluebeech was the only plentiful minor species with great loss. Replacement within these species through birth was slight, thus the decline was real as well as relative.

During 1959-70, birth averaged 270 stems per acre compared to 227 that died. On the average, new stems comprised 27 percent of the 1970 population. Birth was not consistently related to drainage class or tract. Birth was least at Norfolk and greatest at Catlin Wood (Table 7).

Table 7. Birth during 1959-70 as percent of stems in 1959

Site	Gay City	Natchaug	Norfolk	Catlin Wood	All
		Major Species			
Poorly Drained	10	12	1	41	12
Mod. Well Drained	9	16	10	72	28
Well Drained	17		11	98	33
S. Excess. Drained	14				14
All	13	15	8	73	24
		All Species			
Poorly Drained	63	14	1	48	30
Mod. Well Drained	12	20	11	89	35
Well Drained	25		11	93	35
S. Excess. Drained	17				17
All	28	18	8	82	32

Norfolk, with 8 percent birth and 12 percent death, declined slightly in population. Dead sugar maple and yellow birch were not replaced, but birth of beech exceeded death.

At Natchaug, 32 percent death overshadowed 18 percent birth. Half of the red maple that died were replaced, while two black birch arose for each one lost. Birth of chestnut exceeded death four-fold.

Gay City exhibited considerable turnover, 20 percent birth compared to 36 percent death. Birth of maple was nearly twice its death whereas birch replaced only half its losses. Dead white oak and white ash were not replaced. Among the minor species, birth of chestnut was one-third greater than death, while only half the lost witchhazel was replaced. Bluebeech declined greatly because death exceeded birth 15-fold.

In Catlin Wood, 82 percent birth far exceeded the recorded 38 percent death. Few maple and no oak that died were replaced. Birth of birch slightly exceeded death, while birth of beech surpassed death 8-fold. Hemlock and witchhazel, however, swelled the population in 1970. In 1959, hemlock had 103 and witchhazel 85 stems per acre. During 1959-70, hemlock lost none and witchhazel lost about 36, but they gained 226 and 101 stems per acre, respectively. These two species account for about 80 percent of the population increase in Catlin Wood.

Now we see that our stable forest, Norfolk, had both low birth and death rates; some turnover occurred within a persistent species, beech. In the young forests, Gay City and Natchaug, their similar death rates exceeded birth. Turnover was marked for persistent maples and birches. The minor species, chestnut, increased on both tracts. In Catlin Wood death rate differed little from Gay City and Natchaug, and turnover was noted for birch. The greatly increased birth rate, however, was evident only for witchhazel and hemlock. Witchhazel, an understory species declined at Gay City and Natchaug and hemlock, a persistent, tolerant species, remained steady at Norfolk.

We have called Catlin Wood disturbed, yet no disturbance occurred during 1959-70. However, the prostrate remains of large trees indicate sporadic loss of old trees during storms, and thickets of hemlock seedlings often occupy the openings. We can document another disturbance. The reader will recall that greater than 50 percent defoliation occurred in 1956. The field notes of 1959, when the first measurements were taken, indicate that dead red and white oaks from 2 to 12 inches d.b.h were present, and apparently some died in 1958. The notes further record the presence of numerous hemlock seedlings too small to be included in the tally. Therefore, disturbance occurred before 1959, and whether windthrow or defoliation, it permitted hemlock seedlings to grow and encouraged witchhazel to sprout.

The 27 percent loss over all tracts and sites is less than the 34 percent observed during 1957-67 on the Meshomasic tracts (Stephens and Waggoner 1970), largely because of the very low death rate at Norfolk. On the other hand, the average 32 percent birth rate greatly exceeds 19 percent observed in the Meshomasic tracts during 1957-67, largely because of fecund Catlin Wood.

Our analysis so far tells us how many trees died and how many were born. We know that those newly added by birth must be small, but we know not whether those dying were small or large. Later, the section entitled, Growth, will permit us to judge the size of trees lost. But, first, let us examine another facet of population, Single Stems.

Table 8. Birth and death (stems/acre) between 1959 and 1970 in all tracts

	Poorly Drained		Moderately Well Drained		Well Drained		Somewhat Excessively Drained		All Classes	
	Birth	Death	Birth	Death	Birth	Death	Birth	Death	Birth	Death
Major Species										
Sugar Maple	0	0	0	6	16	19			4	7
Red Maple	7	22	15	18	19	8	91	121	18	23
Red Oak	0	13	0	16	8	35	0	10	2	20
Black Oak						8	0	0	0	2
White Oak	2	9	0	34	0	43	0	10	1	28
Yellow Birch	16	13	10	22	5	11			10	16
Black Birch	11	5	24	12	0	3	30	20	15	8
Pignut Hickory	0	7	0	9	5	16			1	9
Shagbark Hickory	0	4			0	0			0	1
Beech	5	0	43	19	43	5			30	9
White Ash	0	9	0	5	0	5			0	6
Basswood	0	5							0	1
Bigtooth Aspen							0	10	0	1
Pepperidge	2	0							1	0
Black Locust	0	2							0	1
Black Cherry			0	2	0	5	0	10	0	3
Sassafras	2	7	0	0			20	10	2	3
White Pine	2	0	13	0	3	0			7	0
Hemlock	22	5	73	0	115	0			64	1
Redcedar	0	2							0	1
Total Major	69	103	178	143	214	158	141	191	155	140

Minor Species										
Chestnut	9	2	33	6	11	16	40	81	21	12
Fl. Dogwood			0	3	24	5			6	3
Bluebeech	0	43	2	6	11	0			3	15
Shadbush	2	9	2	2	5	3			3	4
Hophornbeam	0	5	0	2					0	2
Gray Birch			0	3			10	0	1	1
Witchhazel	22	45	63	48	27	43			39	43
Winterberry	11	11	0	6					3	6
Spicebush	110	5							31	1
Blueberry	2	0	2	0					1	0
Witchhobble			6	0					3	0
Arrowwood	7	0							2	0
Witherod			8	0					3	0
Total Minor	163	120	116	76	78	67	50	81	115	87
All Species	232	223	294	219	292	225	191	272	270	227

Table 9. Single stems (percent of total) of each species in 1959 and 1970 in all tracts

	Poorly Drained		Moderately Well Drained		Well Drained		Somewhat Excessively Drained		All Classes	
	1959	1970	1959	1970	1959	1970	1959	1970	1959	1970
Major Species										
Sugar Maple	100	100	73	79	58	62			66	70
Red Maple	58	46	56	57	47	45	31	31	49	46
Red Oak	78	67	76	72	79	67	70	67	76	69
Black Oak					100		0	0	60	0
Scarlet Oak			100	100			75	75	78	78
White Oak	100	100	100	100	100	100	100		100	100
Yellow Birch	70	62	58	48	75	67			64	56
Black Birch	67	78	79	83	90	89	62	59	78	80
Mockernut Hickory					100	100			100	100
Pignut Hickory	71	75	100	100	57	40			74	61
Shagbark Hickory	100				33	33			60	33
Beech	100	50	72	70	63	72			70	70
White Ash	80	67	80	71	67	50			77	65
Black Ash	100	100							100	100
Basswood	33	0							33	0
American Elm	100	100	100	100					100	100
Bigtooth Aspen							100		100	
Pepperidge	100	50							100	50
Black Locust	100								100	
Black Cherry			0	0	100	100	100		75	75
Sassafras	100	100	100	100			100	80	100	86
White Pine	100	100		100	100	100			100	100
Hemlock	92	93	90	89	79	94			90	92
Total Major	77	72	72	73	70	72	47	44	70	70

Minor Species										
Chestnut	100	100	100	70	100	80	78	80	93	76
Fl. Dogwood			75	67	47	58			56	60
Bluebeech	40	18	50	0	40	33			41	24
Shadbush	40	0	71	57	100	100			64	58
Hophornbeam	100	100	100						100	100
Gray Birch			0					100	0	100
Witchhazel	38	5	38	26	18	15			34	19
Winterberry	43	0	100						64	0
Spicebush	100	15							100	15
Blueberry	0	0	50	20					40	14
Witchhobble			100	17					100	17
Total Minor	45	15	50	35	39	41	78	83	47	30
All Species	68	53	67	63	63	65	50	47	65	60

SINGLE STEMS

We have already seen that over all tracts the number of stems per acre of major and minor species increased 4 percent during 1959-70 and that this increase was due to 4 major and 7 minor species (Table 4). We also observed that the tracts contained a mixture of single stems and sprout clumps. Was the increase in number of stems due to new seedlings or increased sprouting? Single stems, as a percent of total stems, are shown in Table 9. For major species the proportion of single stems remained unchanged over all tracts and sites. However, among major species the proportion of single stems increased in 3 and declined in 12 The change was usually small, suggesting that death and birth affected sprout clumps and single stems similarly. Change in proportions among drainage classes was also slight. Single stems increased on the moderately and well drained soils, but decreased on the poorly and somewhat excessively drained.

During 1959-70 the proportion of single stems in minor species decreased from 47 to 30 percent of single stems. However, this decrease occurred only on the poorly and moderately well drained sites. Slight increases were noted on the well drained and somewhat excessively drained soils.

At Gay City, major species dropped from 67 to 58 percent of single stems, and the decrease occurred on all sites. Minor species also decreased, 46 to 30 percent, but only on the poorly and moderately well drained sites. Although the actual number of single stems increased for sugar and red maple, black birch, and beech, only sugar maple increased proportionately in single stems. Among the minor species, chestnut (which now arises only as sprouts) and flowering dogwood increased their proportion of single stems.

At Natchaug the proportion of single stems scarcely changed for major species, 67 percent in 1959 and 65 in 1970, and decreased slightly for minor species, 33 to 26 percent. On the poorly drained soil the proportion of single stems was about half whereas it was nearly three-fourths on the moderately well drained soil. Only black birch and chestnut increased in actual number of single stems per acre.

In Norfolk there was no overall change during 1959-70. Beech was the only species to increase in number of single stems per acre, primarily on the well drained soils. The proportion of single stems was greatest on the poorly drained soil and decreased as drainage improved.

At Catlin Wood the birth of many hemlocks increased the proportion of single stems among major species from 70 to 76 percent. We also noted that witchhazel increased during 1959-70. However, it must have been mainly through sprouting because the number of its single stems dropped from 60 to 42 per acre. The percentage of single stems over all minor species decreased from 70 to 32.

Thus, we see that increase in single stems of major species occurred mostly at Catlin Wood and was due mainly to hemlock. The proportions of single stems scarcely changed at stable Norfolk or at Natchaug. However, in young Gay City the proportion of single stems decreased, suggesting more birth from sprouting than from seed or more death of single stems than of sprout clumps. Apparently sprouting had some advantage in that young stand, but not in the older.

The proportion of single stems in the Meshomasic tracts was reported to be about two-thirds, and it remained near this level for 40 years (Stephens and Waggoner 1970). In the present study the proportions for major species are slightly greater, about 70 percent for all but the driest site (Table 9). However, this small increase is due to conifers in Norfolk and Catlin Wood. Actually, the proportion of single stems in Gay City and Natchaug, without conifers, is close to two-thirds. The conifers observed do not sprout, and the rare multiple stems usually result from injury. If conifers are plentiful, therefore, the proportion of single stems surely increases. If we ignore the conifers, the proportion of single stems among the remaining major species approaches the two-thirds observed in other stands and changes little with time. Thus, the same conditions affecting sprouting must have applied in all stands.

Single stems of minor species generally decreased during 1959-70 on all tracts except Norfolk where they were rare. This is unlike the trend of increased proportion of single stems of minor species with time noted in the Meshomasic tracts.

BASAL AREA

Basal area, the cross-sectional area of the stem, indicates the size of individuals, whereas population simply enumerates the individuals in the forest. Basal area, summed over all stems, gives the bulk of the forest, but the basal area of a great many small stems is slight whereas that of even a few large stems is great. Therefore, basal area provides an alternative to population for naming or describing the forest.

In 1959, Gay City had the smallest and Norfolk, with nearly twice the basal area, had the greatest bulk (Table 10). Despite decreasing population in all but Catlin Wood, basal area of all tracts increased during 1959-70. The increase averaged about 12 percent of 1959 basal area, ranging from 9 at Gay City to 17 at Catlin Wood. Increases were due almost entirely to major species; only in Catlin Wood did basal area of minor species increase.

Change in basal area of both major and minor species on all tracts was generally unrelated to drainage class. Although poorly drained soils had the greatest gains in all but Gay City, there was no clear relation of other sites to gain. Basal area, however, increased on all drainage classes of all tracts except Gay City (Table 10). There it decreased about 2 percent on the moderately well drained soil.

Table 10. Basal area in square feet per acre

Site	Year	Gay City	Natchaug	Norfolk	Catlin Wood	All
		Major Species				
Poorly Drained	1959	81	60	145	152	113
	1970	94	69	163	185	132
Mod. Well Drained	1959	73	91	155	85	101
	1970	72	104	172	95	112
Well Drained	1959	73		139	193	131
	1970	78		147	224	145
S. Excess. Drained	1959	65				65
	1970	79				79
All	1959	73	81	147	130	109
	1970	80	92	162	151	123
		Minor Species				
Poorly Drained	1959	5.0	2.7		.9	1.9
	1970	3.3	2.5		.7	1.4
Mod. Well Drained	1959	4.0	1.3	<.1	.6	1.2
	1970	2.9	1.3	<.1	1.5	1.3
Well Drained	1959	3.8			.3	1.6
	1970	4.0			.2	1.7
S. Excess. Drained	1959	.4				.4
	1970	.3				.3
All	1959	3.4	1.8	<.1	.6	1.5
	1970	2.8	1.7	<.1	1.0	1.4

We see both striking similarities and differences among these tracts and those reported earlier (Stephens and Waggoner, 1970). For example, basal area of major species in Gay City and Natchaug in 1959 was similar to the 35- to 50-year-old stands of 1937 in the Meshomasic tracts. The large basal area of Norfolk and Catlin Wood was about 50 percent greater than Gay City and Natchaug, and as we shall see, the addition was attributed to the conifers. All tracts of this new series increased in basal area during 1959-70. Among the Meshomasic tracts only Turkey Hill increased during 1957-67.

In 1959 maples comprised 22 percent of basal area; birches, 14 percent; oaks, 27 percent; hemlock, 22 percent (Table 11). On the other hand beech, though numerous, contributed only 3 percent of basal area. During 1959-70 the proportions of basal area changed little; oaks decreased slightly, birch remained constant, while hemlock and maple increased slightly.

Earlier, we called Gay City a maple-birch-oak forest by virtue of its population. However, in 1959 its basal area was 32 percent birch, 29 percent oak and 18 percent maple. During 1959-70 basal area of birch and maple increased slightly. Despite a nearly 50 percent decrease in number of oak, its basal area declined only about 10 percent. Therefore, the tract remained nearly constant and might better be called a birch-oak-maple forest by virtue of its bulk instead of the maple-birch-oak name suggested by mere numbers of stems. Black birch comprises slightly more than half of birch basal area. It predominates on the drier sites, whereas yellow birch prevails on the moister sites. Red oak supplies nearly half of oak basal area and it predominates on the moderately and well drained sites. White oak predominates on poorly drained and scarlet oak on the somewhat excessively drained.

Natchaug, too, was called a maple-birch-oak forest by population. However, in 1959, oak contributed 52 percent of basal area. Red oak supplied half and white oak more than a third of oak basal area. By 1970 the proportions were little changed. Oak decreased slightly to 50 percent; red oak increased while white declined. Red maple comprised nearly all maple basal area and increased from 22 to 26 percent by 1970. Birches, primarily black, decreased slightly from 18 to 16 percent of basal area. Therefore, Natchaug is really an oak-maple-birch forest by bulk.

Norfolk was called a hemlock-beech-maple-birch stand by population. In 1959 maple provided 35 percent, hemlock 28 percent, birch 7 and beech 6 percent of basal area. During 1959-70 maple decreased and hemlock increased slightly but others remained nearly unchanged. Thus, in terms of basal area, Norfolk is a hemlock-maple forest. Red maple predominates on the moister sites while sugar maple prevails on the well drained soil. Red oak supplied a fifth of basal area on the moderately well drained soils and an eighth on well drained.

Catlin Wood was also described as a hemlock-beech-maple-birch forest by population. In 1959, hemlock provided 38 and oak 33 percent of basal area. Maple comprised 12, birch 8, and beech 3 percent of basal area. Although numerous, maple, birch and beech together contributed less basal area than the few large oaks present. By 1970, oak basal area decreased slightly while that of all others increased slightly. Thus, Catlin Wood was really a hemlock-oak forest. Hemlock, white oak and white pine predominated on the poorly drained soils. Hem-

Table 11. Basal area of major and minor species (percent of total) present in 1959 and 1970 in all tracts

	Poorly Drained 1959	Poorly Drained 1970	Moderately Well Drained 1959	Moderately Well Drained 1970	Well Drained 1959	Well Drained 1970	Somewhat Excessively Drained 1959	Somewhat Excessively Drained 1970	All Classes 1959	All Classes 1970
Major Species										
Sugar Maple	.1	.1	5.9	5.7	12.1	10.9			5.7	5.3
Red Maple	25.2	25.3	17.8	19.3	3.5	3.8	27.2	28.3	16.3	17.2
Red Oak	.4	.1	25.5	24.3	25.4	24.9	24.7	25.4	18.1	17.2
Black Oak					.8	.0	5.4	5.3	.4	.2
Scarlet Oak			2.8	2.9			28.4	29.4	2.2	2.3
White Oak	8.4	8.3	8.8	6.8	3.1	2.8	.3	.0	6.8	5.9
Yellow Birch	12.8	12.6	7.0	6.3	.9	1.0			6.7	6.5
Black Birch	2.0	1.0	8.3	8.8	9.8	11.1	10.7	10.9	7.0	7.2
Mockernut Hickory					<.1	<.1			<.1	<.1
Pignut Hickory	1.5	.8	1.8	1.7	2.1	1.8			1.7	1.4
Shagbark Hickory	.2	.0			1.4	1.4			.4	.4
Beech	.3	.4	3.4	4.3	4.8	5.8			2.8	3.4
White Ash	4.5	4.5	2.5	2.5	6.0	5.6			4.0	3.9
Black Ash	.2	.2							.1	.1
Basswood	.1	.0							<.1	<.1
American Elm	.2	.3	.1	.1					.1	.1
Bigtooth Aspen							2.3	.0	.1	.0
Pepperidge									<.1	<.1
Black Locust									<.1	.0
Black Cherry			2.1	1.0	4.8	4.7	.4	.0	2.2	1.7
Sassafras							.2	.4	<.1	<.1
White Pine	3.9	3.9			3.1	2.9			2.0	2.0
Hemlock	38.6	41.3	12.7	15.1	20.7	22.1			22.1	24.3
Redcedar									<.1	.0
Square Feet/Acre	113.3	131.8	100.5	111.5	130.6	145.3	65.3	78.8	109.0	123.1

Minor Species										
Chestnut	.0	.1	.0	.2	.1	.0	.6	.3	.1	.1
Fl. Dogwood			.2	.2	.6	.7			.3	.3
Bluebeech	.8	.3			.0	.1			.3	.1
Shadbush	.1	.0	.1	.1	.1	.0			.1	< .1
Hophornbeam	.1	.0	.1	.0					< .1	< .1
Gray Birch							.0	< .1	< .1	< .1
Witchhazel	.5	.4	.6	.6	.4	.3			.5	.5
Winterberry	< .1	< .1	< .1	.0					< .1	< .1
Spicebush	.0	.2							< .1	.1
Blueberry	< .1	< .1	< .1	< .1					< .1	< .1
Witchhobble			< .1	< .1					< .1	< .1
Arrowwood	.0	< .1							.0	< .1
Witherod			< .1	< .1					< .1	< .1
Square Feet/Acre	1.9	1.4	1.2	1.3	1.6	1.7	.4	.3	1.5	1.4
Total										
Square Feet/Acre	115.2	133.2	101.8	112.9	132.2	147.0	65.7	79.1	110.4	124.5

lock, red maple, red and white oak prevailed on the moderately well drained soils and hemlock and red oak on the well drained soil.

We see that although great changes in numbers of stems occurred during 1959-70 in some tracts, the change in basal area was small. Thus, these tracts appear much the same in 1970 as they did in 1959.

The change we have noted in basal area is net change. To see how persistent trees grew and how much basal area was gained and lost through birth and death we must await the section, Growth. But first we examine Distribution of Diameter.

DISTRIBUTION OF DIAMETER

Population enumerates number of stems, and basal area presents their bulk. Together they indicate whether trees are generally small or large. However, to determine the proportion of trees of different sizes we divided them into four classes: small saplings, 0.5 to 1.5 inches d.b.h.; large saplings, 1.6 to 5.5; poles, 5.6 to 11.5; and sawtimber, greater than 11.5 inches d.b.h. As stands mature, major species will be in all classes, but rarely will the stems of minor species grow beyond large saplings.

Although their populations differed in 1959, the proportion of major species in each size class was the same for Gay City and Natchaug (Table 12). Norfolk and Catlin Wood had proportionally fewer saplings and more pole and sawtimber stems than Gay City and Natchaug. This is not unexpected in the older Norfolk and Catlin Wood. Norfolk had almost no minor species, but in 1959 on the other tracts minor species constituted a fourth to a third of all stems, mostly small saplings.

Table 12. Percentage of major species by diameter

	Small Saplings		Large Saplings		Poles		Sawtimber	
Tract	1959	1970	1959	1970	1959	1970	1959	1970
Gay City	43	42	40	36	15	19	2	3
Natchaug	41	34	41	42	15	17	3	7
Norfolk	17	19	49	45	28	28	6	8
Catlin Wood	28	48	42	32	18	12	12	8
All	33	37	43	38	19	18	5	7

During 1959-70 the proportions of poles and sawtimber remained unchanged or increased on all but Catlin Wood where they decreased (Table 12). The increased proportion at Gay City resulted from fewer saplings; actually the number of poles and sawtimber stems scarcely changed. At Natchaug and Norfolk the increase in sawtimber was real, each gained 16 trees per acre, but the number of poles declined. Nevertheless, loss of saplings was sufficiently great so that the proportion of poles increased or remained unchanged. In Catlin Wood the number of poles and sawtimber stems remained unchanged, but the proportions of both were reduced by the great increase in saplings. Minor species saplings increased in both Gay City and Catlin Wood, but the change was proportionally greater at Gay City.

Over the average of all tracts and drainage classes we note slow movement of stems into pole and sawtimber classes (Table 12). During 1959-70, 3 red maple, 2 each of red oak, black birch and hemlock, and 1 white oak pole per acre became sawtimber (Table 13). Only sugar

Table 13. Diameter class distribution (stems/acre), all tracts

	Small Saplings		Large Saplings		Poles		Sawtimber	
	1959	1970	1959	1970	1959	1970	1959	1970
Sugar maple	7	8	30	25	10	11	1	1
Red maple	54	47	67	67	28	28	3	6
Red oak	10	4	15	6	13	10	9	11
Black & Scarlet oak	1	0	3	1	4	5	1	1
White oak	11	3	21	3	6	5	3	4
Yellow birch	23	19	28	24	13	15	1	1
Black birch	25	29	21	23	14	14	1	3
Beech	48	60	33	41	6	6	0	0
Hemlock	11	57	38	51	14	17	9	11

maple, yellow birch and hemlock poles increased. Sapling losses were greatest in red and white oak and were slight among maples and yellow birch. Saplings increased in black birch, beech and hemlock.

In Gay City, white oak and black birch, each with 4 sawtimber trees per acre, comprised half the sawtimber in 1959. By 1970, 3 additional black birch and 2 red maple became sawtimber. In 1970 poles were numerous among red and scarlet oak, yellow and black birch, red maple and white oak. During the preceding decade the number of poles increased only for yellow and black birch and scarlet oak. Losses of saplings during 1959-70 were great for red and white oak, yellow birch, pignut hickory and white ash. Only red maple increased its saplings.

At Natchaug, in 1959, all sawtimber trees were oak. Red oak supplied 13 per acre, while scarlet and white oak each had 3. During

1959-70 10 additional red oak, 4 white oak and 3 black birch grew to sawtimber. Red maple, white oak and black birch had many poles in 1970, but only red maple had increased in number during 1959-70. The number of red and white oak saplings declined sharply by 1970. Red maple decreased about 20 percent, but black birch saplings increased about 20 percent.

At Norfolk red maple, red oak, black cherry and hemlock comprised 30 of the 38 sawtimber trees per acre in 1959. During 1959-70 red maple and hemlock each added 5 while sugar maple and white ash each contributed 2 sawtimber stems per acre. In 1970, poles were numerous among sugar and red maple, yellow birch, beech, white ash, and hemlock. Only sugar maple and hemlock gained poles during 1959-70. Saplings increased only for beech and decreased among sugar maple, yellow birch, and hemlock.

Catlin Wood had the greatest number of sawtimber trees per acre. In 1959 there were 29 hemlock, 18 red oak, 4 white oak and 4 white pine sawtimber trees per acre. In the decade that followed, red maple and hemlock each produced 2 additional sawtimber stems, but red oak lost 2. Poles were most numerous among red maple, red oak, yellow birch, and beech. During 1959-70 the number of poles increased only in yellow birch and hemlock. Only among beech, hemlock, and white pine did the saplings increase.

Thus, we see that mortality mainly affected the saplings of each species. Apparently few of the larger trees died. Growth into pole and sawtimber classes was slow. Sugar maple, scarlet oak, yellow birch, and hemlock all increased their poles, while red maple, red oak, black birch, and hemlock increased sawtimber stems. Now we can better appreciate the distinction in describing the forest in terms of stem number or basal area. Red maple, although numerous, did not bulk large in basal area because most of its stems were saplings. Red oak, though few in number had a large basal area because nearly half its stems were poles or sawtimber. We go now to a closer examination of growth and loss among species.

GROWTH

We have witnessed a kaleidoscope of change in the forest. Population revealed net change in numbers but nothing of size of individuals. Birth enumerated newcomers and implied they were small, while death indicated only that stems disappeared, but not whether they were small or large. Basal area related net change of the forest's bulk but nothing of its dynamics. Distribution of diameter revealed that mostly small stems disappeared and indicated whether others grew to larger size or did not. We now analyze basal area change in order to learn its dynamics. To do this we separate three components of change: accretion, growth on persistent stems; ingrowth, additions by new stems;

and mortality, loss of those that died. If their sum is positive, growth of the stand has occurred.

We already know that basal area increased on all sites of all tracts except on the moderately well drained soil in Gay City. Let us see the contribution of each component (Table 14). Over all tracts and sites

Table 14. Basal area change (sq. ft./acre), major species

		Poorly Drained	Moderately Well Drained	Well Drained	Somewhat Exc. Drained	All
Gay City	Accretion	21.1	13.4	16.3	17.5	17.0
	Ingrowth	.4	.4	.8	.5	.5
	Mortality	−7.8	−14.6	−11.8	−4.4	−9.9
	Net	13.7	−.8	5.3	13.6	7.6
Natchaug	Accretion	14.3	19.6			17.8
	Ingrowth	2.5	1.7			2.0
	Mortality	−8.1	−8.5			−8.4
	Net	8.7	12.8			11.4
Norfolk	Accretion	23.8	23.5	15.1		21.5
	Ingrowth	.5	.1	.3		.3
	Mortality	−5.7	−6.9	−7.7		−6.6
	Net	18.6	16.7	7.7		15.2
Catlin Wood	Accretion	33.4	20.2	29.7		25.8
	Ingrowth	1.3	2.5	3.6		2.6
	Mortality	−1.9	−11.9	−1.5		−6.8
	Net	32.8	10.8	31.8		21.6
All	Accretion	23.2	19.7	20.4	17.5	20.7
	Ingrowth	1.1	1.5	1.6	.5	1.3
	Mortality	−5.9	−10.2	−7.3	−4.4	−7.9
	Net	18.4	11.0	14.7	13.6	14.1

nearly 21 square feet per acre accrued to basal area of persistent trees. Ingrowth of new trees added a meager 1.3 square feet while mortality withdrew nearly 8 from the basal area present in 1959. Thus, on the average, mortality nullified about a third of all growth.

Accretion was greatest on the poorly drained soils and least on the somewhat excessively drained. However, expressed as a percent of persisting basal area (1959 basal area minus mortality), accretion was greatest, not least, on the somewhat excessively drained, 29 percent, and least on the well drained, 17 percent. Ingrowth was essentially constant; it varied from nearly 1 to less than 2 percent of persistent basal area. On the other hand, mortality varied more than ingrowth. As a percent of the 1959 basal area it varied from 10 percent on moderately well drained sites to about 5 percent on the poorly drained. Net change, similarly expressed, was greatest on the somewhat excessively drained soil, nearly 21 percent; less on the poorly drained, 16 percent; and least on the moderately and well drained sites, about 11 percent. Because ingrowth is nearly constant, net change varied only with the balance between accretion and mortality.

Among the tracts, average accretion ranged from 17 square feet per acre on Gay City to nearly 26 in Catlin Wood (Table 14). As a percent of persistent basal area, however, accretion was greatest at Gay City, 27 percent, and least in Norfolk, 15 percent. Ingrowth was less than 1 percent of persistent basal area at Gay City and Norfolk, but more than 2 percent at Natchaug and Catlin Wood. Mortality was greatest at Gay City, nearly 14 percent of 1959 basal area, and least at Norfolk, less than 5 percent. Nevertheless, net change was nearly equal and least at Gay City and Norfolk, about 10 percent of 1959 basal area, greater at Natchaug, 14 percent, and greatest at Catlin Wood, nearly 17 percent. Thus, the proportional net change among tracts mainly depended on the balance of accretion and mortality, something already seen in the comparison of growth among drainage classes.

At Gay City accretion was less and mortality greater on the moderately and well drained sites than on the others. On the moderately well drained soil, mortality of red and white oak and yellow birch exceeded accretion and ingrowth. On the well drained soil, these species plus black oak and pignut hickory all had great mortality. On the poorly drained, accretion was great and mortality slight for red maple, white oak, yellow birch and white ash. On the somewhat excessively drained soil red maple, red and scarlet oak and black birch all displayed large net increases.

At Natchaug, accretion was greater on the moderately well drained than on the poorly drained soil. Although ingrowth was less and mortality greater, net change on the moderately well drained was nearly 50 percent greater than on the poorly drained. On the poorly drained soil, mortality of black birch exceeded accretion and ingrowth three-fold. On the other hand, net increase of red maple was great. On the moderately well drained site, red oak had much accretion and no mortality whereas mortality of white oak exceeded growth more than two-fold.

In Norfolk, accretion on the well drained site was only two-thirds as great as on the poorly and moderately well drained soils. As drainage improved, mortality increased with the result that net increase on the well drained soil was less than half that on poorly and moderately well drained soils. On the poorly drained site, hemlock, yellow birch, and white ash all increased, but red maple declined. On the moderately well drained soil, red maple, red oak, beech, and hemlock gained in basal area, but mortality of black cherry exceeded growth about 50-fold. On the well drained soil, sugar maple and yellow birch declined, whereas red oak, beech, and black cherry provided nearly all the gain in basal area.

At Catlin Wood net increase on poorly and well drained soils was three times that on moderately well drained soil. Not only was accretion a third less on the moderately well drained soil, but mortality was about six times greater than on the other sites. On the poorly drained soil, hemlock, red maple, yellow birch, and white pine provided nearly all of the gain in basal area. On the well drained soil, hemlock, red oak, red maple, beech, and yellow birch grew much and died little. But on the moderately well drained soil the greater mortality of red oak cancelled more than a third of the gain contributed by red maple, black birch, beech, and hemlock.

The average changes in components of basal area of selected species are shown in Table 15. Accretion and mortality varied among species, but ingrowth was slight for all.

Sugar maple was not found on the driest site and it grew slowly elsewhere; accretion was about 9 percent of persisting basal area. Although mortality was slight compared to other species, it equaled about 60 percent of the growth of sugar maple for the decade. Accretion was greatest on the moderately well drained soils. Red maple, on the other hand, grew more rapidly on all sites. Average accretion was 22 percent of persisting basal area and mortality, 4 percent of 1959 basal area. Both accretion and mortality were proportionally greatest on the somewhat excessively drained soil.

Yellow birch generally grew more than sugar maple but less than red maple. Like sugar maple, it was not found on the driest site. On the average, mortality equaled half the growth. Proportionally, accretion was greatest on the moderately well drained sites, 19 percent, and least on the well drained, 4 percent. Mortality was least on the poorly drained and greatest on the well drained soils. Black birch, on the other hand, grew as well as red maple, and growth was nearly three times mortality. Although accretion was proportionally greatest on the poorly drained sites, the great mortality there caused basal area to decline. On other sites accretion became proportionally greater as drainage improved. Because mortality varied, net increase was greatest on well drained soils. Although black and yellow birch had greatest net increases on well drained soils, yellow birch grew well on the moister and black birch grew well on the drier soils.

Red and white oak occurred on all sites. Average mortality of red oak equaled about two-thirds of accretion while that of white ex-

Table 15. Basal area change (sq. ft./acre), all tracts

Species	Component	Poorly Drained	Moderately Well Drained	Well Drained	S. Excess. Drained	All
Sugar maple	Accretion	.01	.64	1.05		.52
	Ingrowth	.0	.0	.03		.01
	Mortality	.0	−.20	−1.00		−.32
	Net	.01	.44	.08		.21
Red maple	Accretion	5.9	3.9	.88	5.5	3.9
	Ingrowth	.5	.2	.07	.3	.3
	Mortality	−1.7	−.5	−.07	−1.3	−.8
	Net	4.7	3.6	.88	4.5	3.4
Yellow birch	Accretion	2.19	1.13	.03		1.10
	Ingrowth	.16	.05	.64		.22
	Mortality	−.34	−1.17	−.33		−.67
	Net	2.01	.01	.34		.65
Black birch	Accretion	.42	1.72	3.5	2.15	1.81
	Ingrowth	.02	.38	.0	.10	.17
	Mortality	−1.38	−.67	−.2	−.72	−.76
	Net	−.94	1.43	3.3	1.53	1.22
Red oak	Accretion	.05	5.2	5.3	4.4	3.7
	Ingrowth	.0	.0	.2	.0	< .1
	Mortality	−.34	−3.7	−2.5	−.5	−2.3
	Net	−.28	1.5	3.0	3.9	1.5
White oak	Accretion	1.58	1.19	.78	.0	1.13
	Ingrowth	.0	.0	.0	.0	.0
	Mortality	−.14	−2.52	−.78	−.20	−1.30
	Net	1.44	−1.33	.0	−.20	−.16
Beech	Accretion	.07	1.38	2.12		1.10
	Ingrowth	.05	.14	.16		.11
	Mortality	.0	−.19	−.07		−.10
	Net	.12	1.33	2.22		1.12
Hemlock	Accretion	10.6	3.5	4.6		5.5
	Ingrowth	.3	.6	.5		.5
	Mortality	−.3	.0	.0		−.1
	Net	10.6	4.1	5.1		5.9
White ash	Accretion	1.46	.33	.98		.78
	Ingrowth	.0	.0	.0		.0
	Mortality	−.62	−.06	−.81		−.39
	Net	.84	.28	.17		.39
All major	Accretion	23.2	19.7	20.5	17.4	20.7
	Ingrowth	1.1	1.5	1.6	.5	1.3
	Mortality	5.8	−10.2	−7.3	−4.4	−7.9
	Net	18.5	11.0	14.8	13.5	14.1
All minor	Accretion	.16	.30	.29	.06	.25
	Ingrowth	.43	.34	.25	.18	.34
	Mortality	1.06	−.51	−.50	−.34	−.65
	Net	−.47	.13	.05	−.10	−.06

ceeded accretion. On the poorly drained soils, mortality of red oak exceeded growth seven-fold. Although accretion was great on moderately and well drained soils, mortality, too, was large. Hence, net increase of red oak was greatest on the driest site where mortality was least. Conversely, white oak increased its basal area only on the poorly drained sites; on all other sites mortality equaled or exceeded accretion.

Beech and hemlock both grew much and died little. Neither occurred on the driest site and both made maximum gain on the moderately well drained soils. Beech had the greatest proportional rate of net increase, 37 percent of 1959 basal area. Hemlock was second with 24 percent increase.

Mortality of white ash equaled half its accretion. Despite great mortality, net increase was greatest on the poorly drained soils. Although considerable ash was present on well drained soils, mortality was more than 80 percent of accretion.

In summary, we note that red maple grew well on all sites. White oak, white ash, and yellow birch increased most on the poorly drained soils, while red oak increased most on the driest. Hemlock, the rapidly growing beech, and the slow growing sugar maple grew best on the moderately well drained sites. Although all sites remained nearly equally diverse with respect to numbers, change in basal area varied with species and drainage.

CANOPY COMPOSITION

The indistinct outline of the forest seen from afar is its main canopy. The physiognomy of the forest and often its future composition is dictated by the species whose dominant and co-dominant crowns comprise the canopy. Closer inspection reveals intermediate and overtopped crowns, often in a middle or lower story beneath the main canopy. These species, too, are important because they may affect future composition should some catastrophe befall individuals in the main canopy.

What determines participation in the main canopy? In the new forest this is decided by those first appearing and others which grow most rapidly in height. Further, only in the young forest can shrubs and short-statured trees participate in the canopy. However, in the more mature forest other factors predominate. If a species is numerous, likely some of its stems will be in the canopy; if its basal area is great, surely large trees will be present in the canopy. Tolerance to shade is also important unless the main canopy is broken or open. If a species cannot persist in the shade of others, then it must participate in the canopy if it is to exist.

We may consider canopy composition from two aspects. First, what proportion of each species participates in the canopy? If only a small proportion of stems participates in the canopy, then there must

Table 16. Participation in the canopy in 1959 and 1970 in all tracts

	Poorly Drained		Moderately Well Drained		Well Drained		Somewhat Excessively Drained		All Classes	
	1959	1970	1959	1970	1959	1970	1959	1970	1959	1970
PERCENT OF STEMS										
Sugar Maple	0	0	8	15	13	16			11	16
Red Maple	20	31	16	22	3	3	5	5	12	17
Red Oak	0	0	59	89	32	50	50	56	41	63
Black Oak					33	0	100	100	60	100
Scarlet Oak			0	100			75	75	67	78
White Oak	25	33	12	60	5	40	0	0	12	46
Yellow Birch	23	29	8	14	0	17			14	21
Black Birch	17	11	13	14	15	53	6	18	12	21
Beech	0	0	0	2	0	4				2
White Ash	60	83	20	100	67	100			46	94
Black Cherry			100	100	60	100	0	0	63	100
White Pine	100	50	0	0	100	50			100	15
Hemlock	8	21	10	4	16	11			10	13
Total Major	16	25	13	17	13	19	16	19	14	19
PERCENT OF BASAL AREA										
Sugar Maple	0	0	25	45	53	59			41	52
Red Maple	65	77	52	65	15	15	52	56	56	67
Red Oak	0	0	87	99	87	95	72	76	85	96
Black Oak					77	0	100	100	88	100
Scarlet Oak			0	100			84	86	42	93
White Oak	91	94	55	90	56	93	0	0	68	92
Yellow Birch	65	73	25	53	0	43			47	64
Black Birch	57	93	53	66	40	88	30	68	47	77
Beech	0	0	0	16	0	38			0	26
White Ash	96	98	47	100	90	100			81	99
Black Cherry			100	100	100	100	0	0	99	100
White Pine	100	100	0	0	100	100			100	99
Hemlock	50	72	62	68	62	91			55	76
Total Major	62	76	57	74	64	82	65	74	61	77

be many smaller stems tolerant of shade in the understory. Increased participation in the canopy results from death of small stems in the understory or growth of smaller stems into the canopy. In 1959, 14 percent of all major species stems participated in the canopy (Table 16). Slightly more, 16 percent, participated on the poorly and somewhat excessively drained soils and fewer, 13 percent, on the moderately and well drained. By 1970, average participation increased to 19 percent and ranged from 17 percent on the moderately well drained to 25 percent on the poorly drained soils. Increases occurred on all sites. These apparent increases resulted mostly from death of small trees and from a few growing to larger size as seen in distribution of diameter (Table 13). The largest increase in canopy participation occurred on the poorly drained soils.

For example, in 1959, 41 percent of red oak stems participated in the canopy; by 1970, 63 percent participated (Table 16). However, we already know that its saplings declined greatly during 1959-70 (Table 13). Proportionally more stems participated in the canopy because the small stems could not persist in the shade. On the other hand, the proportions of red and sugar maples in the canopy changed little, because few small trees became large and because most of the saplings persisted.

In 1959, few minor species participated in the canopy; only 2 percent on poorly drained and 1 on moderately well drained soils. They were bluebeech, witchhazel, and winterberry. By 1970, no minor species remained in the canopy. Apparently growth of the stands raised the canopy beyond their reach.

We did not measure the area of each crown, but we know the basal area of each stem and its crown class. We can assume that crown or leaf area of a tree is proportional to its basal area. Thus, we can estimate participation in the canopy in a different way.

The proportion of major species participating in the canopy was much greater for basal area than for number, 61 percent in 1959 and 77 in 1970 (Table 16, lower half). In 1959, the proportion ranged from 57 percent on the moderately well drained to 65 on the somewhat excessively drained soil. By 1970 participation ranged from 74 percent on the moderately well and somewhat excessively drained sites to 82 percent on the well drained. Thus, in 1970 we estimate that nearly a fifth of the stems supported about three-fourths of foliage.

The second aspect of canopy composition is the proportion of the canopy occupied by each species. This reveals which species control the forest. In 1959, oaks and birches dominated canopy composition with their numbers (Table 17). During 1959-70 maple remained constant, oaks declined while birches, beech, and hemlock increased. On the poorly drained sites only hemlock increased its participation, all others declined. On the moderately and well drained soils white oaks,

Table 17. Composition of the canopy (percent of total) in 1959 and 1970 in all tracts

	Poorly Drained		Moderately Well Drained		Well Drained		Somewhat Excessively Drained		All Classes	
	1959	1970	1959	1970	1959	1970	1959	1970	1959	1970
NUMBER OF STEMS										
Sugar Maple	0	0	5	7	16	12			5	5
Red Maple	31	31	23	23	3	2	18	16	20	19
Red Oak	0	0	30	21	28	18	29	26	21	15
Black Oak					3	0	12	11	2	1
Scarlet Oak			0	1			35	32	4	4
White Oak	7	5	7	8	3	4	0	0	5	5
Yellow Birch	24	22	7	8	0	2			10	10
Black Birch	2	2	12	12	9	20	6	16	8	11
Beech	0	0	0	3	0	4			0	2
White Ash	14	8	4	9	13	8			8	8
Black Cherry			4	1	9	6	0	0	3	2
White Pine	2	2	0	0	3	2			1	1
Hemlock	14	30	4	4	9	14			7	14
Other Major	1	< 1	2	3	4	8	< 1	< 1	4	3
Total Major	95	100	98	100	100	100	100	100	98	100
CROWN (BASAL) AREA										
Sugar Maple	0	0	3	4	10	8			4	4
Red Maple	27	26	16	17	1	1	22	22	15	15
Red Oak	0	0	39	33	35	29	28	27	26	22
Black Oak					1	0	8	7	1	0
Scarlet Oak			0	4			37	35	2	3
White Oak	13	10	9	8	3	3	0	0	8	7
Yellow Birch	14	12	3	5	0	1			5	5
Black Birch	2	1	8	8	6	12	5	10	5	7
Beech	0	0	0	1	0	3			0	1
White Ash	7	6	2	3	9	7			5	5
Black Cherry			4	1	8	6	0	0	4	2
White Pine	6	5	0	0	5	4			3	3
Hemlock	31	40	14	14	20	25			21	24
Other Major	< 1	< 1	2	2	2	1	< 1	< 1	1	2
Total Major	100	100	100	100	100	100	100	100	100	100

yellow birch, beech, and hemlock were among those with increasing participation in the canopy. On the driest site only black birch increased.

Using the assumed relation between basal and foliage area, we estimate that red maple, red oak, and hemlock contributed about two-thirds of the foliage in the canopy (Table 17, lower half). However, the proportions varied considerably among tracts. Gay City and Natchaug had no conifers. In 1970 at Gay City, birch comprised 38 percent, oak 30, and maple 17 percent of the canopy. At Natchaug, oak constituted 72 percent, birch 13, and maple 8 percent of the canopy. Hemlock was abundant at Norfolk and Catlin Wood. At Norfolk it comprised 26 percent of the canopy and at Catlin Wood, 42 percent. Maples provided 34 percent, oaks, 15 percent and birches 7 percent in Norfolk while at Catlin Wood their proportions were 10, 34, and 5 percent, respectively, in 1970.

You will recall the description given each tract during the discussion of basal area. Description according to canopy composition yields essentially the same result. Gay City remains a birch-oak-maple forest and Natchaug, oak-birch. Norfolk continues as a hemlock-maple forest and, although oak was a small proportion of total basal area, it looms larger in canopy composition. The oaks present were large and in the canopy. Although oaks in the canopy decreased from 45 to 34 percent during 1959-70, Catlin Wood remains a hemlock-oak forest.

We have viewed the changing forest from many vantage points, and we now know what has occurred. But what of the future? We shall use these observed changes to fortell the future in Predicting Change.

PREDICTING CHANGE

Our observations at the beginning and end of a decade enable us to characterize both the present population of the forest and past changes through birth, growth, and death of individuals. However, we would also like to know what the forest will become, barring catastrophe. Transition probabilities are a useful tool for predicting change in unmanaged forests (Waggoner and Stephens 1970, Stephens and Waggoner 1970). We have two sets of observations from which to determine the transitions, and we do so in order to evaluate their reasonableness and to compare them with transitions observed in the Meshomasic tracts.

But first, let us define transition probability. If an object can exist in any one of the several states, transition occurs whenever the object changes state. If change is frequent, then it is probable. By studying many changes among states, we can express each possible transition as a probability, hence, transition probability.

In this study our objects are small plots of land and their state is determined by the kind of vegetation growing upon them. From our observations of many plots at the beginning and end of a decade we determine their persistence in the initial state or their transition to another. A matrix of the probabilities of all possible transitions provides a useful summary of change.

The transects sampled were divided into plots of approximately one-eightieth of an acre. The initial and subsequent states of each plot were determined from the 1959 and 1970 observations. Because Norfolk and Catlin Wood contained many conifers their transitions were determined separately from Gay City and Natchaug. Because there were few plots, all drainage classes were considered together.

Many states could be defined but we will consider only six: maples, oaks, birches, other major species, minor species, and conifers. The last species group or state occurred only at Norfolk and Catlin Wood and consisted mainly of hemlock with some white pine. The assignment of state was determined by the species group with the greatest number of stems per plot. The transitions obtained are in Table 18. We could have defined states based on tolerance to shade

Table 18. Transition probabilities (percent) among species groups during 1959-70 according to number of stems on one-eightieth-acre plots

60 plots from Gay City and Natchaug (no conifers)

Observed 1970 ↓	1959 Maple	Oak	Birch	Other[a]	Minor
Maple	95	14	20	34	11
Oak	0	14	0	0	0
Birch	5	0	70	33	11
Other	0	0	0	0	0
Minor	0	72	10	33	78

68 plots from Norfolk and Catlin Wood (many conifers)

Observed 1970 ↓	1959 Maple	Oak[a]	Birch	Other	Minor	Conifer
Maple	40	0	0	0	0	0
Oak	0	0	20	0	0	0
Birch	0	0	80	0	0	0
Other	33	0	0	88	11	0
Minor	0	33	0	6	78	5
Conifer	27	67	0	6	11	95

[a] Based on three plots

and basal area of stems, but irregular distributions of plots among states in 1959 gave transitions which seemed unreliable.

The diagonal elements from upper left to lower right of each matrix reveal the persistence in initial states. The off-diagonal elements in each column indicate transitions to other states. Where conifers were absent at Gay City and Natchaug, maple, birch, and minor species persisted. Oak showed little persistence due to great mortality and was succeeded largely by minor species. Plots initially dominated by other major species went equally to maple, birch, and minor species. Although this likely reflects the relative increases of maple and birch, we must accept these transitions with caution because only three plots were dominated by other major species in 1959. Study of the matrix suggests that if these transitions continue steadily with time there will be many plots dominated by maple, birch, and minor species, few by oak, and none by other major species.

Where conifers were present at Norfolk and Catlin Wood we see moderate persistence of maple and great persistence of birch, other major species, minor species, and conifers. Oak showed no persistence, but again, we accept this cautiously because only three plots were dominated by oak in 1959. The marked persistence of conifers, combined with transitions of nearly all groups directly to conifer, suggests that conifer will dominate many plots in the future. Further, except for the transition of birch to oak there are no other transitions into maple, oak, or birch. Thus, we anticipate a future forest with many plots dominated by conifer, other major species, and minor species, but eventually none by maple, birch, or oak.

In both matrices of Table 18 the persistence of maple, birch and minor species and the decline of oak resemble the transition probabilities obtained in the Meshomasic tracts during a similar decade, 1957-67 (Stephens and Waggoner 1970). Thus, similar transition probabilities appear to exist for several stands over a large area.

Transition probabilities have useful properties (Ashby 1966). If they are unvarying with time and if they depend only on the present state, that is, if they are independent of antecedent, then they describe a stationary Markov chain (Feller 1950). The transitions for one observation period may be extrapolated to anticipate changes over several and the steady state, or dynamic equilibrium may be calculated. Steady state occurs when the proportion of objects in each state ceases to change; gains to a state are balanced by losses to other states. (The interested reader may wish to refer to a more detailed account by Feller (1950) or Kemeny and Snell (1960).)

Unfortunately, we had only two sets of observations in time so we cannot be certain of the transitions' constancy and there were too few plots to ascertain independence of antecedent. Since the observed transitions in Table 18 are similar to others from the Meshomasic tracts, which appeared Markovian (Stephens and Waggoner 1970), we are encouraged to make the same assumption for the present probabilities. The calculated steady states are in Table 19 .

Table 19. Steady states (percent of total) anticipated from 1959-70 transitions among species groups according to the number of stems on one-eightieth-acre plots

60 plots from Gay City and Natchaug (no conifers)					
Maple	Oak	Birch	Other	Minor	
79	1	14	0	6	
68 plots from Norfolk and Catlin Wood (many conifers)					
Maple	Oak	Birch	Other	Minor	Conifer
0	0	0	18	20	62

As we anticipated from study of the matrix in Table 18, at the calculated steady state most plots in Gay City and Natchaug will be dominated by maple; on some, birch, and minor species will predominate. Oaks will dominate very few plots with their numbers and other major species will dominate none. At Norfolk and Catlin Wood three-fifths of the plots will be dominated by conifers and a fifth each by other major species and minor species.

The transitions anticipate future forests with little oak. Previous work indicates that the decline of oak has continued for at least 40 years but may have accelerated recently (Stephens and Waggoner 1970). Therefore, the outcome of the transitions may be closely related to the events examined in the next section.

DROUGHT, DEFOLIATION, AND DEATH

Drought and defoliation varied among the tracts during 1959-70. In previous sections we have related change to drainage of the site and age of the tract. In this section we will present the effects of drought and defoliation and give the importance of each.

In describing the forests we noted that all tracts received 8 to 15 percent less average annual precipitation during 1959-69 than in the preceeding 6 to 10 years. Despite the reduction of precipitation, however, we can characterize Norfolk as moist, Catlin Wood as moderately moist, and Gay City and Natchaug as moderately dry during 1959-69. Further, we noted that Catlin Wood and a portion of Gay City were defoliated once, while the remainder of Gay City suffered a second defoliation. No defoliation was recorded for Natchaug or Norfolk. An account of the effect of defoliation on these new tracts as well as on the Meshomasic series was published separately (Stephens 1971) because of its great importance in deciding upon insect control measures. The effect of defoliation is also examined here for the benefit of the readers of the present Bulletin.

During our examination of death we found little relation of death to drainage class. Rather, it was more clearly related to population (Figure 3). What are the effects of drought and defoliation? The trend line of death on population removes the effect of population; there is no difference between moist Norfolk (o) and dry Natchaug (x). Thus, drought apparently had little effect on death in undefoliated tracts.

Nor does Catlin Wood (Δ), defoliated in 1956, differ from undefoliated Natchaug and Norfolk. Although newly dead oaks were recorded in Catlin Wood in 1959, either any increased death due to defoliation had already occurred or could not be detected during 1959-70. Thus, a single prior defoliation apparently did not produce a lasting effect on death.

Among the defoliated and droughted sites of Gay City (o) we do discern a difference. Death in the once defoliated dry site (4) and the twice defoliated poorly drained site (1) was no different than on undefoliated sites in other tracts (Fig. 3). On the twice defoliated moderately (2) and well drained sites (3), however, death was clearly greater. These sites, normally optimum for tree growth, had the greatest loss. This is similar to observations made in western Connecticut (Stephens 1963). Thus, abundant soil moisture offset the effect of repeated defoliation.

In Catlin Wood and undefoliated Natchaug and Norfolk, average annual loss of major species ranged from 0.5 to 1.6 percent of the 1959 population. On the moderately well drained site, present in all tracts, average annual loss was more uniform, ranging from 1.2 to 1.6 percent. On the once defoliated dry site of Gay City death was 1.5 percent annually, but it rose to 2.3 percent on the twice defoliated moderately and well drained sites. Thus, repeated defoliation nearly doubled the slight average annual death. During 1957-67, on the Meshomasic tracts which endured both drought and repeated defoliation average mortality varied from 1.6 percent of population on moist sites to 2.3 on the dry (Stephens and Waggoner 1970). The results of both studies are remarkably similar.

Examination of species groups is more revealing. During 1959-70 death of maple stems averaged 15 percent and ranged from 14 to 17 percent on individual tracts. Loss of birch averaged slightly more, nearly 19 percent, and ranged from 17 to 19 percent. Death of oak was considerably greater: death increased from 25 percent at cool, moist Norfolk to 43 percent at Catlin Wood, 47 percent at Natchaug and 55 percent at warm, dry Gay City. The great loss of this species group was concealed in Figure 3 by averaging it with the smaller losses of many other groups. In comparison, death during 1957-67 in the Meshomasic tracts averaged 18 percent for maple, 20 percent for birch and 46 percent for oak.

On the once-defoliated dry site in Gay City, death was only 9 percent for oak, 12 percent for birch, but 20 percent for maple. In contrast, on Gay City's twice-defoliated moister sites death claimed 72 percent of oak, 21 percent of birch, and 9 percent of maple during 11 years. If we consider the climate of Gay City and Natchaug similar, then repeated defoliation increased oak loss from less than 5 percent annually to more than 7 percent; about a 50 percent increase. On the other hand, loss of birch differed little and death of maple was actually greater at Natchaug than at Gay City. Thus, loss of oak exceeded the average for all major species in all tracts. It increased with severity of drought and further increased with repeated defoliation.

In terms of 1959 basal area, mortality of oak during 1959-70 was 8 percent at Norfolk, 10 percent at Natchaug, 12 percent at Catlin Wood, and 24 percent at Gay City. Again, we see little difference between cool, moist Norfolk and warm, dry Natchaug. Nor was Catlin Wood greatly different. At Gay City mortality was only 2 percent of 1959 basal area on the dry site, 7 percent on the poorly drained, but 37 percent on the well drained, and 67 percent on the moderately well drained. During the 11 years, the average annual losses were .2, .6, 3, and nearly 7 percent, dramatically greater on the twice-defoliated sites.

However, average annual losses may be misleading if the period of observation is long. In this report and in the report on the Meshomasic tracts, defoliation occurred near the middle of the observation period. If great losses were sustained during the year or two immediately following defoliation, subsequent mortality might be reduced below normal because of the thinning of the forest. By the end of the period, however, the average might be little different from normal. For example, if a species normally loses 20 percent of its stems during a decade, or 2 percent annually, but suddenly at the midpoint loses 5 percent annually for two years and 1 percent thereafter, the loss for the decade is 23 percent or 2.3 percent annually. Average annual death is little changed despite greater losses immediately after defoliation. We know that oak mortality increases after defoliation. However, only annual observation will determine whether mortality increases sharply and then subsides or whether it varies less dramatically over a longer time.

Oak is a preferred host for many defoliators. Thus, even in years without major defoliation oaks may be attacked. For example, during late spring, 1970, when the tracts were re-examined, the spring cankerworm (*Paleacrita vernata*) and other defoliators were active in Gay City and Catlin Wood. Defoliation of the main canopy was light, less than 25 percent, but many oaks were badly defoliated. If such attacks occur repeatedly, there is little wonder that oak declines.

In Predicting Change we anticipated that the oak population will dwindle. Hopefully, as it does, losses from defoliation will also decrease as insects are deprived of a favored host. Only through continued observation and comparison will we know whether defoliators are speeding the observed decline of oak.

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Common and Scientific Names of Plants Mentioned in This Bulletin

(*Kelsey and Dayton 1942, Fernald 1950, Little 1953*)

Ash, white—*Fraxinus americana*
  black—*Fraxinus nigra*
Aspen, bigtooth—*Populus grandidentata*
Basswood—*Tilia americana*
Beech—*Fagus grandifolia*
Birch, black[1]—*Betula lenta*
  yellow—*Betula alleghaniensis*
  gray—*Betula populifolia*
Bluebeech[1]—*Carpinus caroliniana*
Blueberry, highbush—*Vaccinium corymbosum*
Cherry, black—*Prunus serotina*
Chestnut, American—*Castanea dentata*
Dogwood, flowering—*Cornus florida*
Elm, American—*Ulmus americana*
Hemlock—*Tsuga canadensis*
Hickory, shagbark—*Carya ovata*
  mockernut—*Carya tomentosa*
  pignut—*Carya glabra*
Hophornbeam—*Ostrya virginana*
Locust, black—*Robinia pseudoacacia*
Maple, sugar—*Acer saccharum*
  red—*Acer rubrum*
Oak, white—*Quercus alba*
  red—*Quercus rubra*
  scarlet—*Quercus coccinea*
  black—*Quercus velutina*
Pepperidge—*Nyssa sylvatica*
Pine, white—*Pinus strobus*
Redcedar[1]—*Juniperus virginiana*
Sassafras—*Sassafras albidum*
Shadbush[1]—*Amelanchier arborea*
Spicebush—*Lindera benzoin*
Viburnum, arrowwood—*Viburnum dentatum*
Witchhobble—*Virburnum alnifolium*
Witherod—*Viburnum cassinoides*
Witchhazel—*Hamamelis virginiana*
Winterberry, common—*Ilex verticillata*

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[1] Local name differing from Fernald (1950), Little (1953) or Standardized Plant Names (Kelsey and Dayton 1942).

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James G. Horsfall
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