The Forests Anticipated
from 40 Years of Natural Transitions
in Mixed Hardwoods

George R. Stephens　　　　　　　　　　**Paul E. Waggoner**

A central Connecticut field and woodland as it
looked in 1920. How this unmanaged area had changed
after four decades is shown on the back cover.

CONTENTS

SUMMARY

The natural changes on about 13 acres of transect through 210 acres of four mixed hardwood forests in central Connecticut are analyzed in two ways. First the enumerations of 1927, 1937, 1957, and 1967 are tabulated. Then they are converted into probabilities of transitions on small plots in the forests. These probabilities are sometimes surprisingly similar over the 40 years and permit systematic anticipation of the future.

The tabulations are a summary of the careers of 31 thousand stems. The population halved in 40 years, while the species diversity over the entire sample scarcely changed. For 40 years ingrowth added 80 to 140 new stems per acre per decade, but the change in wood volume was largely in the balance between mortality and the growth of persistent trees. The basal area or cross section of stems rose from 70 to over 90 square feet per acre between 1927 and 1957; then during the drought and defoliation of 1957-67 it declined somewhat in three of the four forests as many hickories and pole-sized oaks died. The decade of drought had little effect where the trees were scarcely defoliated, but the growth of major species decreased while minor species increased where insects did their work.

Fire swept over part of one forest in 1932, and the small stems nearly disappeared. After 35 years, however, the burned forest had largely recovered.

Transition probabilities are most easily grasped in examples. Thus where maple was the most numerous kind of tree in 1927, it was still most numerous in 82 percent of the fortieth-acre plots a decade later. Meanwhile on 7, 2, and 8 percent of the plots once dominated by maple, the most numerous kind became oak, birch and minor species. After a full set of transition probabilities were calculated in this fashion, they were found similar for 1927-37 and 1957-67. Also, when the probabilities for the first decade were multiplied by themselves, the product resembled the transitions of the double decade 1937-57. Further multiplication of the probabilities of the first decade made a product that resembled the changes of the entire 40 years. The steady states extrapolated from either the first or last decade of observations were much alike: many plots were mostly maple or birch, some were mostly minor species, and a few were mostly oak or mostly other major species. When the plots were classified according to the basal area, rather than number of stems, the oaken giants were more dominant and the future was made more uncertain by their frequent death during 1957-67.

When the plots were classified according to the shade tolerance class that was most numerous, the transitions from intolerant were rapid, but the steady state was predominantly moderately tolerant, not one of the more tolerant classes. A synthetic succession starting from all plots dominated by intolerant species passed in only 30 years to a forest of largely moderately tolerant trees.

Although the species diversity on the entire forest scarcely changed, on individual fortieth-acre plots it declined steadily as shown by near constant transition probabilities. The probabilities for basal area and number of stems were not constant from decade to decade. Nevertheless, combining the basal area with the number of stems on a plot makes an interesting way of representing the natural transition from thicket to park in these woods during 40 years.

The Forests Anticipated
from 40 Years of Natural Transitions
in Mixed Hardwoods

George R. Stephens and Paul E. Waggoner

INTRODUCTION

The landscape of Connecticut is changing. To most, the immediate and obvious observation is the succession from rural agraria to sprawling suburbia. Indeed, since 1958, in our state over 62,000 acres of field and over 34,000 of forest have disappeared into the maw of residential, commercial and industrial development. Nevertheless at the same time, nearly 72,000 additional acres of crop and pasture land went out of production, some of which will surely revert to its natural vegetation, forest.[1] Forest occupies much of our land; of Connecticut's 3 million acres, two-thirds are classified as forest. And likely more surprising to some, half of this forest came into being during the past 100 years. Let us then examine more closely our forested landscape.

Connecticut has no vast wilderness; few points in our woodlands lie more than a mile from passable roads. Much of our forest is of the suburbs and the term, "suburban forest," was coined at this Station in 1957 (Hicock, 1957). It is defined as ". . . the land surrounding and permeating the clearings for cities, farms, homes and highways . . . contains sufficient trees to give wooded appearance and is generally excluded from horticulture and agriculture . . . provides . . . a backdrop against which man carries out his daily activities." (Waggoner and Ovington, 1962, p. 10)

To the casual observer, the seemingly immutable mantle of trees which cloaks our hills may impart an aura of changelessness. Yet our forests undergo dramatic change and seethe with the struggle for survival. But because these changes are slow in time as measured by man, they often pass unnoticed. Therefore, let us explore this backdrop in greater detail.

We know that our forest is of two types: that continuously forested and that newly-risen during the last 100 years. Of the first, most was cut or ravaged by fire, but it was never completely cleared for agricultural pursuits. Some is likely little different in general appearance and composition today than when the colonists first landed on this rocky soil. We can

---

[1] Personal communication, R. E. Laramy, Jr., U.S.D.A., Soil Conservation Service, Storrs, Connecticut.

see this on our gaunt ridges, too steep and stony to plow, too rocky to support cattle or sheep. Nonetheless repeating cutting, fire, and the sudden loss of chestnut have altered the composition of this remaining original forest.

Our new forest has grown on land once pastured or plowed. Here the changes are spectacular, clearly visible, and quickly accomplished during man's life span. The unmown meadow and fallow field are quickly invaded · by small-statured shrubs and short-lived pioneers such as sumac and sweetfern, redcedar and birch. The idle furrow is host to the light-seeded birch and aspen, while birds scatter the heavier seed of redcedar and shrubby dogwoods. Often quick to follow are cherry and sassafras, and sometimes pine. Sparsely at first, and then more and more, these pioneers rise up from meadow grass and forgotten field. As 15 or 20 years quickly pass, the shrub-dotted fields are transformed to a tangled thicket that blocks the vista of rolling fields and neat stone walls. Forest, of a sort, now claims the land.

Soon the more majestic, long-term invaders appear. Oak and hickory, maple and ash emerge from the thicket to claim the old field. The lowly pioneers falter and dwindle, unable to remain in the race for the sun. The forest now assumes more of its permanent character, and the insidious struggle of size and numbers, unnoticed by all but the most persistent observer, replaces the dramatic change from field to forest. This Bulletin describes this insidious natural struggle in four mixed hardwood forests of central Connecticut.

Forty-three years ago five men from this Station set out to study this forest, part new, part old, which surrounds us (Hicock et al., 1931). From their detailed records and of those who followed, we now have a unique picture of the struggle for supremacy in four unmanaged hardwood woodlands so typical of Connecticut countryside (Collins 1962, Olson 1965). The cover photos illustrate the dramatic change.

The 1920 view (front cover) near one of the woodlands, shows open field, pioneer birches, and an older forest of pine and hardwood. Note well the stone wall and rock in the foreground. In 1966 (back cover) the stone wall and rock remained in the picture, though barely visible, but field and birches had long since passed from view.

The changes undergone can be expressed in several ways: the appearance and disappearance of species, the rise and fall in population, and the change in size and dominance. Each tells a story, but altogether they complete the picture.

Olson (1965) employed tables of these characteristics for 1927, 1937, and 1957 to show how this silent struggle had gone. In the present Bulletin we have extended his tables to 1967, showing how a full 40 years of change have passed in these four forests. We have repeated some of Olson's descriptions of methods and of the land to smooth the reader's path. The extension of the census to 1967 reveals how the drought and defoliation of that dry decade sped — or did not — the fight for living space in the forest.

But where does this record of the silent struggle lead us and what purpose does it serve?

To keep this Bulletin from becoming a musty chronicle of sylvan history we will show the reader how the past presages the future. The changes of the past provide the probabilities of change or maintaining the *status quo*. But first, we briefly review events of the first three decades and add our account of the fourth.

DESCRIPTION OF THE TRACTS

This study began in 1926 on an 80-acre tract called Turkey Hill in the Cockaponsett State Forest in south central Connecticut. In 1927 study began of the 50-acre Cox tract, the 40-acre Reeves tract, and the 40-acre Cabin tract, all in the Mountain Block of the Meshomasic State Forest in central Connecticut. These were selected as representatives of forests and sites in the mixed hardwood region that covers most of Connecticut. Further, the stands were reasonably uniform in age and density and several important soil types were well represented.

All tracts are near the western end of the Eastern Highlands of Connecticut, a region of metamorphic rocks and glaciated soils. The topography is gently rolling to rugged with considerable rock outcrop. Elevation ranges from 400 to 800 feet. Of the four tracts, Turkey Hill is most exposed to strong southeasterly gales such as those that occurred during the 1938 hurricane.

The forest cover was the mixed hardwood type typical of much of the woodlands in Connecticut, with 37 species represented on the transects. In 1927 the trees varied from 25 to 40 years in age with occasional older trees. Observation and inquiry revealed that portions of each tract had been cleared in the past, but the exact boundaries of clearings could not be ascertained. Thus both the old forest that has never been tilled and the new forest that has arisen on old fields are represented in the tracts but could not be clearly separated. Chestnut was present on all tracts as evidenced by continued sprouting. Since the study was started in 1926 and 1927, disturbance by man has been slight, and most disturbed areas have been eliminated from this study; a burned area on Turkey Hill is analyzed in a separate Chapter.

In the Introduction, the decade from 1957 to 1967 was called a time of drought and defoliation. At Hartford's Brainard Field, which is about 10 miles north of three of the plots, the normal precipitation is 44 inches per year. In the first decade of the census of the tracts, the annual precipitation was 3.6 inches less than normal. In the score of years between 1937 and 1957, it was 1.0 inch above normal. But in the last decade it was 6.9 inches below normal, a very droughty time indeed.

In the middle years of the last decade, 1957-67, gypsy moth (*Porthetria dispar* L.), cankerworm (*Paleacrita vernata* Peck.) and other defoliators flourished and attacked the leaf canopies of all four tracts. Defoliators varied with tract and year, but more important to the forest was the degree of defoliation. Aerial reconnaisance indicated partial defoliation on Cabin,

Cox and Reeves during 1961, 1962 and 1963 and on Turkey Hill in 1964.[2] In 1962 on Cabin, Cox, and Reeves removal of the leaf canopy was estimated to be greater than 50 percent. In 1963 Cabin and Cox were less than 50 percent defoliated while portions of Reeves may have been more than 50 percent defoliated. In 1964 removal of the canopy on Turkey Hill was estimated to be between 25 and 75 percent.

METHODS

All tracts were laid out as rectangles with the long axis east-west. The dimensions were: Turkey Hill, 20 x 40 chains; Cox, 14 x 36 chains; Reeves, 10 x 40 chains; and Cabin, 20 x 20 chains. A chain is 66 feet and an acre is 10 square chains. Transect lines were laid out south to north at 5-chain intervals on Turkey Hill and at 4-chain intervals on the other tracts. Characteristics of site such as soil type, soil depth, soil drainage or moisture, stoniness, humus type, slope, and aspect were determined and mapped along the transect lines. Along a strip 0.25 chain wide centered on the transect lines, each tree 0.6 inch d.b.h. (diameter breast high) or greater was plotted on a map, identified, and described.

Initially, description included d.b.h., crown class (on all tracts except Turkey Hill), and whether or not the tree was a member of a sprout group. Witchhazel was not recorded on Turkey Hill in 1927, but it was in 1937 and 1957. Crown class is defined in Forest Terminology (Soc. Amer. Foresters, 1950).

In 1937 the same information was recorded for stems tallied in 1927. Deaths and new trees (ingrowth) 0.6 inch d.b.h. or larger were noted. Crown class was recorded on Turkey Hill in 1937.

In 1957 the same information was again recorded, but the minimum d.b.h. was decreased to 0.5 inch. In addition, the height of all dominant trees and every tenth tree other than dominants was measured with an Abney level. Trees for which height was measured and any companion sprout were also examined for defects. The defects were in form and symmetry and those caused by injury to the stem or crown and do not include internal defects such as heartrot.

In 1967 all trees larger than 0.5 inch d.b.h. were measured at d.b.h. Also they were classified for crown class, and new sprout numbers were assigned where death had carried one away or a new one had appeared.

In 1932 a resurvey of the Turkey Hill tract was made following a fire which burned approximately 40 percent of the area. In addition to the same information gathered in 1927, the extent of the fire on the transect lines, deaths, new recruits, and crown class were recorded. The information from the burned part of Turkey Hill appears in a separate Chapter in this report.

After the 1957 resurvey, the information from all surveys was transferred to punch cards and summarized by machine. The analyses that follow pertain only to undisturbed sites.

---

[2]Unpublished defoliation maps in the files of the State Entomologist, New Haven, Conn.

SITE CHARACTERISTICS

History of the tracts is undoubtedly important, but unfortunately as we have already said, the exact boundaries of different age classes could not be determined and employed as site characteristics.

Although soil type, depth of soil, internal soil drainage, stoniness, humus type, and aspects were determined along the transects, only internal soil drainage is used here in relating tree or stand characteristics to site because past studies indicated it to be the most important one.

Soil drainage classes were classified according to the Soil Survey Manual (1951). In addition to the 7 classes given in the manual, one was added for the muck site on Turkey Hill. Because the area sampled in some drainage classes was small, the classes were combined into four moisture classes as follows: (A) 7, muck; (B) moist sites which included 0, the very poorly drained, and 1, the poorly drained; (C) medium moist sites which included 2, the imperfectly or somewhat poorly drained (only .06 acre), 3, the moderately well drained, and 4, the well drained; and (D) dry sites which included 5, the somewhat excessively drained, and 6, the excessively drained soils. The area in each combined moisture class is shown in Table 1.

NUMBER OF STEMS

In 1967 the major species averaged 458 stems per acre over all plots and sites with remarkably close agreement among plots (Table 2). Thus although Cox was predominantly the new forest described in the Introduction and Reeves and Cabin were predominantly old, the silent struggle of 1927 to 1967 went much the same in all.

The number of stems has declined steadily since 1927 and major species are now only 46 percent as numerous. The decrease generally occurred over all plots and moisture classes. During the decade of drought and defoliation 1957-67 the decrease in numbers did not accelerate (Fig. 1) and the decrease was, if anything, less on the dry than on the moister sites.

Loss was greatest on Cox and Reeves, nearly two-thirds, and least on Turkey Hill, only 40 percent. However, this is not surprising because there were 40 percent fewer stems on Turkey Hill in 1927 than on the other plots. In fact, since 1927 the number of stems has increased on muck and dry sites of Turkey Hill.

In 1967 minor species averaged 166 stems per acre, 42 percent of the

Table 1. Sample area (acres) of moisture classes, undisturbed sites only

	Muck	Moist	Medium Moist	Dry	All
Turkey Hill	.16	.58	1.57	.09	2.40
Cox	....	.51	2.06	.60	3.17
Reeves	....	.33	1.42	.73	2.48
Cabin	....	.33	1.91	....	2.24
All	.16	1.75	6.96	1.42	10.29
Burned	....	.20	1.09	.30	1.59

number in 1927. However, the number was more variable than for major species. The pattern of change is similar to that of major species, except that since 1957 minor species also have increased on the dry sites of Turkey Hill.

Study of changes among individual species[a] revealed that through 1967 red and sugar maple, yellow and black birch continued to increase in proportion of total stems as other species, for example, redcedar faded out (Table 3). Beech increased in absolute number as well as proportionally. Compared to 1957 the proportion of maples rose from 35 to 39 percent of stems, and birches from 26 to 30. On the other hand, hickories decreased from 4 to 2 percent, while oaks declined from 23 to 14 percent. All moisture classes, except muck, displayed a similar pattern of change.

Among the minor species, chestnut, flowering dogwood, and witchhazel all increased in proportion of stems from 1957 to 1967, whereas bluebeech and hophornbeam declined.
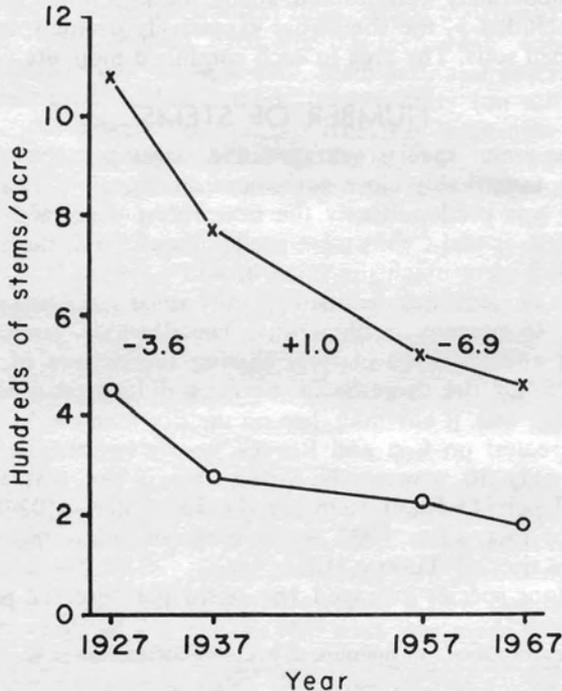
Fig. 1. The number of major (x) and minor (o) species stems per acre. The mean deviation of annual precipitation (inches) from normal during each period is written on the Figure and emphasizes the persistent droughts of the first and last decades.

[a]The present Bulletin is presented characteristic-by-characteristic. For example, here the change in population is discussed. On the other hand, Olson (1965) has written descriptions of behavior species-by-species. The reader interested in particular species will want to refer to Olson's paragraphs.

Moisture affected the population of red maple and red oak surprisingly little. On the other hand, although found on all sites, sugar maple and yellow birch are most abundant on the moist. Black birch and the remaining oaks are more frequent on drier sites. As time has passed the proportion of oaks on all sites has declined, while the proportion of maple and birch has risen.

Table 2.   Number of stems per acre[1]

Site	Year	Turkey Hill	Cox	Major Species Reeves	Cabin	All
Moist	1927	672	1429	827	645	917
	1937	622	902	570	615	693
	1957	550	549	385	479	505
	1967	462	435	330	424	422
Medium[2]	1927	841	1269	1212	1073	1107
	1937	672	761	868	791	771
	1957	566	514	491	506	519
	1967	450	487	441	445	458
Dry	1927	633	1222	1205		1176
	1937	522	852	911		861
	1957	633	518	534		534
	1967	700	473	511		507
All	1927	757	1286	1159	1010	1072
	1937	629	801	841	765	762
	1957	556	520	490	502	517
	1967	462	476	447	442	458
				Minor Species		
Moist	1927	200	1157	491	252	543
	1937	190	569	306	239	331
	1957	314	204	373	352	300
	1967	200	86	258	176	173
Medium	1927	416	873	275	273	483
	1937	373	431	165	177	294
	1957	353	203	159	214	231
	1967	298	117	149	186	183
Dry	1927	189	280	205		236
	1937	167	147	93		120
	1957	78	78	119		99
	1967	89	55	100		80
All	1927	329	806	283	270	452
	1937	298	399	163	186	272
	1957	315	180	176	234	222
	1967	250	101	149	184	166

[1] All site totals for Turkey Hill and All tract totals include the following trees growing on muck. Major species: 1927, 312; 1937, 288; 1957, 438; 1967, 438 stems/acre. Minor species: 1927, 25; 1937, 25; 1957, 75; 1967, 56 stems/acre. Witchhazel was not counted on Turkey Hill in 1927.

[2] Medium moist

Table 3. Number of stems of major and minor species (percent of total), all tracts

	Muck				Moist				Medium Moist				Dry				All			
	1927	1937	1957	1967	1927	1937	1957	1967	1927	1937	1957	1967	1927	1937	1957	1967	1927	1937	1957	1967
Major Species																				
Sugar Maple	0	0	0	1.4	8.2	10.6	14.4	15.8	3.3	4.2	6.4	6.7	1.0	1.1	2.0	1.7	3.7	4.7	7.0	7.3
Red Maple	70.0	76.1	64.3	61.4	29.3	28.5	26.9	26.4	24.1	25.3	27.6	31.8	25.0	23.7	30.3	35.4	25.2	25.9	28.4	32.0
Red Oak	0	0	1.4	1.4	7.7	8.2	7.6	5.0	9.9	9.9	8.7	6.2	8.3	8.3	8.3	6.4	9.3	9.3	8.4	6.0
Black Oak	0	0	0	0	1.1	1.0	.7	.4	2.8	3.1	2.8	2.2	8.0	8.8	7.4	4.9	3.4	3.6	3.1	2.3
Scarlet Oak	0	0	0	0	.9	1.2	.8	.5	1.9	2.0	2.4	1.8	3.5	4.1	4.4	2.9	2.0	2.2	2.3	1.7
White Oak	0	0	0	0	4.2	2.7	2.0	.8	13.1	11.2	5.3	2.3	16.0	16.7	8.8	2.8	12.2	10.7	5.2	2.1
Chestnut Oak	0	0	0	0	1.9	2.8	1.7	1.5	3.3	3.7	4.5	2.4	2.0	2.0	2.4	1.9	2.9	3.3	3.7	2.1
Yellow Birch	2.0	2.2	5.7	4.3	17.1	19.7	21.7	23.5	8.0	8.8	11.7	12.4	.7	.7	1.1	1.2	8.2	9.2	11.8	12.3
Black Birch	0	0	1.4	2.9	4.9	5.2	6.4	8.4	12.8	14.1	15.5	19.1	14.3	15.8	21.4	25.8	11.8	12.9	14.7	18.2
Paper Birch	0	0	0	0	0	0	0	0	.1	.1	.2	.2	0	0	0	0	.1	.1	.1	.1
Bitternut Hickory	0	0	0	0	.2	.2	0	0	.2	.2	.1	<.1	0	0	0	0	.2	.1	<.1	<.1
Mockernut Hickory	0	0	0	0	.4	.2	0	0	1.3	1.3	1.3	.8	1.9	2.0	1.6	.8	1.2	1.2	1.1	.6
Pignut Hickory	0	0	0	0	1.2	1.2	.7	.4	4.2	2.9	2.0	1.2	8.6	8.0	3.8	1.9	4.4	3.4	2.0	1.1
Shagbark Hickory	0	0	0	0	.9	.9	1.1	.9	1.0	1.0	1.1	.8	.7	.7	.5	.1	.9	.9	1.0	.7
Beech	0	0	0	0	.2	.2	3.2	4.6	1.4	1.8	3.1	5.1	2.2	3.1	5.3	10.3	1.3	1.7	3.4	5.7
Tulip	0	0	0	0	1.1	1.4	1.0	1.1	1.3	1.4	1.3	1.4	.2	.2	.3	.3	1.1	1.2	1.1	1.1
White Ash	10.0	13.0	17.1	15.7	6.9	6.2	5.5	4.3	6.8	5.9	3.6	2.4	2.1	2.5	1.1	.1	6.1	5.5	3.7	2.6
Black Ash	2.0	2.2	2.9	5.7	.2	.2	.1	.1	.1	<.1	0	0	0	0	0	.1	.1	.1	.1	.1
Basswood	0	0	0	0	.4	.5	.2	0	.3	.3	.1	.1	0	0	0	0	.3	.3	.1	<.1
Elm	12.0	6.5	7.1	7.1	2.4	2.2	1.7	1.1	.2	.1	.1	.1	.1	<.1	0	0	.5	.5	.4	.3
Bigtooth Aspen	0	0	0	0	3.6	3.0	0	0	.7	.7	.1	.1	1.7	.8	0	0	1.3	1.1	.1	.1
Quaking Aspen	0	0	0	0	.1	.1	0	0	0	0	0	0	0	0	0	0	<.1	<.1	0	0
Pepperidge	4.0	0	0	0	2.1	2.1	2.3	2.7	.5	.6	.6	.7	.3	.2	.3	.1	.7	.8	.8	.9
Locust	0	0	0	0	0	0	0	0	0	0	0	0	.2	.1	.1	.1	<.1	<.1	<.1	<.1
Butternut	0	0	0	0	.4	.1	0	0	.4	.1	0	0	.7	.2	0	0	.4	.1	0	0
Black Cherry	0	0	0	0	3.4	.7	.1	0	.5	.1	0	0	.9	.2	0	0	1.0	.2	<.1	0
Sassafras	0	0	0	0	1.2	.7	1.7	2.2	1.3	1.0	1.2	2.4	1.6	.7	1.1	2.9	1.3	.9	1.3	2.4
White Pine	0	0	0	0	0	.1	0	0	<.1	<.1	.2	<.1	0	0	0	0	<.1	<.1	.1	<.1
Hemlock	0	0	0	0	.1	.1	.1	.1	<.1	<.1	.1	.1	0	0	0	0	<.1	<.1	.1	.1
Redcedar	0	0	0	0	0	0	0	0	.4	<.1	<.1	0	.2	0	0	0	.3	<.1	<.1	0
Stems/acre	312	288	438	438	917	693	505	422	1107	771	519	458	1176	861	534	507	1072	762	517	458

Minor Species

Chestnut	0	0	0	.5	.2	3.8	5.0	2.2	.5	18.6	26.7	12.4	2.9	44.7	61.4	2.6	.6	16.7	25.0
Dogwood	0	0	0	2.6	3.1	4.8	11.6	9.8	14.9	16.1	21.3	9.2	12.9	8.5	11.4	8.2	12.3	13.0	18.8
Bluebeech	75.0	50.0	33.3	45.3	46.2	29.9	21.1	39.0	34.8	21.5	8.8	20.4	24.0	14.2	1.8	39.1	36.5	23.1	10.7
Shadbush	25.0	25.0	11.1	4.2	6.0	1.1	1.0	3.1	4.2	.9	.5	10.1	11.7	2.8	3.5	3.8	5.0	1.1	.8
Hophornbeam	0	0	0	5.2	5.9	9.3	2.0	7.9	7.2	5.4	1.2	6.5	11.7	13.5	.9	7.2	7.2	6.8	1.3
Gray Birch	0	0	0	14.7	10.0	.4	0	13.3	8.9	.4	.1	27.5	23.4	0		14.6	10.0	.4	.1
Witchhazel[1]	0	25.0	50.0	27.6	28.6	50.7	59.4	24.7	29.6	37.1	41.4	13.9	13.5	16.3	21.1	24.6	28.4	39.0	43.3
Stems/acre	25	75	56	598	331	300	173	512	294	231	184	238	120	99	80	481	272	222	166

[1] Witchhazel was not counted on Turkey Hill in 1927.

These changes in proportions have been against a background of declining numbers with all species but one declining in number. The interesting exception is beech, which has increased from 14 to 27 trees per acre.

DIVERSITY

In addition to the sheer change in numbers of stems and a few anecdotes about interesting species, the reader will want to know how big the stems are and how diverse is the collection of species. We will postpone stem size to later sections and discuss species diversity here.

Diversity in a suburban forest is usually assumed to be a virtue. Certainly the pleasure of walking through the woods increases with the number of kinds of plants that the walker discovers. The pleasure from a forest landscape increases if leaves of different tints expand at different times, if various flowers appear in various seasons, and if a spectrum of autumn colors is seen — all because of the diversity of the species. Finally, diversity is assumed to be a sort of insurance because a single pest will not likely attack diverse species.

Since diversity has several facets, however, measuring it is not simple (Pielou, 1966). In a finite forest, such as the transects through the Connecticut forests, the diversity decreases whenever an individual is lost, a species is lost or individuals become concentrated in fewer species. This composite character, diversity, can be measured as

$$\frac{1}{N} \, \log_2 \frac{N!}{N_1! \, N_2! \, \ldots \, Ns!} \quad \text{bits/individual.}$$

N is the total number of individuals on the tract and N_1, N_2 ..., Ns are the numbers in the first, second, ..., and last of s species.

The behavior of this index with changes in the factors (numbers, species, and distribution) has been described fully by Pielou. Here we shall go directly to the changes over the decades in the factors and summarize by examining the change in the index of diversity.

Certainly the number of stems has decreased, Table 3. When the number of stems is large, however, as it is in our tracts even in 1967, both our common sense and Pielou's mathematics say declining numbers will have little effect upon diversity.

The number of species counted on the tracts has remained fairly constant. The table for 1927 shows 37 species, and the table for 1967 still shows 33 species. Only quaking aspen, butternut, redcedar, and black cherry had disappeared, and these four species had contributed only 1 stem in 80 to the total 1927 population.

The distribution of the population among the several species was similar at the beginning and end of the 40 years. This is seen in the percentages in the right side of Table 3, and the distribution was maintained despite the halving of the population per acre.

Since the population has not declined to a sparse one, since few species have been lost, and since the distribution of the population among the species has remained surprisingly similar, one expects that the index of

diversity will not have changed greatly. In fact it was 4.11 in 1927, 4.04 in 1937, 3.93 in1957 and 3.69 in 1967. One might expect that diversity would increase with the development of the forest toward maturity, but this did not happen. Instead diversity was about steady. An explanation is given later. But the inhabitant of the suburban forest may be reassured that he can see nearly as much diversity in trees when he hikes through the woods as his father saw when he looked for the lost cow.

BASAL AREA

Both stocking and maturity of a stand are revealed, not by the number of stems or diversity of species, but by the cross-sectional area of the stems per acre. The cross section is measured at breast height (4.5 feet).

Basal area of major species, as an average over all plots and sites, increased from 63 ft^2 per acre in 1927 to 97 ft^2 in 1957 (Table 4). However, by 1967 it decreased slightly on three plots. The decrease was greatest on Cabin, 8 percent, and least on Reeves, less than 1 percent. The decrease was concentrated on the drier sites.

Turkey Hill, unlike the other three plots, increased its basal area between 1957 and 1967. Initially this plot had fewer, but larger, stems. These have grown steadily in basal area regardless of moisture class. In the last decade, basal area on Turkey Hill has overtaken that on the other plots.

In another example, in 1927 about a sixth of total basal area on Turkey Hill, Reeves and Cabin tracts was comprised of trees larger than 11.5 inches d.b.h. In contrast, less than 1 percent of basal area on Cox occurred among these larger trees. Nevertheless, by 1967 this great disparity nearly disappeared, and all undisturbed tracts had approximately half their basal area in larger trees.

Minor species, on the other hand, have decreased steadily since 1927 in basal area on all plots and sites except muck. By 1967 average basal area was an insignificant 1.8 ft^2 per acre.

Numbers of stems or the proportion of total stems belonging to a species permits only limited insight into stand structure. Small trees are not distinguished from large. Basal area, on the other hand, better describes the importance of a species in the stand. Small trees, though numerous, contribute relatively little to basal area whereas even a few large trees contribute greatly. Therefore, the basal area of single species is presented in Table 5.

In 1967 oaks still predominated with 47 percent of basal area. The contribution of red, black, and scarlet oak remained unchanged, but white and chestnut oak declined nearly one-third in ten years. Maples contributed 16, black and yellow birch nearly 22 percent, and tulip almost 5. Compared to 1957, red and sugar maple, black birch, beech and tulip all contributed proportionally more.

Moisture modified these changes. On moist sites the proportion of basal area of most major species remained unchanged or increased slightly. On medium moist and dry sites, however, the maples, red oak, black birch.

and beech increased their proportion of basal area at the expense of other oaks.

Minor species dwindled from 10 percent of basal area in 1927 to less than 2 percent in 1967. This was a loss of a third in a decade. Only on muck did the basal area of minor species continue to increase. Flowering dogwood and witchhazel contributed most to the basal area of minor species.

Table 4. Basal area in square feet per acre[1]

Site	Year	Turkey Hill	Cox	Reeves	Cabin	All
				Major Species		
Moist	1927	88	70	73	67	76
	1937	93	89	89	88	90
	1957	96	98	112	108	102
	1967	101	99	111	120	106
Medium[2]	1927	61	61	66	67	64
	1937	79	80	88	91	84
	1957	92	96	96	111	99
	1967	100	91	96	98	96
Dry	1927	44	43	53		48
	1937	46	66	74		69
	1957	62	81	94		86
	1967	77	73	94		84
All	1927	66	59	63	67	63
	1937	79	79	84	90	83
	1957	89	94	98	110	97
	1967	97	89	97	102	96
				Minor Species		
Moist	1927	4.8	19.1	5.8	4.8	9.2
	1937	4.2	15.4	4.1	3.6	7.3
	1957	4.6	4.7	3.2	4.2	4.3
	1967	3.1	1.0	2.1	1.8	2.1
Medium	1927	7.7	12.5	2.8	3.3	6.9
	1937	7.2	9.8	2.1	2.4	5.6
	1957	5.1	3.1	1.5	1.3	2.7
	1967	4.0	1.3	1.4	1.4	2.0
Dry	1927	3.0	5.2	3.3		4.0
	1937	2.9	4.1	1.8		2.8
	1957	1.6	.8	.9		.9
	1967	1.9	.8	.6		.7
All	1927	6.4	12.2	3.4	3.5	6.8
	1937	5.9	9.6	2.3	2.6	5.5
	1957	4.6	2.9	1.5	1.7	2.7
	1967	3.6	1.2	1.2	1.5	1.8

[1] All site totals for Turkey Hill and All tract totals include the following trees growing on muck. For major species: 1927, 44; 1937, 52; 1957, 45; 1967, 61 sq .ft./acre. For minor species: 1927, 0.8; 1937, 0.8; 1957, 1.3; 1967, 1.3 sq. ft./acre. Witchhazel was not measured on Turkey Hill in 1927.

[2] Medium moist.

We have already seen that Turkey Hill lost many more stems in the 1957-67 decade than the other plots. Yet it continued to increase in basal area, while the basal area on the other plots declined. This indicates that interesting changes in distribution of stem diameters have occurred.

DISTRIBUTION OF DIAMETER

To determine the proportion of trees of different sizes, they were grouped into four classes: (1) small sapling, 0.5 to 1.5 inches d.b.h.; (2) large sapling, 1.6 to 5.5; (3) pole, 5.6 to 11.5; and (4) sawtimber, larger than 11.5.

First, the major species are considered alone.

During the first decade, 1927-37, the proportion of stems of major species that were large saplings increased to more than half (Table 6). During the next 20 years the proportion of pole and sawtimber sizes increased. In the final decade, however, the proportion of large saplings and pole sizes both decreased, while the proportion of small saplings and sawtimber trees increased, leaving a more even distribution of tree sizes.

Minor species, of course, remained chiefly as saplings (Table 7). Since 1937 they shifted gradually from large to small saplings. Because numbers declined this shift indicates that proportionally more large saplings died than did small. The ingrowth and death of many individuals without moving into the larger classes is, of course, concealed.

The forest is comprised of major and minor species together, however. If we studied the individual tracts, slight differences in distribution among classes, and small changes with time, would be noted. Nevertheless, while the total number of stems declined during the last decade, their distribution among size classes scarcely changed. (Bottom line, Table 7.) This constancy suggests that the average distribution of stems among these arbitrary size classes had approached an equilibrium.

Study of individual species reveals that since 1957 oaks and tulip have become concentrated in sawtimber with corresponding decreases in poles and saplings (Table 7). Maples, birches and beech occur mostly as saplings, and their diameter distribution has changed little since 1957. The concentration of hickories has shifted from large saplings to poles.

Among the oaks the shift from pole to sawtimber was more relative than absolute, and the shift does not reflect actual growth from pole to sawtimber size. In fact, the *number* of sawtimber oaks scarcely changed but the *proportion* of sawtimber increased because fully half the pole trees disappeared. The same was true for hickories. On the other hand, any relative increases in the larger diameter groups among maples, birches, and beech were accompanied by actual increases in numbers, a manifestation of real growth. We shall consider this peculiarity of oak again when mortality is analyzed.

MORTALITY

Since the changes in these forests are "natural" and since the tracts were covered by a canopy of 1500 small trees per acre in 1927, the growth of some means others must naturally fall behind and die in the shade.

Table 5. Basal area of major and minor species (percent of total), all tracts

Major Species	Muck				Moist				Medium Moist				Dry				All			
	1927	1937	1957	1967	1927	1937	1957	1967	1927	1937	1957	1967	1927	1937	1957	1967	1927	1937	1957	1967
Sugar Maple	0	0	0	<.1	4.4	4.5	5.0	5.6	1.3	1.3	1.6	1.9	.2	.2	.2	.3	1.8	1.8	2.0	2.4
Red Maple	84.8	87.2	66.8	62.6	24.6	24.3	20.0	20.6	10.8	10.2	9.6	11.5	11.2	9.5	6.8	8.0	14.5	13.5	11.5	13.4
Red Oak	0	0	.5	.5	6.7	10.3	16.9	17.7	14.0	17.0	22.1	23.3	9.2	12.2	16.3	19.3	11.8	15.1	20.3	21.5
Black Oak	0	0	0	0	1.7	2.1	2.7	2.7	4.4	5.9	8.3	8.7	11.8	15.3	20.3	19.7	4.6	6.2	8.6	8.8
Scarlet Oak	0	0	0	0	1.6	2.5	2.7	2.0	5.0	5.7	7.2	7.0	7.4	9.3	11.7	11.2	4.5	5.4	6.8	6.5
White Oak	0	0	0	0	1.8	2.1	2.1	1.8	10.4	10.1	8.7	5.2	15.5	17.0	13.8	6.7	9.1	9.3	8.0	4.7
Chestnut Oak	0	0	0	0	3.3	4.6	5.8	6.0	7.8	8.6	9.0	6.4	3.9	3.1	3.7	3.2	6.4	7.2	7.7	5.9
Yellow Birch	.1	.3	3.0	3.5	15.1	15.8	16.5	15.9	6.5	6.6	5.6	5.5	1.1	.8	.7	.7	7.7	7.6	6.9	6.9
Black Birch	0	0	<.1	.2	10.7	8.1	10.5	11.6	13.6	13.6	13.3	15.0	15.4	15.4	15.9	19.3	13.1	12.6	13.0	14.8
Paper Birch	0	0	0	0	0	0	0	0	.2	.2	.2	.2	0	0	0	0	.1	.1	.1	.1
Bitternut Hickory	0	0	0	0	.1	<.1	0	0	.1	<.1	<.1	<.1	0	0	0	0	<.1	<.1	<.1	<.1
Mockernut Hickory	0	0	0	0	.1	<.1	0	0	1.0	.9	1.0	.8	1.2	1.2	1.0	.9	.8	.7	.8	.6
Pignut Hickory	0	0	0	0	.4	.4	.5	.1	2.1	1.9	1.8	2.0	4.8	4.5	2.9	2.6	2.0	1.9	1.7	1.7
Shagbark Hickory	0	0	0	0	.8	.8	1.3	1.1	1.1	1.0	1.0	.8	.8	.8	.7	.6	1.0	.9	1.0	.8
Beech	0	0	0	0	.1	.3	.7	1.0	.3	.3	.5	.9	3.1	2.8	3.8	5.1	.6	.6	.9	1.4
Tulip	0	0	0	0	2.5	3.4	4.2	5.1	3.2	3.8	4.0	5.3	.2	.3	.6	.9	2.7	3.3	3.6	4.7
White Ash	2.8	3.9	10.9	13.5	4.6	5.0	4.7	4.8	4.0	3.7	2.5	2.6	2.0	1.9	.4	.1	3.9	3.7	2.7	2.8
Black Ash	.1	.6	4.9	8.0	.5	.4	<.1	<.1	<.1	<.1	0	0	0	0	0	<.1	.1	.1	<.1	.1
Basswood	0	0	0	0	.6	.7	.2	.1	.3	.3	.3	.2	0	0	0	0	.3	.3	.2	.1
Elm	10.1	6.7	11.1	9.8	1.9	1.8	1.7	1.3	1.8	1.5	<.1	<.1	<.1	0	0	0	.5	.4	.4	.4
Bigtooth Aspen	0	0	0	0	5.4	4.4	0	0	0	0	0	.1	2.7	1.4	0	0	2.6	2.0	.1	.1
Quaking Aspen	0	0	0	0	.1	0	0	0	.2	0	.1	0	<.1	0	0	0	<.1	<.1	0	0
Pepperidge	.4	0	0	0	.3	.4	.3	.5	.2	0	.1	.2	<.1	<.1	<.1	<.1	.2	.2	.2	.2
Locust	0	0	0	0	0	0	0	0	0	0	0	0	<.1	0	0	0	<.1	<.1	<.1	<.1
Butternut	0	0	0	0	.4	<.1	<.1	0	.4	.2	0	0	.4	.1	0	0	.4	.1	0	0
Black Cherry	0	0	0	0	.9	.2	.1	0	.2	.1	0	0	.5	.1	0	0	.4	.1	<.1	0
Sassafras	0	0	0	0	.4	.2	.2	0	.5	.5	.4	.3	.5	.2	.1	.2	.5	.4	.3	.2
White Pine	0	0	0	0	<.1	<.1	0	.1	.2	.1	<.1	<.1	0	0	<.1	.1	.1	.1	<.1	<.1
Hemlock	0	0	0	0	0	.1	.1	.1	<.1	.1	<.1	<.1	0	0	0	0	<.1	<.1	<.1	<.1
Redcedar	0	0	0	0	0	0	0	0	.4	.1	<.1	<.1	0	0	0	0	.3	<.1	<.1	<.1
Square feet/acre	44	52	46	61	76	90	102	106	64	84	99	96	48	69	86	84	63	83	97	96

Minor Species

Chestnut	0	0	0	0	<.1	<.1	.1	.1	.1	<.1	.2	.3	.4	<.1	.2	.3	.1	<.1	.2	.3
Dogwood	0	0	0	0	.3	.2	.3	.3	1.2	1.0	.9	.9	.5	.4	.2	.3	.9	.8	.7	.7
Bluebeech	1.7	1.3	2.0	1.4	3.4	2.5	1.9	.6	2.4	1.4	.7	.2	1.3	.5	.1	<.1	2.5	1.5	.8	.5
Shadbush	.1	.1	.4	.3	.3	.4	.1	<.1	.3	.2	<.1	<.1	.4	.4	.2	.2	.3	.3	.1	.1
Hophornbeam	0	0	0	0	1.2	1.0	.7	.7	.9	.6	.3	.1	.6	.4	.2	<.1	.9	.6	.4	<.1
Gray Birch¹	0	0	0	0	4.6	2.7	.1	0	4.0	2.3	.1	<.1	4.3	2.2	0	0	4.1	2.3	.1	<.1
Witchhazel¹		.1	.4	.2	1.4	.7	.9	.7	1.2	.7	.5	.5	.3	.1	.1	.1	1.1	.6	.5	.5
Square feet/acre	.8	.7	1.3	1.2	9.6	7.3	4.3	2.1	7.1	5.6	2.7	2.0	4.1	2.8	.9	.7	7.0	5.5	2.7	1.8
All Species	45	53	47	62	86	98	106	108	71	90	102	98	52	72	87	85	70	88	100	97

¹ Witchhazel was not measured on Turkey Hill in 1927.

Table 6. Percentage of major species by diameter on all tracts

Year	Little Saplings	Large Saplings	Poles	Sawtimber
1927	44	47	8	1
1937	29	52	17	2
1957	30	39	24	7
1967	35	35	21	9

Table 7. Diameter class distribution (stems/acre), all tracts

Major Species	0.5" to 1.5"			1.6" to 5.5"			5.6" to 11.5"			Greater than 11.5"			All Classes		
	1927	1957	1967	1927	1957	1967	1927	1957	1967	1927	1957	1967	1927	1957	1967
Sugar Maple	24	18	14	14	16	16	1	2	3	<1	<1	<1	40	36	34
Red Maple	141	58	60	118	68	62	11	20	22	1	1	2	270	147	146
Red Oak	33	3	2	52	12	3	13	18	10	2	10	12	99	43	27
Black & Scarlet Oak	12	r	<1	33	4	1	12	16	7	1	8	10	58	28	18
White & Chestnut Oak	68	7	2	76	13	4	16	20	8	2	6	5	162	46	19
Yellow Birch	37	22	23	43	27	22	7	13	10	1	2	2	88	61	57
Black Birch	53	22	28	60	30	30	11	19	21	2	4	4	126	76	83
Hickories	38	3	2	31	12	4	3	6	5	<1	<1	<1	72	22	11
Beech	10	10	13	4	6	12	<1	<1	1	<1	<1	<1	14	18	26
Tulip	2	<1	<1	6	1	<1	3	2	2	<1	2	3	12	6	5
White Ash	30	6	3	33	8	3	2	5	6	<1	<1	<1	65	19	12
Other Major	22	7	11	38	7	6	7	5	2	0	<1	<1	66	15	20
All Major	470	157	158	508	204	163	86	123	97	8	34	40	1072	517	458
Percentage[2]	44	30	35	47	39	35	8	24	21	1	7	9	100	100	100
All Minor[1]	348	170	135	131	52	30	1	<1	<1	0	0	0	479	222	166
Percentage[2]	73	77	82	27	23	18	<1	<1	<1	0	0	0	100	100	100
All Species Percentage[2]	52	45	47	41	35	33	6	16	16	1	5	6	100	100	100

[1] Witchhazel was not measured on Turkey Hill in 1927.

[2] Class as percentage of all classes for a year. E.g. 44 percent of all major species stems counted in 1927 were 0.5 to 1.5 inches in diameter.

We have witnessed the drastic decimation during four decades (Table 3). However, differences between decades represent only net loss; that is, total dying less those newly appearing. While net change facilitates our comprehension of the outcome, it may mislead. For if the number dying is near the number appearing, turnover within the population may be overlooked. To avoid oversight, mortality is tabulated, Table 8.

Table 8 reveals the total mortality of each period as a percent of trees alive at the beginning of that period. Since the second interval, 1937-57, spans two decades, the mortality per decade is roughly half the tabular value.

From 1927 to 1957 the mortality of major species per decade decreased. From 1957 to 1967 average mortality remained steady on dry sites, but increased slightly on moist and medium moist sites.

There were differences among species. Fewer maples, black birch and tulip died each decade, while the mortality of yellow birch remained steady. The mortality of oaks, hickories and white ash decreased through 1957, but it rose dramatically during the final decade.

Mortality of minor species was greater than for the major. However, as in major species, it decreased through 1957 and then rose during the last decade. Unlike the major species, the proportion dying during 1957-67 was greatest on the dry sites. Mortality of the tolerant dogwood was similar to maple; it decreased with time. Mortality of the scattered shadbush has increased ever since 1927. All others show decreased mortality during the middle decades. Proportionally fewer chestnut died in the last decade compared to the first, whereas the reverse was true for bluebeech, hophornbeam, and gray birch.

Here again our analysis shows only that trees died. We do not know whether they were little or large. We must await our analysis of growth. But let us first examine the newcomers, called ingrowth.

INGROWTH

As death goes unmourned so birth comes unheralded in the silent struggle of the forest. The newly-arisen, called ingrowth, quickly disappear into the impassive statistic, net change. Yet our persistent pursuit of the details of change causes us to look closely at ingrowth because here may lie the future of our forest.

Table 9 reveals the ingrowth during four decades. Again let us assume that half the tabular value for the double decade, 1937-57, is roughly the ingrowth per decade. We see that over the forest in general the birth rate of major species continued to rise, unslowed by drought or defoliation of the last decade. However, ingrowth increased only on medium moist and dry sites; during 1957-67 it declined on muck and moist sites.

The maples, birches, and beech predominated among new stems, increasing from 62 percent of all ingrowth in the first decade to 85 in the last. On the other hand, the oaks, which currently dominate the forest, decreased from 27 to a mere 2 percent of ingrowth during the same decades.

Ingrowth has appeared against a background of declining numbers, and

Table 8. Mortality (percent), all tracts

	Moist			Medium Moist			Dry			All[1]		
	1927 to 1937	1937 to 1957	1957 to 1967	1927 to 1937	1937 to 1957	1957 to 1967	1927 to 1937	1937 to 1957	1957 to 1967	1927 to 1937	1937 to 1957	1957 to 1967
Major Species												
Sugar Maple	12	34	14	20	32	14	19	31	20	18	33	14
Red Maple	31	45	25	32	48	17	34	51	20	32	48	19
Red Oak	30	39	46	34	44	40	32	46	27	33	44	39
Black Oak	33	50	50	28	41	33	25	50	39	28	45	36
Scarlet Oak	7	50	43	29	25	33	15	38	36	24	31	34
White Oak	52	61	67	44	72	63	28	69	72	41	71	66
Chestnut Oak	10	59	27	31	42	55	39	44	33	30	44	51
Yellow Birch	25	36	23	30	44	30	33	56	12	28	41	27
Black Birch	22	35	12	28	43	17	27	39	10	28	42	15
Bitternut Hickory	50	100		53	78	50				52	82	50
Mockernut Hickory	67	100		30	44	55	22	52	50	30	47	54
Pignut Hickory	32	57	67	53	64	52	38	72	55	48	67	54
Shagbark Hickory	21	18	40	30	30	37	18	67	75	28	32	40
Beech	67	33	0	24	47	8	14	40	8	22	45	7
Tulip	11	53	22	24	45	8	33	0	0	22	45	10
White Ash	36	56	39	42	67	44	23	81	88	40	66	43
All Major	31	45	26	35	50	28	32	54	27	34	50	27
Minor Species												
Chestnut	100	100	40	91	70	50	95	80	56	93	75	50
Dogwood	33	17	12	29	50	19	36	64	8	30	49	18
Bluebeech	48	65	67	52	73	73	46	80	95	50	71	72
Shadbush	34	91	50	29	92	79	47	85	25	34	90	60
Hophornbeam	52	38	90	51	53	86	32	50	100	50	50	89
Gray Birch	62	97	100	62	97	83	59	100		62	98	88
Witchhazel[2]	58	46	47	50	55	42	59	48	44	52	53	44
All Minor	52	61	55	50	66	49	56	75	60	51	65	51

[1] All site values include trees on muck.
[2] Witchhazel was not counted on Turkey Hill in 1927.

Table 9. Ingrowth (stems/acre), all tracts.

	Moist			Medium Moist			Dry			All[1]		
	1927 to 1937	1937 to 1957	1957 to 1967	1927 to 1937	1937 to 1957	1957 to 1967	1927 to 1937	1937 to 1957	1957 to 1967	1927 to 1937	1937 to 1957	1957 to 1967
Major Species												
Sugar Maple	7	24	5	3	11	2	0	4	0	3	12	2
Red Maple	12	28	10	14	42	27	11	63	49	13	45	27
Red Oak	7	4	1	4	3	1	5	6	0	5	4	1
Black & Scarlet Oak	0	0	0	1	1	<1	6	3	1	2	1	<1
White & Chestnut Oak	4	4	0	8	10	1	11	5	2	8	8	1
Yellow Birch	18	22	15	6	22	14	1	3	1	7	20	12
Black Birch	1	9	7	7	19	20	13	32	28	7	19	19
Hickories	1	1	1	2	3	1	6	2	1	2	3	1
Beech	1	15	3	2	9	8	5	12	26	2	10	10
Tulip	1	1	1	0	1	<1	0	0	0	<1	1	<1
White Ash	2	9	1	2	4	1	3	1	0	2	5	1
Other Major	4	8	6	2	7	9	2	2	0	3	6	9
All Major	58	125	50	51	132	84	63	133	120	54	134	83
Minor Species												
Chestnut	1	11	2	<1	42	27	2	44	30	1	37	23
Dogwood	0	6	7	8	15	9	1	3	1	6	12	8
Bluebeech	12	36	7	6	22	3	3	8	1	6	22	3
Shadbush	3	2	0	1	1	<1	1	1	1	1	1	<1
Hophornbeam	5	16	<1	1	3	<1	4	6	1	2	5	<1
Gray Birch	0	0	0	<1	<1	0	1	0	0	<1	<1	0
Witchhazel[2]	30	101	22	15	47	26	2	8	0	15	50	23
All Minor	51	172	38	32	130	66	14	70	41	32	128	57

[1] All site values include trees on muck.

[2] Witchhazel was not counted on Turkey Hill in 1927; therefore ingrowth for this species is likely overestimated for 1927-1937.

almost without exception death has outrun birth. Notable exceptions have occurred. On medium moist and dry sites during 1937-57 more sugar maple appeared than died. On the same sites during 1957-67 fewer red maple died than appeared. Since 1937 beech, and since 1957 black birch ingrowth has exceeded mortality on all sites except muck.

Ingrowth of minor species is interesting only in examining turnover of population and its abundance compared to major species. In the first decade, a time of rapidly decreasing numbers, ingrowth of minor species was but an eighth of mortality. During the double recade, 1937-57, a period of great turnover, ingrowth equalled nearly three-fourths of mortality. In the final decade, when numbers declined less rapidly, ingrowth equalled half of mortality. Thus turnover of population was least during the first decade and greatest during the second and third. Further, a relatively few species accounted for a large proportion of ingrowth.

Between 1957 and 1967 the ingrowth of the intolerant bluebeech, hophornbeam, and gray birch virtually ceased. Ingrowth of the tolerant dogwood increased on moist sites, while the ever-sprouting chestnut and witchhazel have grown in on the drier.

Thus despite the large proportion of ingrowth contributed by minor species, the increase of major species on medium moist and dry sites suggests that minor species did not seriously compete with the major.

The definition of ingrowth here is that a tree reaches a half-inch diameter, but this should not blind us to an important event of the last years. A substantial crop of oak seedlings has appeared. These do not appear in the statistics because the seedlings are much too small to be counted. Nevertheless, this crop may play an important role in maintaining the predominance of oak in these forests — or it may merely stagnate and die in the shade of the established, larger competitors.

The next section, Growth, shows how ingrowth along with mortality and enlargement of persisting trees caused the basal area of the forest to grow.

GROWTH

From the totals of Table 5 we have seen basal area increased until 1957 and then declined slightly in the last decade. But this is net change and the causes are hidden. To simplify learning the causes we can consider basal area as a bank account. From the balance on hand, the initial basal area, we deduct withdrawals, i.e. mortality. The remainder accrues interest called growth. To this we add the deposits, ingrowth. If we conserve our capital and accumulate the interest, our balance will increase regardless of whether we deposit. However, if we squander our capital on mortality and deposit little, then surely our balance will decline.

From mortality (Table 8) we know that trees have died, and at times many, but we know not whether they were small or large. We already know that ingrowth was slight (Table 9), so our deposits were small. Unfortunately, we know nothing of interest on the balance, growth. Accordingly we have analyzed the account in detail and present it in the totals of Table 10.

In general, withdrawals from major species increased with time, both in actual basal area and as a proportion of the balance on hand. During the first three decades, withdrawal of basal area by mortality was less on dry sites than on moist. However, during the final decade mortality on dry and medium moist was equal, but it was a third less on moist sites. Now we see that although loss of tree number decreased with time, loss of basal area increased. From this we deduce that many little trees died in the young forest, but larger trees died later.

As expected, ingrowth was small, but surprisingly the deposit per decade was quite uniform and unaffected by moisture class. In these woodlands, ingrowth was too small to affect the balance of basal area.

Interest on the balance, that is, growth on trees present throughout the period, decreased from the first through the fourth decade on all moisture classes except muck. During the first decade, however, growth equalled 65 percent of basal area surviving on dry sites, but only 40 on moist. Yet in the final decade growth was surprisingly similar, about 16 percent, on all sites. Thus, despite drought and defoliation, the growth of trees surviving the fourth decade was quite uniform. Because growth and ingrowth were similar on all sites during the last decade, we now see that the decreased basal area noted in 1967 resulted directly from increased death, not decreased gain, of basal area on both dry and medium moist sites.

This discussion of growth so far had blended all species together. Our analysis, however, revealed differences among species, and examples are shown in Table 10. Sugar maple has made small, but steady, gains in basal area throughout the 40 years. Mortality was generally a third or less of combined growth and ingrowth. Ingrowth for the first and last decades was quite similar. However, it is not clear whether the increased ingrowth of 1937-57 resulted from increased moisture or disturbance by the 1938 hurricane.

Beech, although not in the Table, behaved much as sugar maple did.

Red maple, too, has gained basal area, but more by flashy spurts rather than by steady plodding. In a period of gain, the first decade, mortality removed basal area equal to a third or more of that gained by growth and ingrowth. The large mortality of 1937-57 on moist and dry sites not only exceeded the gains from growth and ingrowth, but also wiped out the gains of the first decade. Although a surplus of growth over mortality accrued during 1957-67, the losses were a third to a half as great as growth. Thus we see a large turnover in the population.

Red oak grew much and lost little basal area during the first three decades, and black and scarlet did too. Mortality was slight ranging from a tenth to a fourth of growth. During 1957-67, however, ingrowth was slight, growth was reduced and mortality equalled or exceeded growth. Although red oak increased its basal area slightly, black and scarlet oak declined. Thus, decreased growth and increased mortality have halted the breakaway gains of earlier decades.

During 1927-37 white oak, like other oaks, gained basal area, but mortality cancelled a third of the gain. During the next two decades growth

Table 10. Basal area growth (sq. ft./acre), all tracts

Species	Decade	Moist				Medium Moist				Dry				All²			
		GRO¹	INGRO	MORT	NET	GRO	INGRO	MORT	NET	GRO	INGRO	MORT	NET	GRO	INGRO	MORT	NET
Sugar Maple	1	1.0	.04	.4	.6	.3	.02	.1	.2	.05	.00	.01	.04	.4	.02	.13	.3
	2&3	1.6	.21	.9	1.0	.4	.12	.1	.4	.05	.02	.03	.04	.6	.12	.25	.5
	4	.9	.06	.2	.8	.3	.02	.1	.3	.03	.00	.01	.02	.4	.03	.09	.3
Red Maple	1	4.8	.07	2.2	2.7	2.4	.12	1.0	1.5	2.0	.12	1.2	1.0	2.8	.1	1.2	1.7
	2&3	6.3	.22	9.0	—2.5	2.7	.41	2.6	.6	1.0	.25	2.2	—.9	3.1	.5	4.0	—.4
	4	3.7	.18	2.7	1.2	2.2	.22	.8	1.6	1.4	.17	.7	.9	2.4	.2	1.2	1.5
Red Oak	1	4.6	.09	.4	4.5	6.2	.07	.8	5.4	4.3	.04	.4	4.0	5.6	.1	.7	5.0
	2&3	9.3	.04	1.4	7.9	9.8	.05	2.7	7.2	7.4	.06	1.9	5.5	9.2	.1	2.3	7.0
	4	3.9	.00	2.6	1.2	3.6	.14	3.4	.3	3.0	.00	.9	2.1	3.5	.1	2.9	.7
White Oak	1	.7	.00	.2	.5	2.6	.07	1.0	1.7	4.6	.04	.5	4.1	2.5	.1	.8	1.8
	2&3	.6	.02	.4	.2	2.7	.19	3.1	—.2	3.0	.02	3.2	—.2	2.3	.1	2.6	—.2
	4	.4	.00	.7	—.3	.6	.01	4.4	—3.8	.6	.00	6.9	—6.3	.6	.0	4.0	—3.5
All Major	1	25.4	.51	11.7	14.2	27.9	.57	7.8	20.6	26.9	.53	6.6	20.8	27.0	.6	8.2	19.4
	2&3	35.9	1.14	25.4	11.6	35.5	1.56	22.1	14.9	32.0	.77	15.2	17.5	34.6	1.6	21.8	14.4
	4	17.3	.70	13.6	4.4	15.4	.85	19.6	—3.4	13.8	.69	16.9	—2.4	15.5	.8	18.0	—1.6
All Minor	1	1.7	.58	4.2	—1.8	1.2	.42	2.9	—1.3	.6	.11	1.9	—1.2	1.2	.4	3.0	—1.3
	2&3	1.0	1.01	5.0	—3.0	.6	.65	4.1	—2.9	.2	.30	2.4	—2.0	.6	.7	4.0	—2.7
	4	.4	.20	2.8	—2.2	.4	.30	1.4	—.7	.2	.13	.5	—.2	.3	.3	1.5	—.9

¹ GRO is basal area increase on trees present throughout the period; INGRO is basal area of trees appearing for the first time in the period; MORT is the basal area of trees dying during the period (based on their diameter at the beginning of the period); NET is net change in basal area,
NET = GRO + INGRO — MORT.

² All site values include trees on muck.

declined and mortality cancelled all gains. During 1957-67 growth was slight, and the abrupt increase in mortality, especially on medium moist and dry sites, erased all gains made in 30 years. Thus in 1967 basal area was but 71 percent of that in 1927. Chestnut oak behaved similarly except that mortality exceeded growth only during 1957-67. Consequently, basal area was reduced to midway between that in 1927 and 1937.

During the recorded history of these tracts minor species have never exceeded a tenth of total basal area except on Cox. Since 1927 minor species have declined steadily in basal area. Of all minor species only chestnut has increased in basal area, mainly from ingrowth. The tolerant dogwood barely matched mortality with growth. Thus, in the absence of major disturbance, the minor species will likely remain merely a pleasant, diverting curiosity in the forest.

COMPOSITION OF THE CANOPY

The landscape, the view of the forest from afar, is the canopy of dominant and codominant trees. This canopy is also important to the working of the forest as it is to our eyes. These tall trees absorb the lion's share of the life-giving light, passing only flecks and diffuse light down to the saplings beneath, and only after death letting candidates emerge into the sun. In 1967 only a sixth of the stems were in the main canopy. These giants contributed full three-fourths of the basal area.

Only in young stands with short trees can minor species play a role in the canopy. Hence, in 1927 minor species provided about a fifth of the individuals in the canopy, but they have been almost absent since.

From the beginning in 1927, the oaks were the most numerous genus in the canopy (Table 11). In 1967, 43 percent of the dominant and codominant trees were still some kind of oak. Maples and birches together comprised another 41 percent, and white ash and tulip supplied 9 percent.

Although the same names led the list of contributors to the canopy from the earliest years, significant changes occurred in the 1957-67 decade. Participation in the canopy by red and scarlet oak remained steady, and black oak declined slightly. But white and chestnut oaks plummeted to half their contribution. Meanwhile hickories and birches remained much the same. The increase was in the maples; their contribution rose by nearly two-thirds.

The preceding paragraphs tell what happened to the number of stems contributed by each species to the canopy of the forest. But not all stems and crowns are of the same size. If an adjustment is made for the size of crown, one can estimate what proportion of the canopy is made of leaves of each species.

We did not, however, measure the span of the crowns of each tree. But it is reasonable to assume that the span of the crowns increases as the diameter of the stems, which was measured. Thus an estimate of the proportion of the canopy made of leaves of each species is gotten by calculating the basal area of the dominant and codominant trees. To make interpretation clearer in the paragraph that follows we speak of the

Table 11. Number of dominant and codominant stems in the canopy (percent of total), all tracts

Major Species	Moist			Medium Moist			Dry			All[1]		
	1927	1957	1967	1927	1957	1967	1927	1957	1967	1927	1957	1967
Sugar Maple	3	4	6	1	1	2	<1	0	0	1	1	2
Red Maple	25	22	26	11	7	12	10	1	2	14	10	15
Red Oak	7	15	12	15	22	22	12	21	23	13	21	20
Black & Scarlet Oak	3	4	3	10	16	14	20	42	37	10	17	14
White & Chestnut Oak	5	8	4	15	19	10	15	21	14	13	17	9
Yellow Birch	12	16	19	6	4	6	1	0	0	6	0	7
Black Birch	5	12	12	14	16	19	16	6	11	12	14	16
Hickories	1	4	3	5	5	5	6	7	8	4	5	5
Beech	<1	<1	<1	<1	<1	1	<1	1	2	<1	<1	1
Tulip	2	3	3	3	4	5	2	0	2	3	3	4
White Ash	5	7	10	5	3	4	6	<1	1	5	3	5
Other Major	15	3	<1	5	1	1		<1	1	7		2
All Major (Stems/acre)	216	113	110	210	119	100	211	94	82	210	114	101
Minor Species												
Gray Birch	16	<1	0	10	0	0	11	0	0	11	<1	0
Other Minor[2]	<1	1	<1	<1	1	0	<1	0	0	<1	1	<1
All Minor (Stems/acre)	41	2	1	26	1	0	26	0	0	28	1	1

[1] All site values include trees on muck.

[2] Witchhazel was not included on Turkey Hill in 1927.

relative proportions of the canopy leaves that are contributed by each species. But the reader will realize that the estimate is in fact for the proportion of the basal area of trees in the canopy.

During the decade 1957-67 the maples, the birches, red oak, white ash and tulip all increased their contribution to the leaves of the canopy. Black and scarlet oak, on the other hand, made a smaller contribution in 1967 than in 1957, while the contributions of white and chestnut oak diminished greatly. It is interesting that the contribution of the oaks to the number of dominant and codominant trees fell fully 12 percent, but their contribution to canopy leaves fell only 7 percent. This reflects the loss of medium-size oaks but the persistence of the giants, an event that was anticipated in the discussion of mortality.

Whether viewed as number of trees or area of crown, however, the change in a trend is clear. Reporting on the changes from 1927 to 1957 Olson (1965) wrote, "On all moisture classes of all tracts . . . the canopy became increasingly dominated by oaks." The decline in the oaks, although small, that is reported now for the decade that followed Olson's survey may signal the end of the growing ascendency of oak.

HEIGHT

The height of dominant trees at a given age is called the site index and indicates the quality of a site for forest growth. In 1957 when the stands were 55 to 70 years old, the average height of the taller trees was 68 feet on the moist and medium moist sites that comprised most of the sample area. This was slightly better than medium quality sites in Pennsylvania (McIntyre, 1933), indicating that the central Connecticut sites were medium or slightly better in quality.

In 1967, however, no increase in the heights could be detected in a sample of trees on Reeves and measurement was abandoned. Evidently the advancing age of the trees, drought and defoliators had allied to slow the growth in height to an indetectable change in a decade.

SPROUTS

In our account of numbers of trees, no distinction was made between single stems and those arising from sprout clumps. Yet we often ascribe superiority to trees that grow from seeds instead of sprouts. Has the inferiority attributed to sprouts caused their proportion in the population to decrease?

All trees that were members, survivors, or recruits of a sprout group were classified as sprouts. The remainder were classified as single trees or stems because they had not visibly been members of a sprout group during the 30 years. Some of these single trees undoubtedly originated as sprouts, but their origin was not apparent between 1927 and 1957. The true proportion of trees originating as seedlings, therefore, is equal to or less than the percentage of single trees shown in Table 12.

Among the major species, the proportion of single stems has remained

Table 12. Single stems (percent of total stems), all tracts

	Moist			Medium Moist			Dry			All[1]		
	1927	1957	1967	1927	1957	1967	1927	1957	1967	1927	1957	1967
Major Species												
Sugar Maple	58	79	81	64	68	76	44	33	50	62	70	77
Red Maple	37	37	46	50	52	59	35	45	46	45	47	54
Red Oak	70	63	70	73	66	73	71	67	72	72	66	72
Black Oak	67	83	67	83	87	90	81	80	86	81	85	88
Scarlet Oak	80	86	100	69	80	88	90	88	90	75	82	89
White Oak	78	83	100	80	84	88	79	69	85	80	80	88
Chestnut Oak	70	73	100	66	65	85	64	67	57	66	66	83
Yellow Birch	42	42	52	41	46	48	42	88	67	41	45	50
Black Birch	59	72	79	64	76	76	58	67	78	62	74	76
Bitternut Hickory	100			100	100	100	75	67	50	100	100	100
Mockernut Hickory	67			93	96	88	90	83	93	88	90	80
Pignut Hickory	100	100	100	91	84	76	82	75	100	91	84	82
Shagbark Hickory	71	70	86	66	66	58	17	40	62	69	67	66
Beech	67	61	62	47	55	61	100	100	62	40	53	61
Tulip	61	67	75	60	57	61		100	100	61	60	65
White Ash	67	57	66	66	62	67	83	50	100	68	62	68
All Major	57	56	63	65	64	67	64	62	65	63	62	66
Minor Species												
Chestnut	80	100	100	65	89	82	62	86	91	65	89	84
Dogwood	67	64	74	49	59	69	36	42	69	49	59	70
Bluebeech	36	36	50	29	37	40	17	25	100	30	36	44
Shadbush	18	33	67	45	43	50	24	0	25	35	36	50
Hophornbeam	72	76	100	49	48	93	46	58	100	52	58	96
Gray Birch	45	50		50	67	100	54			50	62	100
Witchhazel[2]	14	16	17	16	16	15	11	22	8	16	16	15
All Minor	35	34	37	34	43	48	36	57	69	35	42	47

[1] All site values include trees on muck.

[2] Witchhazel was not counted on Turkey Hill in 1927.

nearly two-thirds since 1927. During 40 years the proportion of single stems has varied little among moisture classes. Most noticeable between 1957 and 1967 was the change on moist sites where the proportion of single stems increased by an eighth.

The minor species have about half the proportion of single stems that the major have. Among the minor, the proportion of single stems has changed little except on the dry sites where the proportion of non-sprouts has reached two-thirds. In essence, then, although numbers have declined markedly since 1927, the division of stems into sprout and single stems remains unchanged. Thus, sprouts have not proven inferior to seedlings in their ability to survive as an important part of the population.

FIRE

All results presented so far were from portions of the tracts undisturbed except by hurricane and defoliation. However, in 1932 fire swept across nearly 40 percent of Turkey Hill, including almost 1.6 acres of sample. Here is a careful chart (Fig. 2) of the effect of the wildfires that ravaged so much of our woodland in the past.

In 1927 the part of the forest that would burn and the part that would escape were similar (Table 13). Both were similarly populated (Fig. 2, 1927), and maples and oaks comprised similar proportions on both. The part that was destined to burn, however, supported more hickories, more white and chestnut oaks, fewer other oaks, and fewer black birch than did the rest of the forest. Distribution among size classes was similar on both: about 85 percent of all stems were saplings and about 13 percent were poles. Despite the similarity of distribution, the part that was to burn supported about a tenth more basal area than did the unburned.

The observations of the unburned forest were taken at the same time as in all undisturbed areas previously discussed. In the burned forest, however, observations were taken in 1932 rather than 1937.

In 1932, fire swept over the portion above the line in Fig. 2, 1937. It drastically altered the population. After the fire only a fifth of the stems present in 1927 remained alive (Fig. 2, 1937). Although never abundant, redcedar, aspen, basswood, butternut, cherry, and sassafras were eliminated. The numbers of all of the remaining species decreased. The proportion of oak changed little and hickories declined, while maples and birches increased. Because almost no trees grew in, the difference in population between 1927 and 1932 was mainly loss in the fire.

Over 90 percent of small saplings, three-fourths of large saplings, and nearly half the poles succumbed. But basal area on the burned forest was reduced only a third because mostly small trees died.

In contrast, during the first 10 years in the unburned forest, the number of stems declined only a sixth and basal area increased by a fifth. The proportions of oak and hickory declined slightly, while those of maple and birch increased. Distribution among size classes shifted slightly upward. Change in the unburned forest, although perceptible, was small.

Quantitatively, the fire decimated the population and changed the
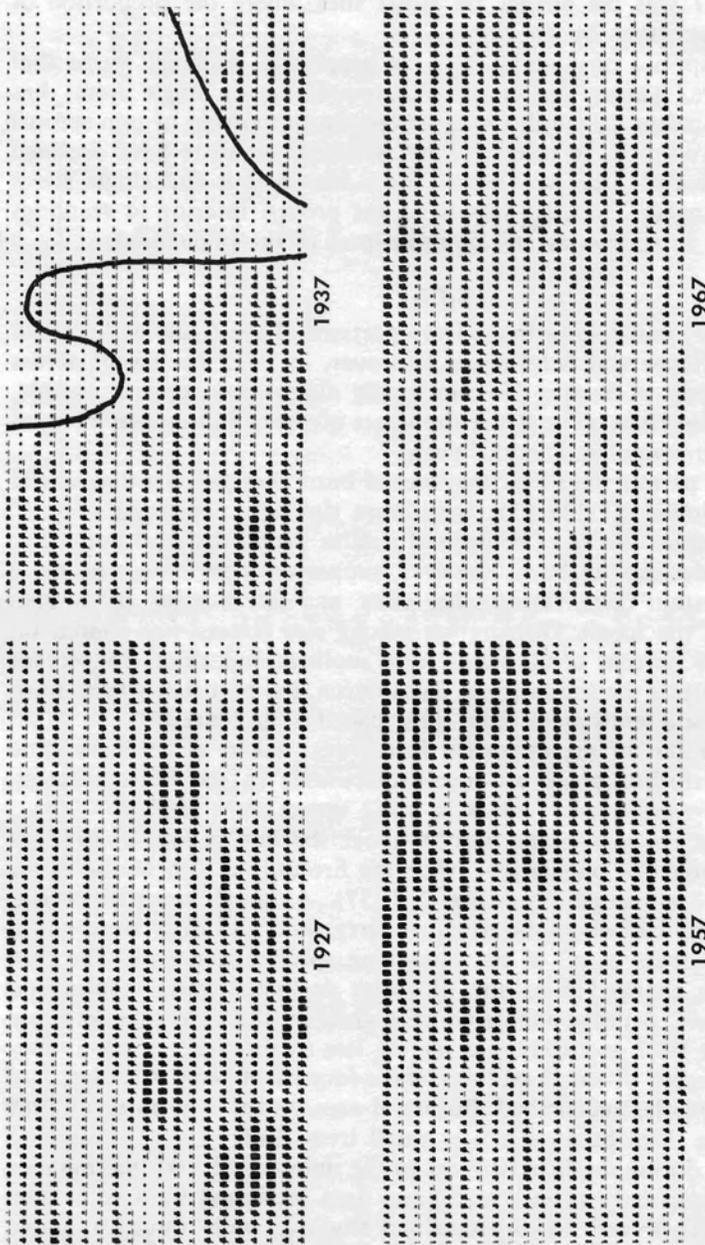
Fig. 2. Effect of fire on number of stems on Turkey Hill. Darker areas indicate a greater number of stems. The years of the enumerations are shown on the four parts of the Figure. The burned portion of the forest above the solid line in the 1937 Figure was examined in 1932. The great increase in number on the burned portion in 1957 is clearly seen. Although the effect of the fire can still be seen in 1967, distribution of stems on the burned and unburned forest is more uniform than in 1957. Thomas Siccama of the Yale School of Forestry kindly supplied the computer plotting technique.

Table 13. Comparison of burned and unburned portions of Turkey Hill

	Number (stems/acre)				Basal area (sq. ft./acre)				Ingrowth (stems/acre)		Sprouts (%)	
	1927	1932¹	1957	1967	1927	1932¹	1957	1967	1932¹-57	1957-67	1927	1967
Major species Burned	741	166	1332	906	73	49	80	96	1243	46	51	40
Major species Unburned	757	629	556	462	66	79	89	97	188	56	31	32
Minor species² Burned	262	1	661	352	6	<1	6	4	660	39	58	73
Minor species² Unburned	329	298	315	250	6	6	5	4	176	70	51	66

	Number (stems/acre) Percent of major species						Basal area (sq. ft./acre) Percent of all species						Ingrowth (stems/acre) Percent of major species			
	Burned			Unburned			Burned			Unburned			Burned		Unburned	
Major Species	1927	1957	1967	1927	1957	1967	1927	1957	1967	1927	1957	1967	1932-57	1957-67	1937-57	1957-67
Sugar Maple	10	9	14	6	14	17	8	6	7	2	2	3	9	31	19	16
Red Maple	10	14	19	17	21	24	5	5	6	20	14	14	14	22	29	25
Red Oak	8	10	10	12	9	6	6	11	12	5	11	11	10	8	6	3
Black Oak	3	3	3	2	2	2	6	5	6	3	6	7	3	3	<1	0
Scarlet Oak	3	4	3	2	2	1	3	3	3	3	3	2	4	0	2	0
White Oak	8	7	4	6	5	4	10	12	12	6	8	8	6	4	5	1
Chestnut Oak	9	12	10	6	6	4	10	13	12	7	6	6	12	5	9	1
Yellow Birch	7	4	5	16	16	15	8	6	5	16	16	14	4	5	10	15
Black Birch	10	18	19	9	10	11	17	19	20	15	14	14	18	7	5	8
Hickories	13	8	7	5	4	3	7	4	3	4	4	4	9	3	3	0
Beech	2	2	2	3	3	5	<1	<1	<1	<1	<1	1	2	3	3	16
Tulip	1	4	2	1	1	1	2	6	6	2	4	5	4	4	<1	0
White Ash	8	2	1	7	4	3	5	2	1	3	3	3	2	1	4	1
Other Major Species	8	3	1	8	3	4	5	<1	2	7	3	3	3	4	4	14

¹ 1932 for burned, 1937 for unburned.
² Witchhazel was not counted in 1927.

diameter distribution, but qualitatively, it changed the main components of the forest little.

The subsequent 25 years, 1932 to 1957, was a time of recovery in the burned forest. By 1957 the number of stems had risen eight-fold (Fig. 2, 1957), and basal area increased nearly two-thirds.

Ingrowth outstripped mortality sixteen-fold. Red and sugar maple contributed nearly a fourth of all ingrowth. The fecund black birch supplied more than a sixth of the ingrowth, and white and chestnut oaks together provided another sixth, while the other oaks contributed still another sixth.

Species representation changed little. The proportion of maples declined about a fourth, oaks increased by a fourth, and hickories doubled. Birches, despite the contribution by black birch, declined by a fifth.

The great influx of small trees completely changed diameter distribution. In 1957 nearly 95 percent of all stems were saplings. Only a few poles grew large enough to become sawtimber. Apparently much of the increased basal area was derived from the many new, small trees. Thus in 1957 the burned forest had the number of stems, the diameter distribution and the basal area of a stand at least 30 years younger than the unburned forest, and it resembled Cox or Reeves in 1927 (Tables 2 and 4).

By comparison, the period 1937 to 1957 on the unburned forest was one of great turnover but slow change. The number of stems decreased by an eighth, while basal area increased an eighth. Mortality, though great, was but a third more than ingrowth.

During the final decade, 1957-67, the number of stems on the burned forest declined nearly a third (Fig. 2, 1967). Mortality prevailed and exceeded ingrowth ten-fold. Mortality of sugar maple cancelled ingrowth, while mortality of red maple was four times ingrowth. The high mortality of hickories, oaks, and birches greatly exceeded their insignificant ingrowth. Death of oaks and hickories increased the proportion of maples by a third. Despite losses, the proportion of birches also increased slightly. Although in 1927 their numbers were nearly equal, by 1967 black birch outnumbered yellow birch about four to one.

During 1957-67 basal area increased about a fifth and in 1967 equalled that in the unburned forest, again demonstrating the trend toward similarity among the tracts. Within that simple total of basal area, however, an interesting shift in its nature could be seen. Although the species composition was about the same, the basal area was made of different sized trees. The loss of large saplings and poles in the fire of 1932 had left few candidates for poles and sawtimber in 1967. Therefore, despite equal basal area on burned and unburned tracts in 1967, fire had made the number of pole and sawtimber trees on the burned a third and a seventh less.

So far we have not mentioned the effect of the fire on minor species. In 1927 minor species contributed nearly a third of all stems in the unburned and about a quarter in the burned forest. Dogwood and bluebeech predominated, but the reader will recall that witchhazel was not recorded on Turkey Hill in 1927. Nevertheless, the abundance of witchhazel on the unburned tract in 1937 suggests that it was abundant on both portions in

1927. Nearly all stems of the minor species were saplings and their basal area was about a twelfth of that of the major species.

The fire of 1932 almost completely eliminated the small and susceptible stems of minor species. By 1957, however, their number increased to two and a half times that before the fire, with dogwood and witchhazel predominating. Also, their 1957 basal area nearly equalled that of 1927. Although their numbers then declined nearly half and their basal area a third during 1957-67, there were 40 percent more minor species stems and a seventh greater basal area in the burned than in the unburned forest in 1967.

Because fire killed mostly smaller trees one might reasonably expect increased sprouting in the burned forest. A high proportion of the woody plants that sprout readily are shrubs (Smith, 1962). First, let us examine the second line of Table 13: where there was no fire the proportion of sprouts among major species did not change from 1927 to 1967. Where the fire burned, line one in Table 13, the sprouting actually declined rather than increased. Among minor species the percentage of sprouts increased 15 percent on both burned and unburned. Clearly this fire did not increase sprouting.

The fire of 1932 had arrested the forest and in an instant turned back time fully three decades. Yet the phoenix of the new forest rose, little changed, from its ashes. The treeless state of old field or clearcut forest was not achieved because fire removed mainly small stems. Consequently, three and a half decades later the forest was a curious mixture of young and old forest. The great number of stems and large proportion of saplings suggest a young forest but the large basal area, an older one. Twenty-five years was fully ample to allow restocking and recovery, and after 35 years the forest had characteristics of maturity: mortality was great and the basal area was slowly increasing as in the unburned forest fully three decades earlier.

The fire scarcely changed the distribution among the major species. However, this need not surprise us. If wildfire prevailed in the past, and it likely did, then selection of species resistant or adapted to fire has likely long since occurred. Indeed, with increased fire protection and prolonged absence of fire, the changes in composition may come in unburned rather than burned forests. Unlike the disturbance of fire, the events treated next are not growing rarer.

DROUGHT AND DEFOLIATION

In the Introduction the last period, 1957-67, was referred to as the decade of drought and defoliation. Unfortunately, the events were confounded, but let us see if their effects can be separated. During the last decade Turkey Hill was defoliated but once, 1964. Cox and Cabin tracts were partially defoliated in 1961, 1962, and 1963. Reeves was partially defoliated in 1961 and 1962 and severely in 1963. We know of no other major defoliation during the last 40 years.

Therefore, we can classify the recorded history of the tracts into three

intervals: 1927-37, a time of moderate drought without defoliation; a moist middle interval spanning two decades without defoliation; and finally, 1957-67, a decade of severe drought with light defoliation on Turkey Hill, burned and unburned; moderate defoliation on Cox and Cabin; and heavy defoliation on Reeves.

The effect of drought and defoliation might be assessed by mortality, ingrowth or growth of the persistent trees. At first glance mortality seems the proper measure because favorable conditions should decrease and unfavorable conditions should increase mortality. Because mortality (Table 8) changed as the forest aged, however, it is likely a poor indicator. Since ingrowth was small and generally unaffected by site and decade (Table 9), it, too, is useless by itself. The growth or accretion of the basal area of stems measured and living throughout an interval should, on the other hand, reveal the effect of conditions during that interval.

Accordingly, the growth of trees present throughout an interval is presented in Table 14. The growth percentages are the accretions as a percentage of the basal area of those same trees at the beginning of the interval. The reader should note that the first interval on the burned area was but five years; therefore, this value should be doubled to estimate performance during a full decade. Similarly, the second interval on the burned was 25 years compared to 20 for the unburned, and values for the burned should be reduced a fifth to make them comparable to those on the unburned site.

Generally, the major species grew little if any faster in the moist second period than in the dry first period. On the burned area the major species grew slightly more than five times as much between 1932 and 1957 as they did between 1927 and 1932. But on the four unburned plots, growth was a half to a quarter slower in the second period.

Effect of drought during the fourth decade can only be appraised on Turkey Hill where defoliation was slight. Since growth there was at least half as great during dry 1957-67 as during the moist double decade 1937-57, drought alone evidently had little effect.

Now, how did the plots fare according to defoliation during the last decade? The growth in all major species in the last decade relative to the preceding period is our clue. This percentage index decreased from 140 percent in lightly defoliated Turkey Hill to 72 and 62 in the intermediate and on to 52 percent in severely defoliated Reeves. Thus, defoliation evidently decreased basal area growth, something that we could not detect when we considered all tracts together in Growth.

On the other hand, minor species were less affected by drought and defoliation. In fact, as defoliation of the canopy increased so did the growth of the basal area of the minor species in the understory. Earlier in a Connecticut wood the understory grew more rapidly when the shade of the canopy giants was removed by defoliation (Collins, 1961), and now we can see the same spurt in the minor species beneath the defoliated canopies of Cox, Cabin and Reeves.

The harm to large trees and benefit to small during the last decade is reflected in the Probability of Change.

Table 14. Growth of basal area on residual trees (percent of initial basal area), all sites

Species	Decade[1]	Burn	Turkey Hill	Cox	Cabin	Reeves
			← INCREASING DEFOLIATION →			
Sugar Maple	1	8	36	56	24	34
	2&3	133	85	58	27	39
	4	33	31	23	11	17
Red Maple	1	11	22	41	34	32
	2&3	91	41	43	36	25
	4	48	25	28	19	20
Red Oak	1	22	91	78	70	63
	2&3	151	129	79	84	78
	4	39	27	20	18	19
White Oak	1	16	30	45	49	56
	2&3	133	62	32	43	45
	4	21	17	11	6	18
Yellow Birch	1	14	34	46	54	35
	2&3	31	27	52	40	33
	4	21	12	24	19	16
Black Birch	1	13	33	74	62	41
	2&3	57	40	56	61	43
	4	23	17	27	20	16
Beech	1	33	21	67	80	14
	2&3	—	106	55	106	73
	4	35	43	84	44	18
Tulip	1	27	67	106	52	36
	2&3	98	112	115	68	58
	4	45	30	28	24	25
All Major Species	1	15	36	53	52	47
	2&3	85	55	61	55	66
	4	32	39	22	17	17
All Minor Species	1	28	33	34	23	20
	2&3	9	45	42	19	35
	4	23	20	30	43	40

[1] For all unburned plots: 1 = 1927-37, 2&3 = 1937-57, 4 = 1957-67.
For the burned portion of Turkey Hill: 1 = 1927-32, 2&3 = 1932-57, 4 = 1957-67.

PROBABILITY OF CHANGE

In the Introduction we promised to use the surveys to anticipate the future. Now we shall try.

First, what do we mean by "anticipate"? Consider the example of a tract that is now predominantly covered by Red trees. We do not expect to say whether the tract will surely be covered by White trees a decade hence or surely by Red ones. Rather, we shall attempt to say what the probability is that the tract will be covered by a predominantly Red or White forest. This estimation of probabilities is anticipating the future.

Transition Probabilities

The probabilities of transition can be illustrated by the simple example of a tract that has either a Red or White forest upon it. Suppose that 200 tracts have been classified at the beginning and end of a decade. At the beginning, 100 are Red and 100 are White. At the end, 90 of the Red and 80 of the White remain unchanged, while the remainder have become forests of the other sort. The frequencies can be written thus:

	Beginning	
End	Red	White
Red	90	20
White	10	80

The transition probabilities are then simply:

	Beginning	
End	Red	White
Red	0.90	0.20
White	0.10	0.80

That is, if a tract is covered by a forest that is primarily Red, there are 9 chances out of 10 that it will still be covered by Red a decade later. If these probabilities could be estimated, then we would say that the future of the tract, so far as the predominant tree is concerned, was anticipated.

Estimating these probabilities could be very complicated if they were variable. If, on the other hand, the probabilities were constant, estimating them would be very simple. One would only have to observe them over a suitable interval, such as a decade, and then go on extrapolating them into the future.

For example, the transition probabilities among oak and maple on the tracts will be calculated for the 1927-37 and 1957-67 decades. If they are similar despite the great lapse of time and change in population, the probabilities will be proposed as an anticipation of the future. On the other hand, if the transitions are different from decade to decade, they provide a summary of the response of the forest to age and weather.

Before this investigation is undertaken, the properties of the constant transition probabilities should be identified. If they do not depend upon how the forest got to the state it is in but only upon what state it is in, we are dealing with a Markov chain. If the probabilities do not change as the decades pass, the chain is stationary and has convenient mathematical properties (Feller, 1950).

One convenient property allows the probability of a change over, say, two decades to be derived from the probability of a change over one decade. To do this, the matrix of probabilities for one decade is simply multiplied by itself according to the rules of matrix algebra.

This operation can be seen easily in the simple example of the Red or White forest. The probability of a Red forest remaining continually Red for two decades is 0.90×0.90 or 0.81. But if we observed the forest only at the beginning and end of the two decades, the forest would also seem to remain Red when, in fact, the Red became White in the first and returned to Red in the second decade. The probability of this latter course

is 0.10 × 0.20 or 0.02. Therefore, the probability of a Red forest standing on a tract at the beginning and end of two decades is 0.81 + 0.02 or 0.83. If the multiplication is continued for all rows and columns of the matrix, then a new matrix of probabilities is obtained, and it is for the transitions over two decades.

The matrix for two decades can serve two purposes. First, it is an estimation of the change over 20 years that can be derived from observations over ten years. Second, it can be used in testing whether the changes over the single decade of 1927-37 are comparable to those over the double decade of 1937-57.

Another useful characteristic of a Markov chain with constant transition probabilities is seen in estimating the changing states and even the equilibrium or steady state. The estimate of the number of Red plots after one period is (0.9 times 100) plus (0.2 times 100) or 110. After the process is repeated a second time, the number of Red plots becomes 117.

The steady state is also easily calculated. After the transitions have gone on for a long time, individual trees will still be dying and growing into our ken, but the percentage of plots dominated by a certain species, or some other characteristic, will remain near an equilibrium. The simple calculation is easily described with the Red and White species. The reader has just seen that the proportion of Red plots at the end of a period is (0.9 times the proportion of Red at the beginning) plus (0.2 times the proportion of White at the beginning of the period). Once equilibrium is reached, this proportion at the end of a period is exactly the same as at the beginning of the period. In algebraic terms,

$$r = 0.9\,r + 0.2\,w$$

The second rule says that the sum of the Red and White proportions is 1.0. In algebraic terms,

$$r + w = 1.0$$

The solution of these equations: at equilibrium the proportions will be two-thirds Red and one-third White.

The estimated future states and, especially, the steady state, like all extrapolations, put short-term conclusions to a severe test, revealing some ridiculous ones. If, however, the extrapolation makes common sense, it is an adequate anticipation of the future. Further, the steady state is a summary of the entire matrix of probabilities, telling where they are heading.

Forests have been analyzed before in terms of probabilities. For example, Usher (1966) has set down the recruiting of stems into the smallest class and their transition to larger classes as a matrix of probabilities. Our contribution is in using probabilities in two other ways. First, to analyze changes in kind as well as size of trees. Second, to see whether the transition probabilities are constant from decade to decade, making a stationary Markov chain and easy calculation.

With this introduction to transition probabilities, which are delineated by Ashby (1956) and thoroughly discussed by Feller (1950), the actual frequencies of change in the Connecticut forests are now examined. First, the changes in the predominant species, much as the simple foregoing

example of the Red and White classification, are examined. Then the changes in diversity, in stem numbers, and in basal area are investigated.

Each chain or 66-foot-length of transect through the forest was considered as a plot of ground where the change over a decade could be examined. It is a sample of the forest seen through a window, and the viewer wonders how it will change in 10, 20, or 40 years. Since the transects are a rod or 16½ feet wide, the plots are 1/40 acre. Excluding all tracts wholly burned in the 30's or otherwise disturbed, and those even partly on muck or dry sites, a sample of 327 fairly uniform plots is left for analysis.

The next task is classifying the trees upon the tracts into a few groups. Only a few classes can be made lest the sample in some classes be too small. Also, the classes must be easily grasped by the reader if they are to convey any information. Finally, good fortune must attend this process, since the constancy of the probabilities depends upon the skill of classification.

Predominant Species

The first classification of the tracts according to predominant species was merely asking which group of species contained the most stems on each of the 327 plots. It may be said that the most numerous class "dominates." Five species classes were set up: maple, oak, birch, other major species, and minor species. Thus if more stems on a plot were in the maple class than in any other single class, the population on that plot was classified "maple."

The transitions from 1927 to 1937 are tabulated in Table 15. The classes contained reasonably large numbers at the beginning of the decade, ranging from 29 plots in the "other major species" to 99 in the "minor species" class. The transitions would be more frequent with smaller, rarer with larger plots, but we shall stick to the fortieth-acre plots.

The clearest phenomenon was the persistence of the classes, which is seen in the large percentages along the diagonal from upper left to lower right. More than 80 percent of the plots that were maple or birch in 1927 retained the same class in 1937. Therefore, a surprisingly accurate anticipation was, "Whatever predominates at the beginning of the decade will still predominate at the end."

Being transition probabilities, the numbers of Table 15 not only tell how frequently forest stayed as it was but also what else it became. For example, the matrix shows that one oaken plot in six became maple. Or the fourth of the minor species plots that changed were evenly distributed to other classes. But we want to know how constant these transition probabilities were before applying them to the future, and we turn to the 1957-67 transitions which are tabulated in the lower part of Table 15.

At the beginning of the last decade the sample sizes ranged from 18 in other major and 34 in oak to 116 in the minor species class. Thus the probabilities for other major species must be taken with a grain of salt.

Leaving minor fluctuations aside for the present, one has to marvel at

Table 15. Ten-year transitions in classes of species according to number of stems per plot. "Other" means the most numerous are major species other than maple, oak and birch. Probabilities as percentages

Observed 1937	Maple	Oak	1927 Birch	Other	Minor
Maple	82	16	13	7	7
Oak	7	72	2	3	7
Birch	2	8	83	7	7
Other	0	0	2	69	7
Minor	9	4	0	14	72
Observed 1967	Maple	Oak	1957 Birch	Other	Minor
Maple	85	15	8	22	17
Oak	1	35	0	0	2
Birch	6	12	82	6	15
Other	3	6	3	50	2
Minor	5	32	7	22	64

how similar the transitions are for the first and last decade of the survey. After all, a great time has passed. The first decade began when Lindy flew the Atlantic, Coolidge was President, and people traveled over dusty roads in Model T's. And the last decade ended with astronauts ready to fly to the moon, LBJ in the White House, and traffic jams on 8-lane highways.

The interesting difference in probabilities between the decades is for oak. Clearly oak became something else more frequently in the drought and defoliation of the last decade than in the first decade.

The surprisingly similar probabilities of the two dissimilar decades encouraged us to multiply the 1927-37 probabilities by themselves and compare them to the observed changes 1937-57, Table 16. The chief disparity is as in the earlier comparison: the oak was less persistent in the later period than in 1927-37. Nevertheless, the similarity between probabilities

Table 16. Twenty-year transitions in classes of species according to number of stems per plot. The first matrix was obtained by multiplication of the 1927-37 matrix. Probabilities as percentages

Anticipated 20 Years	Maple	Oak	1927 Birch	Other	Minor
Maple	69	25	22	13	13
Oak	12	53	4	6	11
Birch	5	14	69	12	12
Other	1	1	3	49	10
Minor	13	7	2	20	54
Observed 1957	Maple	Oak	1937 Birch	Other	Minor
Maple	68	29	9	25	5
Oak	2	39	4	4	4
Birch	8	17	63	0	9
Other	0	2	2	46	3
Minor	22	13	22	25	79

derived from the first decade and another period, the score of years 1937-57, is encouraging.

Since the probabilities have proven reasonably stable in the two comparisons made so far, we were emboldened to ask, "How accurate is anticipating the full 40 years by multiplying the matrix of the first decade by itself?" Table 17 gives the answer. The chief error of anticipation concerns oak. In the long pull, it was less persistent than in the first decade.

The transition probabilities were calculated for the two plots, Turkey Hill and Cabin, that had fewer stems per acre in 1927 and for the other two plots. Much the same transition probabilities were obtained from both. The same pattern was also obtained by calculating the transitions separately for the moist, the medium moist and the dry sites. The transitions of the last decade on the repeatedly defoliated plots revealed an acceleration toward minor species but little else.

A surprising number of things were anticipated from the probabilities calculated in all ways.

First is the outstanding persistence of maple and birch. Also anticipated were the frequent transitions from oak to maple, from birch to maple, from "other" to maple and minor species, and from minor species to maple and birch.

The transition probabilities are now used and hence tested in another way. Figure 3 shows the changing state of the forest as changing heights of blocks that make a column for the end of each decade. The top row of blocks represents minor species; the second, dark row represents other major; the middle row represents birch; the dark row next to the bottom represents oak; and the bottom row represents maple. The imprecise sizes of the blocks should convey to the reader that the gross features, not precise details, are to be glimpsed.

The first column on the left shows the composition of the forest in 1927. Maple and oak each then dominated about a quarter of the forest. Birch and other species each dominated a few plots, and minor species was the most numerous class on nearly a third of the plots.

Table 17. Forty-year transitions in classes of species according to number of stems per plot. The first matrix was obtained by multiplication of the 1927-37 matrix. Probabilities as percentages

Anticipated 40 Years ↓	Maple	Oak	1927 Birch	Other	Minor
Maple	53	35	32	22	23
Oak	16	33	8	11	15
Birch	11	19	50	18	18
Other	2	2	4	26	11
Minor	18	11	6	23	33
Observed 1967 ↓			1927		
Maple	62	32	22	45	20
Oak	0	15	0	0	4
Birch	16	23	54	10	21
Other	2	7	2	17	5
Minor	20	33	22	28	50
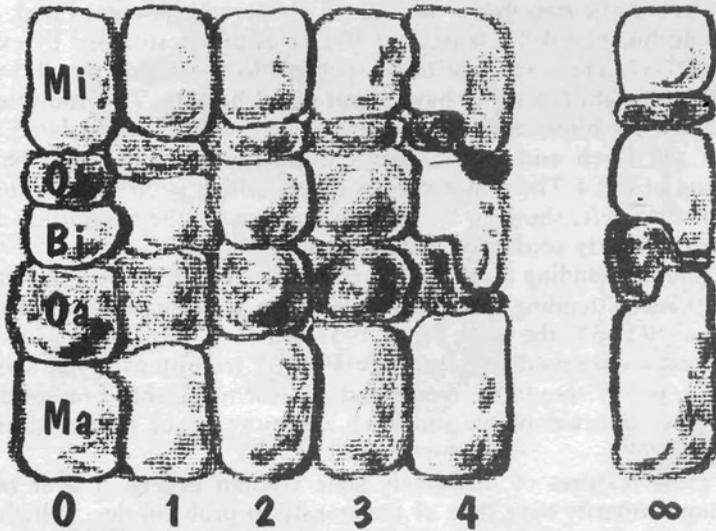
Fig. 3. The changes in the kinds of trees dominating the stem population on fortieth-acre plots. The height of the blocks represents the proportion of the plots dominated by a class of species. The top row represents minor species; the next (dark), other major species; the next, birch; the next (dark), oak; and the bottom, maple. The first column shows the state of the forest in 1927, the second in 1937. The third and fourth columns represent 1947 and 1957 and were obtained by extrapolating the 1927-37 transitions. The left side of the fifth column shows the extrapolation from 1927-37 to 1967, but the right side shows the proportions actually observed in 1967. The column standing alone on the right depicts the steady state of the forest; the left side was obtained from the transitions of 1927-37, the right from 1957-67.

The second column is the state of the forest a decade later in 1937. Maple and birch enlarged their domains and the other three classes lost some ground.

The third column is an extrapolation of the 1927-37 transitions. It was made by multiplication of the 1937 state and the 1927-37 matrix of Table 15 and represents the state of the forest at the end of two decades of change. The fourth column was obtained by another multiplication, and it represents the forest at the end of three decades and the beginning of a fourth.

The fifth column contains two sorts of information. Its left side is, like the column next to it, an extrapolation. The right side, however, is actuality. The heights of the blocks on the right side of the fifth column were set by the proportions of the forest dominated by the stems of the five classes in 1967. Hence the steps in the tops and bottoms of the blocks in the fifth column reveal differences between extrapolation and observation.

The blocks of the fifth column are now examined in detail. The bottom block is nearly level on top, indicating that the extrapolation from 1927-37 accurately foretold that maple would predominate on about a third of the

plots in 1967. The step in the dark block above, on the other hand, shows that the decline in oak from 1937 to 1967 was underestimated by extrapolating 1927-37. The birch and other species blocks, which are above oak, have left and right sides that have about equal heights. This indicates that the increase in birch and other species were fairly extrapolated. (The steps in the birch and other species blocks were caused by the overestimation of oak.) The minor species block, which is on top, is longer on the right than left, showing an underestimation of the proportion of the forest most thickly settled by minor species.

The column standing alone on the right side shows the steady state that the forest seems tending toward. The left side was obtained by extrapolation from 1927-37, the right from 1957-67.

The steady state predicted from the 1937-57 transitions is not shown in the figure, but it should be mentioned. It resembles that predicted from 1957-67, except fewer maple and birch and more minor species plots were anticipated.

The gross features of the steady state column in Fig. 3 bear out the surprising similarity over time of the transition probabilities. Whether the transitions of the thickets of 1927-37 or forest of 1957-67 were extrapolated, the prediction was about the same: the anticipated forest is one of plots that are mostly maple or birch, some minor species and few oak and other major species.

A comparison of the tendencies, that is steady states, from each interval shows that the last decade of drought and defoliation was not of a different quality from those before. The trend from oak and minor species to maple and birch may have become greater, but the seeming difficulties of the last decade did not change the direction of the trends that were already evident. This predictability will please the person who wants to anticipate what stems will be most numerous on a plot, but the classes must be changed if one is interested in which class will dominate the plot with its bulk, not numbers.

Table 18. Transition probabilities for single decades for classes of species according to basal area per plot. Probabilities as percentages

Observed			1927		
1937 ↓	Maple	Oak	Birch	Other	Minor
Maple	84	1	1	2	0
Oak	8	96	10	8	22
Birch	8	2	86	9	0
Other	0	1	3	79	19
Minor	0	0	0	2	59
Observed			1957		
1967 ↓					
Maple	91	6	3	0	15
Oak	0	89	3	6	0
Birch	3	3	92	6	14
Other	3	2	2	88	14
Minor	3	0	0	0	57
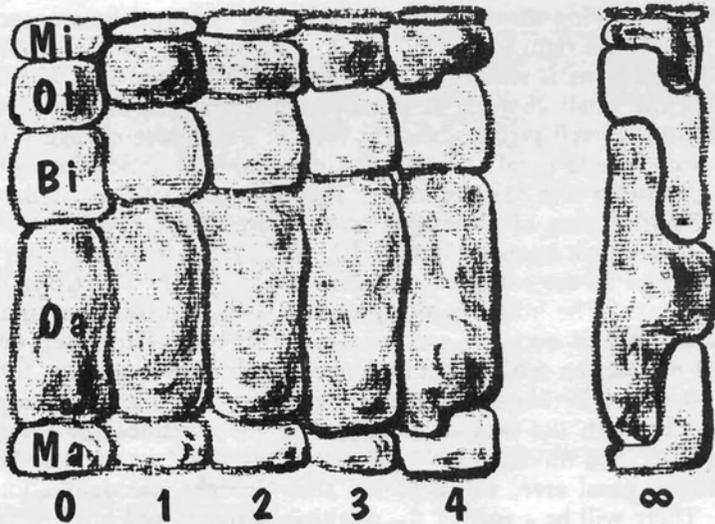
Fig. 4. The changes in the kinds of trees dominating the basal area or cross section of stems. The conventions are the same as in the preceding Figure. In the present Figure concerning classes by basal area, the steady state anticipated from transitions of earlier decades has considerably more oak and less maple than the state anticipated from the last decade; this is evident in the bottom (maple) and next to bottom (oak) blocks of the column standing alone on the right.

The chain-length plots along the transects were again classified into maple, oak, and so forth. But this time, the plots were identified with the species class that contained the greatest basal area or cross section of stem. Previously a plot that contained many witchhazel stems and a large oak would have been classified as "minor species," but it would now be classifield "oak" in calculating the probabilities of Table 18.

The striking effect of changing from a criterion of stem numbers to one of basal area is, of course, the greater persistence of the major species and lesser persistence of minor species (Table 18). However, this should come as no surprise for the reader has already seen how basal area of minor species declined steadily after 1927 (Table 5).

The transitions in the basal area classification underwent a subtle change in the dry decade 1957-67 when a considerable number of pole-size oaks died. This decreased the persistence of oak a few percent in Table 18, while the persistence of maple, birch and other species increased slightly. The change seems slight until the steady states are examined.

The transistions in the plots are depicted in Fig. 4 by the now-familiar blocks. The first four columns show the slow increase in the predominance of the oaken giants observed in 1927-37 and extrapolated to 1947 and 1957. The fifth column represents on its left the extrapolation to 1967 and on its right the actual state observed in 1967. As in the transition probabilities, the difference in extrapolation and actuality seems slight.

The column standing alone on the right shows the steady state that the

forest seems tending toward. The left side was obtained by extrapolation from 1927-37, the right from 1957-67. The steady state predicted from the 1937-57 transitions is similar to that from 1927-37, and it is not shown.

Clearly the small changes in transition probabilities between 1927-37 and 1957-67 foretell greatly different forests. This great change for these classes according to basal area makes it impossible to anticipate the future as a continuation of a Markov chain. The change in 1957-67 is, however, a clear manifestation of something foreseen by Olson (1965). He wrote - that the lack of oak recruits "indicate[d] a . . . trend toward greater diversity of species in the canopy as opposed to the [1927-57] trend toward increased oak." The initial predominance of oak, a prolific sprouter, was likely a heritage of both fire and repeated clear cutting for fuelwood and charcoal production which occurred over much of Connecticut for more than 100 years. Perhaps the trend away from oak that has long been indicated by both the lack of recruits and the classification for species according to stem number, and now the recent trend in the classification according to basal area, will continue after drought and defoliation have passed. There will be a race of the established maple and birch versus the oak seedlings that have now appeared on the plots.

Tolerance

The classification of the plots according to maple, oak and so forth tells much to the viewer of the landscape, but the role of a kind of tree in succession might more logically be appraised in terms of its tolerance of shade, and we turn to that now.

Braun (1950) has succinctly related tolerance and succession:

> "Observation will reveal that young individuals of certain species of trees are commonly seen only in the open while others are seen within the shade of the forests, that some are intolerant, others tolerant. [Tolerance is the ability to develop and grow in the shade of, and in competition with, other trees.] Ecologically, tolerance is of great importance for differences in relative tolerance of species *in part* determine the progress of succession. Pioneers are generally intolerant species, and often are incapable of growing in their own shade. . . . Some less intolerant species will grow beneath them, and in time will replace the earlier growth. More and more tolerant trees appear with the progress of succession until finally, in climax communities, the canopy species are ones which can successfully reproduce and maintain . . . the community."

She goes on to say that, of course, the tolerance of a species may vary from region to region. Nevertheless, the transition from intolerant to tolerant is generally expected as succession proceeds.

The transition among the following four classes on the plots have been examined: very intolerant and intolerant (one class, I), moderately tolerant (MT), tolerant (T), and very tolerant (VT). The classification of each species is shown in Table 19 and was taken from Baker (1950) or Fowells (1965). Each of the 327 plots employed before was classified into whichever tolerance category had the most stems.

Table 19.   Tolerance to shade (Baker 1950, Fowells 1965)

Intolerant (I)	Moderately Tolerant (MT)	Tolerant (T)	Very Tolerant (VT)
Redcedar (VI)[1]	White Pine	Red Maple	Hemlock
Bitternut Hickory	Shagbark Hickory	Basswood	Sugar Maple
Mockernut Hickory	Red Oak	Shadbush	Beech
Pignut Hickory	Black Oak		Dogwood
Scarlet Oak	White Oak		Bluebeech
Paper Birch	Chestnut Oak		Hophornbeam
Tulip	Yellow Birch		
Bigtooth Aspen (VI)	Black Birch		
Quaking Aspen (VI)	White Ash		
Pepperidge	Black Ash		
Locust	Elm		
Butternut	Chestnut		
Black Cherry	Witchhazel		
Sassafras			
Gray Birch (VI)			

[1] Very intolerant (VI)

Where the classifications go is seen in the transition probabilities, Table 20. For example, in both the first and last decades, several plots dominated by very tolerant changed to moderately tolerant classification, and several dominated by tolerant moved one notch down the scale of tolerance. The moderately tolerant classification was most persistent, while the intolerant was fleeting.

The trends in each interval can be appraised by the steady states that the forest seems tending toward. Since the transitions are similar from decade to decade, the steady states are, too (Table 21). Thus the forest seems to be working much like a simple Markov chain, imparting confidence to prediction. As expected, the intolerant class will be rare at equilibrium. The surprise is in the persistence of the large moderately tolerant class. Although a fair proportion of the plots seems likely to be

Table 20.   Transition probabilities for single decades for tolerance classes according to number of stems per plot. The species in each class are shown in Table 19. Probabilities as percentages

Observed	1927			
1937	Very	Tolerant	Moderately	Intolerant
Very	80	2	2	27
Tolerant	0	73	7	0
Moderately	18	25	91	33
Intolerant	2	0	0	40
Observed	1957			
1967				
Very	70	0	5	0[a]
Tolerant	11	83	7	0[a]
Moderately	19	17	88	75[a]
Intolerant	0	0	0	25[a]

[a] Small sample.

Table 21. Percentage of plots dominated by each tolerance class according to number of stems per plot in 1927 and 1967 and the steady states anticipated from the transitions of four intervals

	Very	Tolerant	Moderately	Intolerant
Observed:				
1927	18	13	64	5
1967	16	18	66	<1
Anticipated from:				
1927-37	11	17	71	1
1937-57	16	14	69	1
1957-67	10	31	59	0
1927-67	13	21	66	0

dominated by the tolerant class, no evidence of a large trend on to the very tolerant class has been found.

Thus both phenomena mentioned by Braun (1950) are visible in the Connecticut forests. First, the succession away from intolerant is clear. But the superficial expectation that succession would go on to very tolerant has been confounded by the regional bounds of species. The very tolerant hemlock, sugar maple, and beech have so far been unable to prevail in Central Connecticut. The long life of many moderately tolerant species undoubtedly contributes to the persistence of that class. Hence the four forests needed only lose a few intolerant trees to reach essential equilibrium, midway in the classes of shade tolerance.

Since the transition probabilities are similar in the two widely separated decades, they can reasonably be used to simulate the succession that follows an invasion and complete domination of an old field by the pioneering intolerant species. The rapidity and realism of the synthetic succession is demonstrated in Fig. 5. Here the heights of the blocks represent the proportion of forest plots dominated by each of the four tolerance classes.

The changes in the forest have been calculated from both the 1927-37 and 1957-67 transitions. The state of the forest predicted from 1927-37 is shown on the left and the state predicted from 1957-67 is shown on the right side of each column except the first. Since the forest of 1927-37 was a thicket and the forest of 1957-67 suffered from drought and defoliation, the characteristics that they have in common must be robust ones. Thus the gross features seen in predictions from both times should be reliable.

In the left column or initial state of the synthetic succession (Fig. 5) intolerant species hold full sway just as the intolerant gray birch did in the real view near Cabin in 1920 (front cover). In the foreground is an old field still covered by grass. On the side of the hill between the grass and Cabin is land dominated by gray birch as is visualized in the synthetic succession. Later we shall return to the real forest, but first we shall follow the synthetic to its steady state.

At the end of the first decade, which is depicted by the second column, the pioneering intolerant species have lost about two-thirds of their territory and rule over only a third of the land. The moderately tolerant species

are represented by the dark blocks above the light intolerant blocks. By the end of the first decade they have appeared in force, occupying more land than the intolerant. The tolerant have yet to appear, but extrapolation from the 1927-37 experience indicates that the very tolerant have taken over a few plots.

At the end of the second decade, which is represented by the third column, the once-prevalent intolerant species have declined until they dominate a quarter or fewer of the plots. The moderately tolerant have maintained but not increased their territory. The tolerant have appeared, and the very tolerant have a foothold, too, whether the extrapolation from 1927-37 or 1957-67 is examined.

After the third and fourth decades, the intolerant have declined further, and the tolerant and very tolerant have held their own. The moderately tolerant class continues to hold a large, but not increasing, proportion of the plots.

The column standing alone at the right of Fig. 5 represents the forest that has succeeded after many decades to the tract once held by the intolerant pioneers. In the steady state, anticipated from either the 1927-37
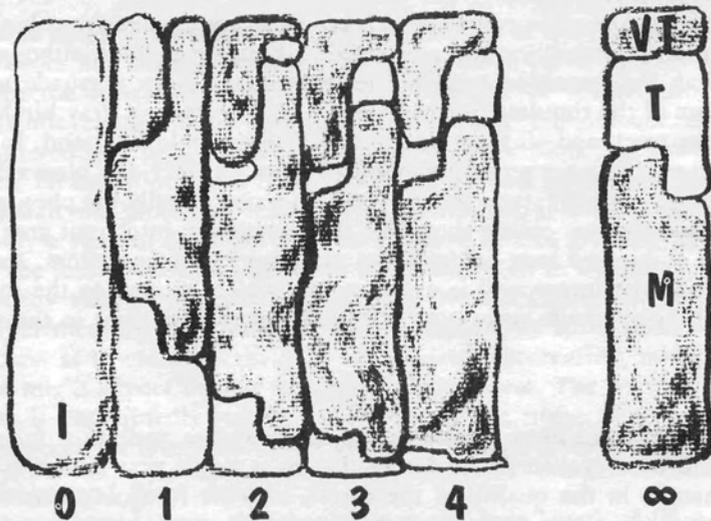
Fig. 5. The changes in the tolerance classes dominating the stem population on fortieth-acre plots. The height of the blocks represents the proportion of the plots dominated by a tolerance class. In the initial state, represented by the first column, all plots are dominated by the intolerant class. The columns to the right represent the state of the forest 1, 2, 3 and 4 decades later. The intolerant class, shown by the bottom row of blocks, shrinks quickly; the shrinkage calculated from the 1927-37 transitions is shown by the left and from the 1957-67 transitions by the right side of the blocks. The contribution of the abundant moderately tolerant class is depicted by the second block from the bottom. The contribution of the tolerant class is represented by the light blocks that appear in the next rank above in the third and later columns. Finally the very tolerant class is represented by the dark blocks on the top of the columns. The column standing alone on the right depicts the steady state of the forest.

or 1957-67 transitions, the intolerant class has disappeared, and the moderately tolerant class predominates over more than half the plots. The tolerant class dominates about a quarter of the tracts, and the very tolerant a few.

The reader may doubt the rapidity of this synthetic succession, especially when confronted by Bard's (1952) well-known estimate that 100 years would be required for oaks and hickories to dominate that in the New Jersey Piedmont. However, Bard was considering the time required to change from grassy field to hardwood forest. In our example we assumed the tract occupied by intolerant trees. Further, Bard's tract contained no gray birch but was dominated by redcedar. Lutz (1928) said, ". . . the higher the percentage of gray birch in the [redcedar-gray birch] association, the faster succession will move. Gray birch stands usually deteriorate between thirty to sixty years old. On better sites red cedar is usually over-topped and dies when it is sixty to eighty years old." In 1927 our tracts contained many gray birch but few redcedar (Table 3) and the transition probabilities were derived from plots with trees, not grassy fields. Hence, the relatively short time required for intolerant hardwoods to disappear seems reasonable.

Since much the same course of succession is anticipated from both sets of transition probabilities, it seems reliable. Some anecdotes, although less sound than the transition probabilities themselves, help persuade one of the realism of the simulated succession. In 1927 crowds of gray birch grew on the Cox tract, and 40 years later few remnants could be found. In 1927 intolerant species were predominant on 15 plots. In 1937, this class retained control of six; in 1957, two; and in 1967, only one. Finally the photographs on the front and rear covers show that the pioneering, intolerant gray birch had been eliminated long before by its more tolerant competitors. And the large tree in the foreground is a red maple, which belongs to the tolerant class that the synthetic succession of Fig. 5 makes prominent in the steady state forest.

Diversity

The viewer who likes variety in his landscape as well as a man who wants insurance against forest destruction by a single pest is interested in other changes in the quality of the forest, and the foregoing classes will not serve. Rather, the viewer and the insurer want to anticipate whether the forest will become more or less diverse. The diversity index (Pielou, 1966), which was introduced earlier in this Bulletin, is a criterion that indicates an increasing number of stems and species and a broader distribution of stems among species. It was, therefore, calculated for the 327 chain-lengths of transect, and the transition probabilities are tabulated in Table 22.

The probabilities are much the same for the first and last decade, and hence, the transitions of the entire 40 years are well anticipated by simply multiplying the probabilities of the first decade. Since the number of stems per plot decreases, it is not surprising that the diversity also tends to decrease as Table 22 shows, but one is surprised at how similar the transition

Table 22. Transition probabilities for single decades for diversity per plot. The classes are:
Low, less than 1.80; B, 1.80 to 2.09; C, 2.10 to 2.40; High, greater than 2.40.
Probabilities as percentages

Observed		1927		
1937 ↓	Low	B	C	High
Low	80	55	14	6
B	18	39	48	12
C	2	5	35	48
High	0	1	3	34
Observed		1957		
1967 ↓				
Low	89	66	34	25ᵃ
B	10	25	49	13ᵃ
C	1	9	15	50ᵃ
High	0	0	2	12ᵃ

ᵃ Small sample.

probabilities are for the 1927-37 and 1957-67 decades. That is, despite
great differences in weather and a difference in forest age, the diversity
decreased from a given level in a similar fashion in the first and last decade
of the survey. Although the stability of the diversity of the total of all
plots was noted in an earlier section, the diversity of trees on the individual
small plots has surely declined and the trend is for a further decrease.

Since the foregoing "diversity" is a function of several things, it is
worthwhile calculating a simpler index, merely the number of species
encountered in a plot. In 1927, 10 percent of the plots had fewer than 6
species, 28 had 6 or 7, 29 had 8 or 9 and 33 had more than 9. In 1967
nearly half the plots had less than 6 species, about a third had 6 or 7,
and only a sixth of the plots had more than 7 species growing upon them.
Since the loss of species was faster in the last than in the earlier decades,
the steady state is difficult to anticipate. Nevertheless, the indication of
the other measure of diversity is sustained: On the small plots — not in
the forest as a whole — diversity of species is decreasing, not increasing
as one might expect during the aging of the forest. The reason for fewer
species is undoubtedly merely the growth of the trees; after each decade
there is room for fewer and fewer kinds as the trees grow larger and larger.

Population and Basal Area

The number of stems, the populations, per chain-length of transect were
next classified into classes of 0-9, 10-14, 15-19, 20-29, 30-39, 40-49, and
more than 50. Fewer stems are likely, of course, after each decade.

The trend of stem numbers has not been constant during the entire 40
years. Thus after 1927-37 it seemed that half the plots would have 600
to 1200 stems per acre and in 1967 it seemed that in the steady state
half the plots would have fewer than 600 stems per acre. Nevertheless,
one trend has always been apparent: at the steady state the plots will have
a great diversity of stem densities. The steady state anticipated from the
1957-67 transitions gives the flavor of this assortment: Fully 28 percent
are expected to have fewer than 400, and 33 percent more than 800 stems
per acre, a great range around the expected average of about 500 per acre.

The distribution of these stems among diameter classes wants examination as an introduction to the subject of basal area. Superficially, one might expect that the percentage of the stems that are small saplings might decrease steadily as the forest matures. Table 7 has, however, shown that this percentage did not decrease from 1957 to 1967. Instead it changed from 45 to 47, implying an equilibrium distribution of diameters had been reached. Do transition probabilities sustain this conclusion?

The 327 fortieth-acre plots were classified into many (more than 60%), moderate number, or few (less than 30%) small saplings. The steady states implied by the transition probabilities of either 1937-57 or 1957-67 were near the state of 1967: about a third of the plots with many, half with a moderate number and a fifth with a few small seedlings. This confirms that a steady state of a variety of stem diameters has been attained on the plots.

A related characteristic of a plot of land is the basal area or bulk of wood that it will sustain. A glance at Table 23 reveals, however, that the increase of basal area is no stationary Markov chain with the transitions from one class to another constant decade after decade. Rather, in the first decade most plots seemed moving regularly upward in their basal area. In the last decade, on the other hand, most plots merely maintained their basal area, perhaps having reached a steady state more quickly than the transitions of the first decade indicated.

The ease of strolling through the wood and the pleasure of glimpsing vistas will grow as the frequency of stems diminishes. On the other hand, the serenity of an arching canopy requires large stems and a large basal area per acre. Thus the landscape made of the small plots can be envisioned and its trend anticipated from a classification that encompasses both the basal area and the number of stems per acre. Since nine classes were employed, more sample was needed and the dry sites were added, raising it to 387.

The classes were set, not to divide the sample evenly, but to depict the

Table 23. Transition probabilities for single decades as percents for classes according to basal area per plot. The classes expressed as square feet per acre.

Observed			1927		
1937 ↓	≤ 36	40-52	56-76	80-116	≥ 120
≤ 36	41	1	2	0	0
40-52	39	20	2	0	3
56-76	20	60	43	2	0
80-116	0	19	53	51	7
≥ 120	0	0	0	47	90
Observed			1957		
1967 ↓	≤ 36	40-52	56-76	80-116	≥ 120
≤ 36	83	24	8	1	3
40-52	14	52	19	1	1
56-76	3	24	44	24	1
80-116	0	0	29	61	15
≥ 120	0	0	0	13	80

landscape. If a wood has more than 1000 stems per acre, each stem on the average occupies less than 40 square feet or stands less than 8 feet from its neighbor. Given the accompanying slender saplings that are smaller than we measured, this makes a thicket. On the other hand, in a forest of less than 400 stems per acre each stem on the average stands about 12 feet from its neighbor. This sparser population will be a park of large trees or a field with scattered saplings according to the basal area of the stems.

If the cross section of stem is greater than 100 square feet per acre, the land is covered by a respectable forest. If, on the other hand, the cross section is less than 50, the wood is paltry.

The state of the forest in 1927 is shown in the first of three matrices in Table 24. Half the plots had 50 to 100 and 29 percent had less than 50 square feet of basal area per acre. Nearly three-quarters of the plots had over 1000 stems per acre.

The second matrix shows how the plots had changed by 1967. Then three-fourths of the plots had only 400 to 1000 stems and one plot in six had fewer than 400. And about half of the plots had more than 100 square feet of basal area per acre.

If more than 1000 stems is called a thicket, a man could walk through 20 plots in 1967 before he was entrammeled in a thicket. In 1927 he was ensnarled in them three-quarters of the time. If a wood with fewer than 400 stems per acre and more than 100 square feet of stem is a park, the walker of 1927 could scarcely find one, but the walker of 1967 found 5 percent of the land was a park.

The transitions among these nine classes are far from constant over the 40 years, partly because of the small sample in some of the categories. The steady state that the 1957-67 transitions are tending toward, however, seems reasonable. It is not far different from the 1967 state. The chief difference is a tendency toward more plots with fewer stems, but not with more basal area. This tendency is a reflection of the death of pole-size trees,

Table 24. Percentage of plots with given basal area and stems per acre of land

Stems/acre	Basal area, sq. ft./acre		
	Small	50 to 100	Great
		Observed in 1927	
Few	3	<1	<1
400 to 1000	10	10	5
Many	16	39	16
		Observed in 1967	
Few	5	5	5
400 to 1000	15	24	40
Many	<1	2	3
		Steady state from 1957-67	
Few	18	5	6
400 to 1000	22	16	30
Many	1	1	1

a mortality that the reader has already learned of. As we have written above, these changes are not following a simple, unvarying chain, and only time can tell whether the changes are a passing fluctuation in a long reign of oak or the first omen of their eclipse.

This finishes the transition probabilities and requires a summary of the anticipations for these woodlands — and many other mixed hardwood forests like them.

The transition probabilities have proven surprisingly constant from decade to decade, permitting the comparison of one with two decades, the simulation of succession, and the anticipation of steady states toward which the fortieth-acre plots in the four forests are tending.

When the plots were classified according to the species with the most numerous stems, they were clearly tending toward plots nearly half dominated by maple, a quarter by birch, a few by minor species, and very few by oak and by other major species. When they were classified according to the species with the greatest basal area of stem, however, the future was not so clear: the prediction from the three earlier decades said that more than half the plots would be dominated by oak, while the prediction from the most recent decade said that a third of the plots would be dominated by maple and a third by birch.

When the plots were classified according to the tolerance class with the most numerous stems, a clear prediction followed: The intolerant species would disappear and the moderately tolerant would continue to dominate with a small but steady proportion of the plots held by the more tolerant classes. When a simulated succession from an old field dominated by intolerant trees was made from the transition probabilities, the intolerant were reduced to an insignificant proportion and the moderately tolerant reached their commanding position within 30 years.

Diversity can be measured by an index that decreases with the number of stems and the breadth of their distribution among species. It can also be measured simply as the number of species encountered on one of the fortieth-acre plots. By either measure, the diversity has decreased and promises to decrease further, no doubt because the enlargement of the individual trees simply leaves room for fewer kinds.

The changes in the population of stems and in their basal area were inconstant during the 40 years of the survey. The basal area that once seemed going very high has now leveled off. The population, on the other hand, is falling ever faster. One characteristic of the decline in population seems invariant, however: the trend has always been toward a stem population varying from place to place.

When the population and basal area of stems was combined into a single index of whether the woodlands were thickets or parks, the transition from thicket to park in the past 40 years was clearly reflected. The uncertainty about the future enlargement of the stem cross sections, however, leaves us uncertain how stately the declining number of stems will become.

Having foreseen some features of the future forest — and left some for the woodland protagonists to settle for themselves, we conclude this Bulletin.

COMMON AND SCIENTIFIC NAMES OF PLANTS
MENTIONED IN THIS BULLETIN
(Little, 1953)

Ash, white — *Fraxinus americana*
Ash, black — *Fraxinus nigra*
Aspen, bigtooth — *Populus grandidentata*
  quaking — *Populus tremuloides*
Basswood — *Tilia americana*
Beech — *Fagus grandifolia*
Birch, black[1] — *Betula lenta*
  yellow — *Betula alleghaniensis*
  paper — *Betula papyrifera*
  gray — *Betula populifolia*
Bluebeech[1] — *Carpinus caroliniana*
Butternut — *Juglans cinerea*
Cherry, black — *Prunus serotina*
Chestnut, American — *Castanea dentata*
Dogwood, flowering — *Cornus florida*
Elm, American — *Ulmus americana*
Hemlock — *Tsuga canadensis*
Hickory, bitternut — *Carya cordiformis*
  shagbark — *Carya ovata*

Hickory, mockernut — *Carya tomentosa*
  pignut — *Carya glabra*
Hophornbeam — *Ostrya virginiana* .
Locust, black — *Robinia pseudoacacia*
Maple, sugar — *Acer saccharum*
  red — *Acer rubrum*
Oak, white — *Quercus alba*
  chestnut — *Quercus prinus*
  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*
Tulip[1] — *Liriodendron tulipifera*
Witchhazel — *Hamamelis virginiana*

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

LITERATURE CITED

Anonymous, 1951. Soil survey manual. U.S. Dept. Agr., Agr. Handbook 18. 503 p.

Ashby, W. R. 1956. An introduction to cybernetics. Science Editions. John Wiley & Sons, Inc. New York, N.Y. 295 p.

Baker, F. S. 1950. Principles of silviculture. McGraw-Hill Book Co., Inc. New York, N.Y. 414 p.

Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecol. Mono. 22: 195-215.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia, Pa. 596 p.

Collins, S. 1961. Benefits to understory from canopy defoliation by gypsy moth larvae. Ecology 42: 836-838.

Collins, S. 1962. Three decades of change in an unmanaged Connecticut woodland. The Conn. Agr. Expt. Sta. Bull. 653. 32 p.

Feller, W. 1950. An introduction to probability theory and its applications. Vol. 1. John Wiley & Sons, Inc. New York, N.Y. 419 p.

Fowells, H. A. 1965. Silvics of the forest trees of the United States. U.S. Dept. Agr., Agr. Handbook 271. 762 p.

Hicock, H. W. 1957. The suburban forest. Frontiers of Plant Science 10(2):2 The Conn. Agr. Expt. Sta., New Haven, Conn.

Hicock, H. W., M. F. Morgan, H. J. Lutz, H. Bull, and H. A. Lunt. 1931. The relation of forest composition and rate of growth to certain soil characters. The Conn. Agr. Expt. Sta. Bull. 330. 73 p.

Kelsey, H. P., and W. A. Dayton. 1942. Standardized plant names, 2nd ed. J. Horace McFarland Co. Harrisburg, Pa. 677 p.

Little, E. L., Jr. 1953. Check list of native and naturalized trees of the United States (including Alaska). U.S. Dept. Agr., Agr. Handbook 41. 472 p.

Lutz, H. J. 1928. Trends and silvicultural significance of upland forest successions in southern New England. Yale Univ. School of Forestry Bull. 22. 68 p.

McIntyre, A. C. 1933. Growth and yield in oak forests of Pennsylvania. Penn. Agr. Expt. Sta. Bull. 283. 28 p.

Olson, A. R. 1965. Natural changes in some Connecticut woodlands during 30 years. The Conn. Agr. Expt. Sta. Bull. 669. 52 p.

Pielou, E. C. 1966. Species - diversity and pattern - diversity in the study of ecological succession. J. Theoret. Biol. 10:370-383.

Smith, D. M. 1962. The practice of silviculture. 7th ed. John Wiley & Sons, Inc. New York, N.Y. 578 p.

Society of American Foresters, Committee on Forest Terminology. 1950. Forest Terminology Society of American Foresters, Washington, D.C. 93 p.

Usher, M. B. 1966. A matrix approach to the management of renewable resources with special reference to selection forests. J. Appl. Ecol. 3:355-367.

Waggoner, P.E., and J. D. Ovington [ed]. 1962. Proceedings of the Lockwood Conference on the suburban forest and ecology. The Conn. Agr. Expt. Sta. Bull. 652. 102 p.