



Promoting the Science of Ecology

Reconstructing Forest History from Live and Dead Plant Material--An Approach to the Study of Forest Succession in Southwest New Hampshire

Author(s): J. D. Henry and J. M. A. Swan

Reviewed work(s):

Source: *Ecology*, Vol. 55, No. 4 (Jul., 1974), pp. 772-783

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1934413>

Accessed: 06/04/2012 13:54

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

RECONSTRUCTING FOREST HISTORY FROM LIVE AND DEAD PLANT MATERIAL—AN APPROACH TO THE STUDY OF FOREST SUCCESSION IN SOUTHWEST NEW HAMPSHIRE¹

J. D. HENRY² AND J. M. A. SWAN

Harvard University, Harvard Forest, Petersham, Massachusetts 01366

Abstract. The purpose of this study is to see if it is possible to determine the course of forest succession over several hundred years by the dissection and close scrutiny of live and dead plant material. The study area was a one-tenth-acre (0.04-ha) square plot in a forest that had never been cut, located near Ashuelot in southwestern New Hampshire. Within it stem-location and growth-rate data were collected from three different classes of stems: 1) living trees, 2), dead unburied stems and stem fragments, and 3), woody remnants buried in the forest floor.

The vegetational history of the plot was reconstructed from before 1665 to 1967. During this time, autogenic succession did not contribute significantly to compositional changes, whereas disturbance was an important mediator of such changes.

Furthermore, changes in forest structure were often manifestations of species behavior: each tree species had a distinctive stem-distribution pattern in relation to microtopography, mode of germination, and growth. The approach seemed to provide a useful means to obtain evidence about forest change through time that may help prediction and illuminate ecological theory. Limits and modifications of the procedure are discussed.

Key words: Climax; disturbance; fire; forests; history; hurricanes; New England; New Hampshire; succession; theory.

INTRODUCTION

We see a forest at a particular time and often study then the spatial disposition of its stems—their numbers, sizes, and species. Studies of the forest at different times are more difficult. Long-term changes in vegetation (since the ice age) have been explored through pollen analysis by many (for example, Davis 1963, Deevey 1939, Frey 1951, Potzger and Otto 1943, Walker and Hartman 1960, Zumbege and Potzger 1956). However, the detailed study of short-term forest change with time (several hundred years) has lagged, presumably because of practical difficulties. Yet, this is an important area for study since it bears on ecological theory and on the practical matter of predicting vegetational change in given areas.

Indirect approaches are often used to study short-term forest succession. For example, a number of plots with progressively more recent origins for their forest vegetation may be compared as if they were different stages in a time sequence (Cowles 1899, Spurr 1956a, Flaccus 1959, Viereck 1966). Here, different habitat conditions among the plots must be assumed to have little effect on the vegetation: changes in space may be mistakenly thought to rep-

resent changes in time. Alternatively, available historical records (travelers' journals, surveyors notes) that describe a past forest are compared with the living forest (Sears 1925, Stearns 1949). This provides only a general picture of change.

Analyses of vegetational changes based on periodic inventories and large-scale maps of tree spacing have proved valuable (Leak 1970, Stephens and Waggoner 1970, Waggoner and Stephens 1970). Yet, there are few areas where suitable records have been obtained over many years.

Another approach is the direct study of rotting wood fragments and microtopography within a forest. This technique has seldom been used to reconstruct forest history. Yet wood fragments can often be traced to their place of germination and can be used to obtain diameter and age estimates for the original tree. Furthermore, the superposition of live on dead vegetation often permits an estimate of the time down stems fell from the living forest. Stephens (1955, 1956) was able to reconstruct in detail the history of an old woodlot on the Harvard Forest, Petersham, Massachusetts since 1800 and to obtain information about the destruction wrought upon it by hurricanes as far back as 1635. Yet, because logging operations had disturbed much of the evidence, he was unable to document the history of the forest for more than 150 yr.

We had at our disposal a 20-acre (8.1-ha) tract in the Pisgah Forest of southwestern New Hamp-

¹ Manuscript received September 1, 1971; accepted November 6, 1973.

² Present address: Dept. of Biology, The University of Calgary, Calgary, Alberta, Canada, T2N 1N4.

shire. It is one of the rare old growth stands still undisturbed by man in central New England. It seemed that an analysis of changes in forest-tree populations over several hundred years might be possible in this area because of the occurrence, in place, of wood fragments from trees long since dead.

Our aim was to clarify the problems and determine the potential of reconstructing a forest history directly from available evidence. Specifically, for a single plot in the Pisgah Forest, we wished to investigate over time changes in tree-species composition—all trees over 6 in (15 cm) tall, their places and times of germination as related to environmental conditions, diameter growth for the life of each tree, and the development of vertical strata in the forest. From these data we hoped to determine the ecological value of the approach and the feasibility of the method for future studies.

STUDY AREA

The 20-acre Harvard Tract is 7 miles (11.3 km) northwest of Winchester, New Hampshire, only a few miles from Vermont to the west and Massachusetts to the south. The tract is located within the privately owned 5,000-acre (2,025-ha) Pisgah Forest acquired by Harvard University in 1927.

Elevation of the Pisgah Forest ranges from 700 ft (214 m) to 1,300 ft (397 m) above sea level. There are many ridges and valleys separated by steep slopes. The area was heavily glaciated 12–14-thousand years ago (Schafer and Hartshorn 1965) and the summits of the ridges are mostly bare rock while elsewhere the ground is mantled by rough, stony land soils (Gloucester soil material, Simmons et al. 1949). These soils were studied by Griffith et al. (1930). Their work has often been cited as evidence for the influence of vegetation on soil genesis.

The mean annual precipitation for the area is 38 in (96.5 cm), usually well-distributed throughout the year. The average frost-free season extends 120 days (Cline and Spurr 1942). The prevailing winds are northwesterly. Excessively high winds, occasionally of hurricane force, occur at very infrequent intervals, sometimes in connection with severe electrical or ice storms (Cline and Spurr 1942). Cline and Spurr (1942) review historical treatises that also report infrequent severe fires for this area.

The forests lie within the maple–beech–birch cover type (Ferguson and Jensen 1963). Cline and Spurr (1942) reported 19 tree species in the area. The most abundant are: White pine (*Pinus strobus* L.), hemlock (*Tsuga canadensis* [L.] Carr.), red spruce (*Picea rubens* Sarg.), beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), black birch (*Betula lenta*

L.), white birch (*Betula papyrifera* Marsh.) and white ash (*Fraxinus americana* L.).

METHODS

Selection of study quadrat

A one-tenth-acre (0.04-ha) square (66 ft × 66 ft) quadrat within the Harvard Tract was chosen for the study. This was the largest area that could be sampled within the time available (autumn of 1967). It was placed in an area where rotting material was abundant since it seemed that this would provide an optimum opportunity to reconstruct forest history.

Sampling and analysis

Our main problem was to establish the time relationships between the living stems, the dead unburied trees, and the dead buried tree fragments. To achieve this, all stems and stem fragments were accurately mapped using a string grid with coordinates at 11-ft (3.4-m) intervals along each 66-ft (20.1-m) side of the quadrat. The plot was systematically studied: first, the living vegetation; second, the dead unburied stems; third, the buried fragments.

Living vegetation.—Each tree was numbered. Its species, location, height, diameter (breast height, outside bark), origin (seedling or sprout), place of germination, and injuries (evidence from branch or stem damage) were noted. An increment core was taken 9 in (23 cm) aboveground from every tree to obtain age- and growth-rate estimates. When the growth rings were indistinct they were stained with safranin (Newsome 1963). This was often necessary for hardwoods, less so for conifers.

The age of each tree was calculated in two steps. First, the rings of increment cores taken 9 in aboveground were counted on three separate occasions to obtain an average age and estimated error. With few exceptions, independent counts for each hemlock and beech differed by no more than 2 yr and by no more than 1 yr for red maple and black birch. Core counts differing by more than these amounts were re-counted to obtain a more accurate age estimate. Second, 10 trees of each common species were cored both at ground level and at 9 in (23 cm) to determine the number of years by which the cores taken at 9 in were short of stem age. For hemlock the average difference was 6 yr with a standard deviation from the mean difference of ± 3 yr, 5 ± 2 yr for beech, 3 ± 1 yr for black birch and red maple. Combining error estimates we believe the reported ages are correct within the following limits: for hemlock ± 5 yr, for beech ± 4 yr, for black birch and red maple ± 2 yr. Since our conclusions are unaltered even when the maximum error value is added

or subtracted from the age of each tree we make no further reference to the estimated error.

Each core was examined for major suppressions or releases in growth (those probably related to major changes in the forest environment). We hoped such changes might mark interesting historical events. We used arbitrary criteria to decide whether a suppression or release was to be recorded: a changed growth rate had to extend for at least four consecutive growth rings. Only an increase of 2.5 or more over the previous rate (more than double the previous rate) was recorded as a release, and only a decrease of 0.4 or less of the previous rate (less than half the previous rate) was recorded as a suppression.

Dead unburied stems.—Information on location, species, size, origin, and injuries was likewise collected for the dead unburied trees. In addition the fallen position and direction of each tree was mapped.

The year of death for each tree was determined by a number of approaches. For example, if tree *a* falls and injures tree *b*, which survives to the present, the year tree *a* fell can be dated from the year of injury on tree *b*, the survivor. Further, if the date of fall is known for one tree, all down stems beneath it must predate it while all stems lying above must have fallen later. Each stem was treated as an independent case for which all available evidence was pieced together as coherently as possible. Usually the year of fall became evident from these analyses so that a tree life span and growth record could be extended back in time from the fall date.

To obtain a growth record for each dead unburied tree, a cross sectional disc was cut near the base of each stem. The rings of the disc were counted on three separate occasions, and agreement between readings was high (within 5 yr). On several trees a second disc was cut 4 ft (12 decimeters) further up the bole and an age-correction factor was calculated for each species. This age-correction factor (number of years per foot of growth) was used if the cross-sectional disc was taken more than 1 ft (3 dm) above the base of the stem. From the high agreement in age counts and lack of variation in the age-correction factors, we feel the ages of the old-growth trees are correct to within ± 10 yr.

In several instances decay at the center of the disc made it necessary to estimate the number of missing rings—the radial width of the missing portion was divided by the average ring width of the readable surface. Throughout this study estimates of missing rings are used as supplementary information and no interpretations are based solely on them.

Buried stems.—To discover old buried boles and old windthrow mounds all leaf litter was removed. The organic layer was systematically overturned. Scattered throughout the plot we found fragments

of charcoal and deposits of rotting wood. Stem remains were traced in the soil and their positions mapped where possible. Also, notes were made on evidence that seemed to bear on the origin and growth of each stem remnant.

Wood and charcoal samples were embedded in paraffin and 10-micron sections were prepared. Species identification was made by using the anatomical characteristics of the wood structure (Johansen 1940, Brown and Panshin 1940, Sen 1963). When a fragment was sufficiently large (over 1 in [2.5 cm] of circumference intact) for an arc of curvature to be calculated, tree size was estimated from it. Age was also estimated whenever possible. Since we did not know how much wood had rotted from the outside of each fragment, these values are minimum estimates.

All information was assembled into two master diagrams (not presented here), one showing tree growth over time, the other all stem locations on the plot. The results are all extracted from the information in these diagrams.

RESULTS

The forest on the study plot was traced back more than 300 yr during which it was destroyed by two catastrophes—a fire in about 1665 and a hurricane in 1938. The data are presented chronologically under three headings that relate to these disturbances: (1) the forest before 1665, (2) the forest between 1665 and 1938, (3) the forest between 1938 and 1967.

The forest before 1665

Charcoal fragments were found directly above the mineral soil in every part of the study quadrat. In six places charcoal deposits were traced along the forest floor in broad continuous lines extending up to 25 ft (7.7 m) within the study plot. Some deposits continued beyond the plot but were not traced further. Sixteen burnt stems were located from charcoal deposits. Many stems were charred to the center. Hence, little can be said of the size and age of stems in the prefire forest. However, a stem diameter of at least 12 in (30 cm) was estimated from the largest charcoal fragment—a fragment with 3 in (7.6 cm) of circumference intact. A tree with this basal diameter might be 50 or more ft (15 m) tall and about 40 yr old in a living forest. Fragments from two stems had large growth rings near the center and smaller rings further out. The prefire forest may itself have developed in the open following some previous catastrophe.

Fragments from 16 trees were identified microscopically. The forest was largely coniferous (11 of 16 stems). We recorded the number of stems: *Pinus*

TABLE 1. 1907 stand table of a one-tenth-acre forest plot, Harvard Pisgah Tract, SW New Hampshire. The distribution of stems among dbh classes was calculated from growth rate data. Numbers in parentheses are stems still alive in 1967

Dbh classes (inches)	All stems per class	Hemlock	White pine	Beech	Paper birch
6.0" high-0.4 dbh	7 (7)	6 (6)		1 (1)	
0.5 dbh -0.9	6 (6)	4 (4)		2 (2)	
1.0-1.9	4 (4)	3 (3)		1 (1)	
2.0-2.9	2 (2)			2 (2)	
3.0-3.9	3 (3)			3 (3)	
4.0-4.9	1 (1)	1 (1)			
5.0-5.9					
6.0-6.9					
7.0-7.9	1			1	
8.0-8.9	1				1
9.0-9.9	1				1
10.0-10.9					
11.0-11.9					
12.0-12.9	1				1
13.0-13.9	1	1			
14.0-14.9	2	2			
15.0-15.9	2	1	1		
16.0-16.9	1	1			
17.0-17.9	3	3			
18.0-18.9	1		1		
19.0-19.9					
20.0-20.9	1	1			
21.0-21.9	1	1			
22.0-22.9	1	1			
23.0-23.9					
24.0-24.9	2	1	1		
25.0-25.9					
26.0-26.9					
27.0-27.9					
28.0-28.9					
29.0-29.9	1		1		
30.0-30.9					
31.0-31.9					
Total	43 (23)	26 (14)	4	10 (9)	3

strobis L., 7; *Quercus alba* L., 3; *Tsuga canadensis* (L.) Carr., 2; *Picea* A. Dietr. spp., 2; *Acer rubrum* L., 1; *Populus* L. spp., 1.

The year the fire destroyed this forest can be estimated from the age of stems that followed it. Five old-growth conifers blown down in the 1938 hurricane (evidence for windstorms to be discussed under Results) had charcoal directly beneath their places of germination but no evidence of fire scars along their boles (two of these trees germinated immediately adjacent to the study plot). Their germination dates were 1665, 1673, 1677, 1678, and 1687. Hence, 1665 appears to be the latest date the fire could have occurred. Further, all old-growth white pine in the study plot or within 100 ft (31 m) of it (seven trees in all) germinated between 1665 and 1687, six of these in the first 13 yr. Eleven (80%) of the 14 old-growth hemlock within the plot germinated within the first 37 yr (1665-1702). The completely charred stems in the organic layer as well as the similar ages for trees following the fire indicate that this disturbance was sufficiently severe to initiate a completely new forest.

Living trees in a forest are probably not charred to the center by a severe fire. Hence, the stems in the prefire forest may have been dead and down at the time of the fire. The storm track of a severe hurricane passed through the area in 1635 (Channing 1939) and the forest may have blown down at that time. During the 30 yr between hurricane and fire fallen trees would dry sufficiently to be almost completely consumed by fire.

The forest between 1665 and 1938

The forest that became established following the 1665 fire grew on the plot until 1897 without a major disturbance. After this date four windstorms, culminating in the 1938 hurricane, completely destroyed the canopy trees and set in motion the growth of a new forest. Although the canopy was destroyed, its character can be reconstructed in some detail. Our record of stems above 2 in (5 cm) dbh (diameter at breast height) accounts for 393 B.A. (Basal Area) ft/acre (87 m²/ha) in 1907 distributed among 26 stems within the one-tenth-acre plot.

Table 1 is a stand table of the forest in 1907.

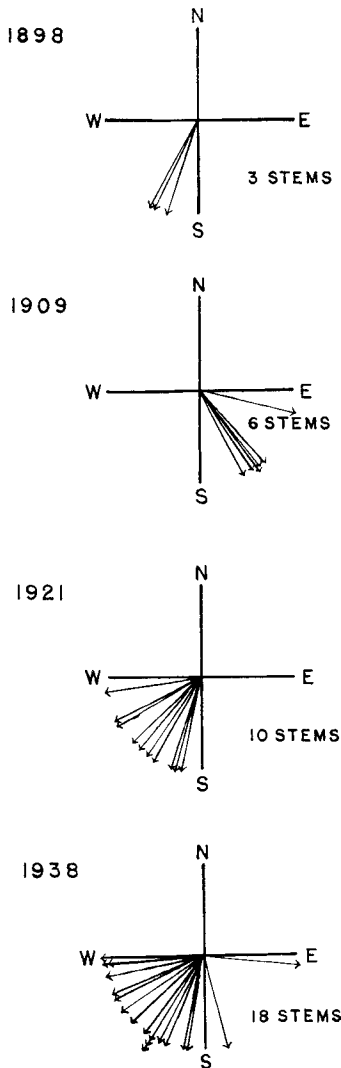


FIG. 1. The year and direction of fall (arrows) of stems blown down in four windstorms on the Harvard Pisgah Tract, SW New Hampshire. Stems in the diagram were rooted within a one-tenth-acre (0.04-ha) study plot, or they fell into it.

This is one of the earliest years for which all strata are comprehensively represented in the data.

Since we had recorded the final diameter of dead trees, the 1967 diameter of living trees, and the growth rate changes of each tree throughout its life (measured as noted under "Living vegetation"), we were able to estimate the 1907 diameter of a stem from the equation:

$$Y = A(w) + B(x) + C(z) + \dots$$

where Y is the tree diameter in 1907 (inches dbh);

A , B , and C are the number of years at growth rates w , x , and z respectively; $A + B + C \dots$ is the age of the tree in 1907.

In Table 1, stems below 7 in diam survived all windstorms and now form part of the living forest. All larger stems were removed by these storms. Of these, the stems of white pine (*Pinus strobus*) were largest and the hemlock (*Tsuga canadensis*) of lesser diameters but more abundant. These two species dominated the old growth forest throughout its history. Beneath were small beech and hemlock stems and three of paper birch of intermediate size. The heights of large trees destroyed by the windstorms matched their diameters. The five stems of white pine that could be measured for height ranged 87–101 ft (26.5–30.8 m) fallen length. These five include two stems that germinated within the plot and three that germinated within 100 ft (31 m) of the plot. Two other of white pine inside the plot had detectable lengths that were obviously shorter than the height of the trees at the time of their death. The five largest stems of hemlock had heights between 65 and 85 ft (19.8 and 25.9 m). Height measurements for the two of paper birch were 53 and 66 ft (16.2 and 20.1 m).

Fig. 1 is a diagram indicating the time of fall and direction of fall for all windthrown trees. We determined this from vegetational evidence alone but climatological records confirmed our conclusions about the times and severities of windstorms. Only three dead unburied stems are not accounted for in this diagram. One fell before 1845, one in 1912 and one tree, standing as a snag for some years after its death in 1921, disintegrated in place.

The diagram includes windthrown trees that germinated outside the plot but fell into it. Three stems fell in 1898, 6 in 1909, 10 in 1921 and 8 in 1938. Strong northerly winds were responsible for almost the entire destruction of the postfire forest. It seems that the times of these storms were correctly estimated from the vegetational data alone because of close agreement with weather records (USDA Climatological Data, New England section, before 1940). Damaging storms for central New England were recorded as a wind and rain storm in August 1898, a windstorm in February 1909 (since this windstorm occurred between the growing seasons of 1908 and 1909, dates of tree fall were registered on surviving trees as damage to tissues laid down in 1908), a tornado in the summer of 1921, and a hurricane of September 1938. Other damaging storms recorded in the climatological data left no detectable mark on the study quadrat.

We examined details of forest growth before the storms by mapping places of germination, and then by noting relative growth rates, heights, and diam-

TABLE 2. 1967 stand table of a one-tenth-acre forest plot, Harvard Pisgah Tract, SW New Hampshire. Numbers in parentheses are stems alive in 1907 (compare Table 1.)

Dbh classes (inches)	All stems per class	Hemlock	Black birch	Red maple	Beech	Sugar maple	Paper birch	Striped maple
6.0" high-0.4 dbh	30	26		2	2			
0.5 dbh -0.9	15(1)	7	4	2	2(1)			
1.0-1.9	77	25	21	22	6	3		
2.0-2.9	51(2)	16(2)	18	13	2	1		1
3.0-3.9	33(3)	9(2)	10	9	3(1)		2	
4.0-4.9	16(1)	6(1)	4	3	3			
5.0-5.9	9(3)	7(3)		2				
6.0-6.9	9(6)	6(3)			3(3)			
7.0-7.9	4(3)	1			3(3)			
8.0-8.9	1(1)	1(1)						
9.0-9.9	2(2)	1(1)			1(1)			
10.0-10.9	1	1						
11.0-11.9								
12.0-12.9	1(1)	1(1)						
Total	249(23)	107(14)	57	53	25(9)	4	2	1

eters. The object was to produce a picture of relational growth among species. Our findings are limited by the small size of the study plot. However, we list observations of ecological interest.

1) The larger-size classes of the old-growth forest (over 8 in [20 cm] dbh) on the study plot contain more hemlock (12) than pine (4). This is accounted for by the continued successful reproduction of hemlock after stand establishment. The white pine germinated between 1665 and 1687 (for 22 yr) while hemlock continued to invade between 1684 and 1780 (for 96 yr).

2) Judging from the spatial distribution of stems of the two species (pine scattered among hemlock) and stem heights, the top surface of the forest canopy was probably two layered.

3) The two-layered structure of the forest canopy may be explained by the significantly larger height-growth rates of white pine as compared with hemlock. The probability that the overall height-growth rates of these two species are the same is less than 0.002 using the nonparametric-runs test (Siegel 1956). (The smaller stature of hemlock does not seem to be due to overstory domination by pine. Judging from stem locational data, slower growing trees of hemlock were not specifically beneath white pine crowns.)

4) Two stems of paper birch became established between 1742 and 1770. (A germination date of 1795 was estimated for a third.) These incursions took place about 100 years after stand establishment. However, all stems were adjacent in the northwestern quarter of the plot on shallowly buried outcrops (organic matter 3-5 in [7-13 cm] deep, no mineral soil). All organic matter was probably burned from these outcrops in 1665, the severe fire making these sites unavailable for any tree species until sufficient litter had accumulated.

5) There was no relationship between charcoal and stem positions in the postfire forest. Hence, the prefire forest had no visible effect on the spatial disposition of stems invading after the fire.

6) Abrupt releases and suppressions were recorded for trees down after the hurricane using a similar technique to that used for the living vegetation (discussed under Methods). The average number of abrupt growth rate changes per 10 yr in the old-growth forest was 1.68 (SD = 1.66, sample size = 28). Most changes appear to be clustered around the time of crown closure when the forest was 60-130 yr old. Frequency of abrupt changes decreases after this with one exception. Between 1836 and 1839, four adjacent stems (3 of paper birch and 1 of hemlock) in the northwest corner of the plot had between them a total of six growth-change events. We know that one tree on the plot fell before 1845. Perhaps some minor interim disturbances of the long-standing forest (possibly a windstorm) may have occurred at this time. Over the total time 1667-1938, thirty-seven (74%) of the abrupt growth changes were for hemlock.

7) At its final destruction, 55% of the old-growth canopy was made up of postdisturbance trees—stems that had germinated between 1665 and 1702. The remaining 45% consisted of three stems of paper birch (which germinated in an opening on the plot after stand establishment) and six of hemlock which grew into the lower reaches of the canopy. Between 1790 and 1860, three of red oak (*Quercus borealis* Michx.) entered the plot but died. Their final breast height diameters were 5.2, 6.1, and 8.5 in (13.2, 15.5, 21.6 cm), but age estimates indicate they must have been in the forest for at least 32, 40, and 53 yr respectively. Beech (*Fagus grandifolia*) first became established in 1815, but it entered at such a slow rate that only six stems (average dbh: 2.3 ± 1.9 in,

TABLE 3. Distribution of stems among age classes for stems of four common species alive in 1967 on a one-tenth-acre forest plot, Harvard Pisgah Tract, SW New Hampshire*

Age classes	Hemlock	Black birch	Red maple	Beech
1-9	2		1	1
10-19	1	3	4	1
20-29	10	21	15	6
30-39	23	18	22	4
40-49	15	11	5	2
50-59	12	3	4	2
60-69	7			2
70-79	5			2
80-89	1			1
90-99				1
100-109				1
110-119				1
120-129				1
130-139	1			
140-149				
150-159				1
160-169				
Total	77	56	51	25

*Age data for six stems (3 hemlocks, 1 black birch, 2 red maples) are missing from the record; 27 hemlocks, 0.6 in diam or less than 9 in above ground, are not in the tally. An average age of 23 ± 15 yr was obtained from age counts of seven of these stems.

5.8 cm) were present at the time of the first windstorm (1898).

We must conclude that autogenic succession—a directional change in composition—could not be clearly defined during the 273 yr between severe disturbances, although an increase in the proportion of hemlock was indicated.

The forest between 1938 and 1967

The origins of the forest growing on the study plot in 1967 are the stems that became established both before and after the windstorms of 1909, 1921, and 1938. Hence the analysis examines vegetational changes about these disturbances.

Forest structure.—In a stand table (Table 2), the number of stems in each size class that predates 1907 is indicated in parentheses. A comparison of these values with those in 1907 (Table 1) shows that many of the stems then beneath the forest canopy presently occupy it.

The living forest on the quadrat is a very dense growth of small trees (249 stems per tenth acre (0.04 ha) as compared to 43 trees per tenth acre in 1907). In the living forest stems over 2 in (5.1 cm) dbh account for 139 B.A. ft/acre (31 m²/ha), whereas in the prehurricane forest they accounted for 393 B.A. ft/acre (87 m²/ha). Twelve to 12.9 in (about 31–33 cm) is the largest stem-diameter class in the living forest, whereas 31–32 in (about 79–81 cm) was the largest class in the preceding forest. Although

TABLE 4. Distribution of stems among height classes for stems of four common species alive in 1967 on a one-tenth-acre forest plot, Harvard Pisgah Tract, SW New Hampshire. Numbers in parentheses are trees alive in 1907

Height classes (ft)	Hemlock	Black birch	Red maple	Beech
0.5-4.9	23		4	2
5.0-9.9	12			2(1)
10.0-14.9	22(1)	9	8	6(1)
15.0-19.9	14	17	12	5(1)
20.0-24.9	13(4)	20	8	5(3)
25.0-29.9	8(1)	6	6	1(1)
30.0-34.9	4(1)	4	8	3(2)
35.0-39.9	3(2)	1	3	1
40.0-44.9	5(3)		3	
45.0-49.9	2(2)		1	
50.0-54.9	1			
Total	107(14)	57	53	25(9)

the two forests have beech, paper birch, and hemlock in common, their composition differs in that the current forest also contains red maple, black birch, sugar maple, and striped maple (*Acer pennsylvanicum* L.). It contains no white pine as did the prehurricane forest.

Age and growth history data (releases, suppressions, injuries) were obtained for 216 of the 249 living stems on the study plot. Of the remaining stems, 27 hemlock, 0.6 in (1.5 cm) dbh or less, could not be reliably aged in the field, and ages for six other stems (1 of black birch, 2 of red maple, 3 of hemlock) were missing from the record. Thus, we have a growth history for 77 of the 107 of hemlock, 56 of the 57 of black birch, 51 of the 53 of red maple and all 25 of beech on the plot (209 stems in all). The remaining seven stems for which age- and growth-history data were recorded belong to three species infrequently encountered in the quadrat (Table 2). Only the four common species are treated in our analysis.

There is a parallel between dbh growth (Table 2) and age (Table 3). The youngest species are red maple and black birch. These occupy the smaller diameter classes. Conversely older stems (of hemlock and beech) occupy larger classes. Little relation exists between height (Table 4) and time. Young red maple, while remaining small in dbh, is taller than beech and often as tall as hemlock. Hence the species already present in the forest about the time of a disturbance are not necessarily those that will dominate the forest (although this is true for hemlock). Table 5 presents the average-diameter-growth rates for black birch, beech, hemlock and red maple germinating within different 10-yr periods. For each stem the growth rate was obtained as the dbh outside bark divided by the age of the tree and ex-

TABLE 5. Changing growth rates over time for four common tree species calculated for stems alive in 1967 on a one-tenth-acre forest plot, Harvard Pisgah Tract, SW New Hampshire. Average growth rates within successive 10-yr periods are expressed as inches per 10 yr; each entry is an average for stems germinating within that 10 yr period; numbers of trees used to calculate growth rates are in parentheses*

Years	Hemlock	Black birch	Red maple	Beech
1810-1819				0.5(1)
1820-1829				
1830-1839	0.3(1)			
1840-1849				0.6(1)
1850-1859				0.9(1)
1860-1869				
1870-1879				1.1(1)
1880-1889	6.5(2)			0.7(3)
1890-1899	6.7(5)			
1900-1909	6.6(8)	0.6(2)		0.7(3)
1910-1919	4.2(18)	0.6(1)	0.8(4)	0.4(1)
1920-1929	2.0(11)	0.7(13)	0.8(1)	0.6(3)
1930-1939	1.9(24)	0.8(29)	0.8(26)	0.7(6)
1940-1949	1.4(5)	0.7(9)	0.8(9)	0.7(4)
1950-1959	0.3(2)	0.6(2)	0.5(4)	
1960-1967	0.2(1)		0.5(1)	0.2(1)
Total	77	56	51	25

* Growth rate data for six stems (3 hemlocks, 1 black birch, 2 red maples) are missing from the record; 27 hemlocks, 0.6 in diam or less than 9 in aboveground, are not included in the tally.

pressed as a 10-yr increment. The average growth in diameter for hemlock far exceeds that for any of the remaining three species. Further, there is a decrease in growth rate for stems germinating closer to the present. This is probably because stems beneath the old forest and presently dominating the living vegetation have been able to take full advantage of the crown opening about the time of the windstorms; those established later were suppressed.

Spatial pattern.—We tried to relate the plot distribution, germination time, and growth changes of each species to the sequence of openings created in the forest by the windstorms between 1898 and 1938. Four plot diagrams were made for each species for stems germinating in the periods 1800-1905, 1906-15, 1916-30, 1931-67. The first of these diagrams showed all stems alive in 1967 that germinated within the postfire forest before and including the time of the first wind disturbance in 1898. The remaining diagrams were for stems germinating about the time of each of the succeeding windstorms. In addition, plot diagrams were made of soil depth and the openings in the forest crown before and after each of the major windstorms. No patterns of species establishment could be related to soil depth or crown location. Nor was there any apparent relation to down stem or charcoal locations. However, the stems of black birch, red maple and hemlock were aggregated. We are presently able to give some explanation for

the aggregation of black birch and red maple stems but not for hemlock stems.

Thirty-two stems of black birch (56% of the living black birch) grew on windthrow mounds, although these mounds represent only about 7% of the total area. This is the only species that grew on such areas. In addition, 13 black birch stems (23% of the black birch) occupy stony outcrops which represent another 11% of the total area. Thus, 79% of the black birch occur on 18% of the total area: there is a definite correlation between black birch-stem distribution and certain microhabitats of the forest floor.

A third of the young red maple stems (18 out of 53 stems on the quadrat) occur in the pits left by windthrown trees and other microswales, which together represent only about 9% of the total quadrat area. Over a quarter of the red maple are of sprout origin (15 of 53 stems). Since only one red maple sprout occurs in a pit, these two processes concern different stems and together affect more than half of all red maple (32 of 53 stems).

Although little could be done with plot diagrams, a detailed study, by species, of the times of germination for living stems and their diameter-growth changes (suppressions and releases), clearly points to the significance of the windstorms in shaping the living forest.

Germinations.—For all living stems germination times are presented in Fig. 2. The number of germinating stems rises to a peak in the 1930's and rapidly declines thereafter. We will examine the germination behavior of the four common species on the plot: hemlock, black birch, red maple and beech. Fig. 2 shows the number of successful germinations (those surviving to 1967) in each year for each species.

Hemlock.—Most hemlock has made its entrance since 1900. The sharp rise in hemlock following 1900 indicates an opportunistic establishment in relation to windstorms. Apparently seedlings 2-3 yr old before the 1921 and 1938 windstorms were well able to take advantage of crown destruction because the number of fresh stems rises sharply at these times. After the 1938 hurricane there is a rapid decline in the invasion of hemlock. However, it is still entering the plot beneath the new forest canopy.

Black Birch.—This is the second most abundant species. It first appeared on the plot in 1909: during the growing season that immediately followed the first of the three 20th-century windstorms. From that time it rapidly invaded the plot until the late 1930's. No black birch has entered the quadrat since 1954. Of particular interest are the rises in numbers about the years of the 1921 and 1938 storms. In fact, over half (32 of 57 living stems) of the black birch germinated within 3 yr of these storms. This

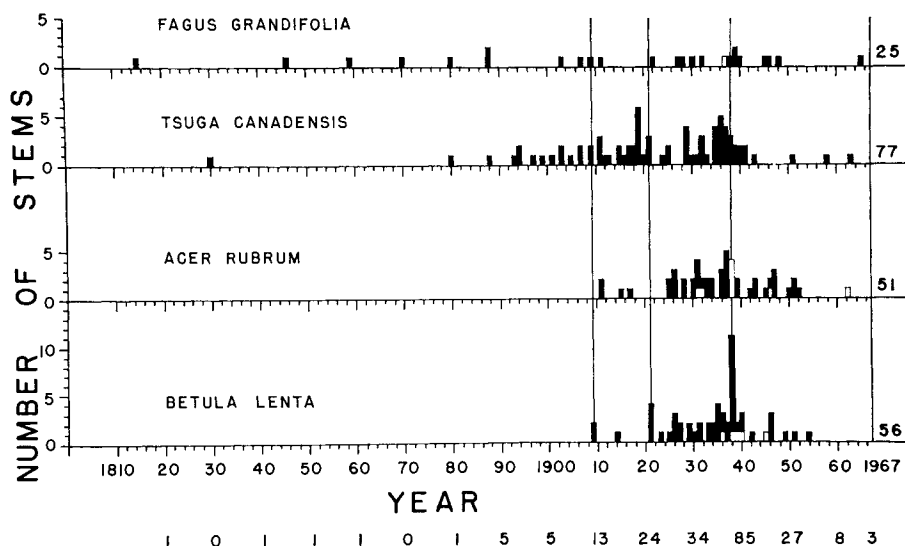


FIG. 2. Number of successful germinations (those surviving to 1967) in each year for the four common tree species on a one-tenth-acre (0.04-ha) forest plot, Harvard Pisgah Tract, SW New Hampshire. The numbers beneath the years are the number of stems established in the preceding decade (e.g., 34 stems were established 1920–1929, 85 stems 1930–1939). To the right of each histogram is the total number of stems/species. White areas in histogram are sprouts, black areas seedlings.

is partly caused by the creation of a new micro-environment—the tree-throw-mound—which, as already mentioned, favors black birch.

Red Maple.—The invasion of red maple is similar to that of black birch but with a less pronounced rise in the numbers of invading stems about the times of the 1921 and 1938 windstorms.

Beech.—Like hemlock, beech entered the quadrat long before the disturbances of the 20th century (first stem in 1815). But unlike hemlock approximately one beech tree entered the quadrat every decade and there is only a slight increase in numbers about the time of forest disturbance. All stems but one seem to have originated as seedlings.

Growth releases and suppressions.—Table 6 is a summary of the data on major abrupt releases and suppressions for each species. The values are the percent for each species of all stems that show a pronounced abrupt growth rate change—a suppression, a release, or both.

Beech and hemlock, the two species in the forest before the windstorms, are represented by more stems with releases than with suppressions. Red maple and black birch, the species first germinating during these disturbances, are more frequently suppressed than released. Hemlock is the only species for which there are many trees each having both releases and suppressions during their lifetime.

Hemlock and beech, because they were present in the old growth forest as well as in the living forest,

provide an opportunity to study changes in suppression-release patterns about the times of disturbances

Hemlock releases occurred between 1885 and 1963 but 50% of these (25 in 50) were between 1937–41 and 12 occurred in 1938 (of which 11 were in the under-0.6-in (1.5-cm) dbh class). There is a definite relationship between hemlock releases and the 1938 hurricane. Only nine suppressions were noted in hemlock during the total time studied before the hurricane. Four of the 32 suppressions for hemlock occurred in 1938. But in the 30 yr following this storm there were 19 suppressions. The growth rate of hemlock is sensitive to canopy closure.

Hemlock shows abrupt growth-rate changes more

TABLE 6. The growth increment changes of four common tree species on a one-tenth-acre forest plot, Harvard Pisgah Tract, SW New Hampshire. For each species, values are the percent of stems alive in 1967 that had at least one pronounced abrupt growth rate change—a release, a suppression, or both. Releases were recorded as more than double, and suppressions as less than half the adjacent previous growth rate

Growth change	Species: % of trees			
	Hemlock	Black birch	Red maple	Beech
Releases	47	2	8	24
Suppressions	33	11	18	8
Releases and suppressions	23	2	4	0
Any growth-rate change	57	11	22	32

frequently than the other tree species (Table 6). In particular, stems are released at the time of windstorms and suppressed as the canopy closes. Also, two or more growth-rate changes in the same stem are more frequent in hemlock than for other tree species on the plot (38% of hemlock stems have two or more rate changes, 4% of beech stems, 3% of red maple, and 2% of black birch). Thus, hemlock has greater flexibility in growth-rate response to environmental events than do the other tree species on the plot.

For beech, the species with the second-highest frequency of releases and suppressions, five of the 17 trees that germinated before the 1938 hurricane showed a marked change in growth rate that approximately coincided with the windstorms. However, the rest (12 stems) had major or abrupt changes in growth at some other time.

DISCUSSION

We have concentrated on developing a rapid technique of plot analysis that provides direct evidence about forest change over time. This is significant because theories about forest change have often been based on speculation (Kershaw 1964) and limited evidence. Our conclusions have an evidential bearing on ecological theory.

Theoretical relevance

The importance of disturbance relative to autogenic change probably varies in its effect on forest composition from place to place. Clements (1916), Cline and Spurr (1942), Oosting (1956), and Daubenmire (1952) have all emphasized the importance of autogenic succession. On the other hand, Raup (1957) and Olson (1958) have indicated the importance of catastrophic disturbance and the adjustment of vegetation to it, thereby deemphasizing succession. Therefore, through plot analysis, we have tried to approach the study of forest change without making any a priori assumptions about the nature of forest processes. We conclude that disturbance in the Pisgah Forest has been the predominant occasion for change and that autogenic processes did not cause any significant alteration of forest composition over the 300-yr history. The major species changes are all initiated at the time of the disturbances. Hence, the attention paid to compositional changes associated with openings in the forest canopy (Spurr 1956*b*, Leak and Wilson 1958, Marquis 1965, 1967) is also justified for the Pisgah Forest.

Specifically our finds have a bearing on a long-term ecological debate. Curtis and McIntosh (1951), Curtis (1959), Whittaker (1956, 1960), Whittaker and Niering (1964), and Maycock (1963) have provided some crucial evidence to support Gleason's

view (1926) that, as the environment changes over space, each species acts in its individual way. Our data show the distinctive behavior of each species over time. These are but two aspects of the same phenomenon: each species has a detectable and specific behavior as regards germination, growth, and spatial distribution of stems that underlies its visible ecology.

We believe, as do Stebbins (1966) and Janzen (1968), that the behaviors of plants are a part of their adaptive machinery. Contrast, for example, the response of hemlock and black birch to the 1938 hurricane. Young hemlock is not limited to a single microhabitat on the forest floor, it becomes established and survives beneath a closed canopy and is often released when the crown opens. Black birch is a specialist: it primarily occupies rocky outcrops and windthrow mounds. The mounds are microhabitats created only during a windstorm and, in this study, black birch was largely established at such times (16 stems germinated within 2 yr of the 1938 hurricane). The different distribution, germination, and growth behavior of these two species may represent two integrated strategies each suited to the domination of disturbed areas.

According to our data hemlock is the only species common to the forest throughout the time examined. Since its growth rate is also somewhat superior to other species, it seems fair to assume that it could always be included in predictions about forest growth on this plot. However, our data also indicate the latitude of variability in vegetational composition that one site can support. With the exception of hemlock the three forests on the plot appear to have had divergent compositions. There are major gaps in our knowledge of changes in forest vegetation associated with different kinds and intensities of disturbance on different sites. For example, the post-fire origin of white pine and its absence from the posthurricane forest suggest that fire may favour the establishment of this species. Jones (1945), Lutz (1930), Maissurow (1941), Spurr (1956*a*) all suggest a postfire origin for white pine in presettlement forests, but present little or no evidence supporting their claim. Hemlock appears to be as well suited to the invasion of burned ground as to the invasion of blow-down areas (contrary to Cline and Spurr (1942), Oosting (1956)).

As summary and hypothesis for forests of the Pisgah region we can say that tranquillity does not appear to be an important mediator of change, but that external events (fire and windstorms) are extremely important. The vegetational composition on one site may change considerably over time, and studies that examine compositional change associated

with disturbance may provide a key to predicting its progress.

Evaluation of the technique

In evaluating our procedure we noted four difficulties. First, our study plot was small. A single crown tree in the old-growth forest was a relatively large part of the total-canopy sample. We were unable to determine precisely the time of fall for three such trees and attempts to match growth-ring patterns of these trees to stems of known age were not successful. (Dendrochronological comparisons were not useful in this study.) Hence, it is hardly surprising that we could not observe any correspondence between the locations of recently-germinated stems and openings in the forest canopy. A larger quadrat size is indicated for future work. Second, the forest history becomes less complete the further it extends back in time. We were able to account for only 42 B.A. ft/acre (9.3 m²/ha) in the prefire forest. However, this material was sufficient to indicate differences in forest composition before and after a fire in 1665. The significance of this difficulty will doubtless vary from one study to the next. Third, it may sometimes be difficult to locate areas where human activities have not removed much of the evidence of early forest composition. But disturbed areas themselves may be profitably analyzed. Stephens (1955), working on a plot where timber had been periodically harvested for 150 yr, was able to reconstruct disturbance history from tree-throw mounds. Fourth, where natural disturbances have not occurred recently, it may be difficult to date the fall of a down stem, both because of the deterioration of evidence and because of the mutually-reinforcing evidence of the catastrophe that the fall of many stems at similar times tends to provide.

These problems are outweighed by the advantages of the approach. A major difficulty with successional studies—one not often faced—is that the establishment and growth of each stem in the forest is subject to a different immediate set of environmental influences. The growth rate of one stem may particularly depend on the adjacency of another. Many attributes must be reviewed before conclusions can be reached about succession. For example, stem numbers, species, age, size, and growth rate must be studied in relation to stem location. A distorted view of succession is likely to emerge if average values are obtained for many stems using a few attributes only (i.e., number-per-acre values in different layers of the forest). Plot analysis focuses attention on individual stems and their history. It reconstructs forest history by a method that is not excessively time consuming. The field work and evaluation of our data were completed in about 8 mo.

An equally useful alternative to time studies in a forest is periodic forest inventory at intervals following severe disturbance. Work in this field is already underway (Leak 1970, Stephens and Wagoner 1970).

We can suggest a new but untried approach to time-plot studies. With information on ages, stem locations, growth rates—and with a movie camera—a sequence of models might be used to create a time-lapse film of forest growth. A plot may be represented as a pegboard on which dowels of different heights, diameters and colors indicate the size (diameter and height) and species of different stems. A dynamic picture of the forest as changing populations over time should emerge and possibly suggest its responses to local canopy openings, shade, and microenvironment.

ACKNOWLEDGMENTS

This paper is based upon a thesis submitted by the first named author for a Master's Degree in Forest Science, Graduate School of Arts and Sciences, Harvard University. The authors wish to thank the staff of the Harvard Forest, Petersham, Massachusetts for their help and advice throughout the study.

LITERATURE CITED

- Brown, H. P., and A. J. Panshin. 1940. Commercial timbers of the U.S. McGraw-Hill. 554 p.
- Channing, W. 1939. New England hurricanes. Walter Channing, Boston. 16 p.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Inst. Washington Publ. 242. 512 p.
- Cline, A. C., and S. H. Spurr. 1942. The virgin upland forest of central New England: A study of old growth stands in the Pisgah Mountain section of southwestern New Hampshire. Harv. For. Bull. 21. 58 p.
- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz. 27:95-117, 167-208, 361-391.
- Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. Wisconsin Press, Madison. 657 p.
- Curtis, J. T., and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32:476-496.
- Daubenmire, R. F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol Monogr. 22:301-330.
- Davis, M. B. 1963. On the theory of pollen analysis. Am. J. Sci. 261:897-912.
- Deevey, E. S. 1939. Studies on Connecticut lake sediments. Am. J. Sci. 237:691-724.
- Ferguson, R. H., and V. S. Jensen. 1963. The timber resources of New Hampshire. U.S. For. Serv. Resour. Rep. NE-1:1-46.
- Flaccus, E. 1959. Regeneration on landslides in the White Mountains. Ecology 40:692-703.
- Frey, D. G. 1951. Pollen succession in the sediments of Singletary Lake, North Carolina. Ecology 32:518-533.

- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* **53**: 7-26.
- Griffith, B. G., E. W. Hartwell, and T. E. Shaw. 1930. The evolution of soils as affected by the old field white, pine-mixed hardwood succession in central New England. *Harv. For. Bull.* **15**: 82 p.
- Janzen, D. H. 1968. Reproductive behaviour in the Passifloraceae and some of its pollinators in Central America. *Behaviour* **32**:33-48.
- Johansen, D. A. 1940. *Plant microtechnique*. McGraw-Hill, New York. 523 p.
- Jones, E. W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. *New Phytol.* **44**:130-148.
- Kershaw, K. A. 1964. *Quantitative and dynamic ecology*. Edward Arnold, London. 183 p.
- Leak, W. B. 1970. Successional change in northern hardwoods predicted by birth and death simulation. *Ecology* **51**:794-801.
- Leak, W. B., and R. W. Wilson. 1958. Regeneration after cutting of old-growth northern hardwoods in New Hampshire. *U.S. For. Serv. Northeast. For. Exp. Stn. Pap.* **103**: 8 p.
- Lutz, H. J. 1930. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. *Ecology* **11**:1-30.
- Maissurow, D. K. 1941. The role of fire in the perpetuation of virgin forest of northern Wisconsin. *J. For.* **39**:201-207.
- Marquis, D. A. 1965. Regeneration of birch and associated hardwoods after patch cutting. *U.S. For. Serv. Res. Pap. NE-32*. 13 p.
- . 1967. Clearcutting in northern hardwoods: results after 30 years. *U.S. For. Serv. Res. Pap. NE-85*. 13 p.
- Maycock, P. F. 1963. The phytosociology of the deciduous forests of extreme southern Ontario. *Can. J. Bot.* **41**:379-438.
- Newsome, R. D. 1963. A report of studies preparatory to an analysis of forest stand ages. Unpubl. rep. Univ. Saskatchewan. 6 p.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Bot. Gaz.* **119**:125-170.
- Oosting, H. J. 1956. *The study of plant communities*. W. H. Freeman, San Francisco. 440 p.
- Potzger, J. E., and J. H. Otto. 1943. Post-glacial forest succession in northern New Jersey as shown by pollen records from five bogs. *Am. J. Bot.* **30**:83-87.
- Raup, H. M. 1957. Vegetational adjustment to the instability of site. *Proc. Pap. Union Conserv. Nature Nat. Resour.*, p. 36-48.
- Schafer, J. P., and J. H. Hartshorn. 1965. The quaternary of New England. The quaternary of the United States. Princeton Univ. Press, Princeton, N.J. 3 p.
- Sears, P. B. 1925. The natural vegetation of Ohio. 1. A map of the virgin forest. *Ohio J. Sci.* **25**:139-149.
- Sen, J. 1963. Fine structure in degraded, ancient, and buried wood II. *Bot. Rev.* **29**:230-242.
- Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York. 312 p.
- Simmons, C. S., W. J. Latimer, M. H. Layton, W. H. Coates, W. H. Lyford, and P. N. Scripture. 1949. *Soil survey of Cheshire and Sullivan Counties, New Hampshire*. U.S. Dep. Agric. 1937, No. 23. 82 p.
- Spurr, S. H. 1956a. Forest associations in the Harvard Forest. *Ecol. Monogr.* **26**:245-262.
- . 1956b. Natural restocking of forests following the 1938 hurricane in central New England. *Ecology* **37**:443-451.
- Stearns, F. S. 1949. Ninety years change in a northern hardwood forest in Wisconsin. *Ecology* **30**:350-358.
- Stebbins, G. L. 1966. Adaptive radiation and trends of evolution in higher plants. *Evol. Biol.* **1**:101-142.
- Stephens, E. P. 1955. The historical-development method of determining forest trends. Unpubl. Ph.D. Thesis. Harvard Univ. 29 p.
- . 1956. The uprooting of trees: a forest process. *Soil Sci. Soc. Am. Proc.* **20**:113-116.
- Stephens, G. R., and P. E. Waggoner. 1970. The forests anticipated for forty years of natural transitions in mixed hardwoods. *Bull. Conn. Agric. Exp. Stn., New Haven.* **707**: 58 p.
- USDA Climatological Data, New England Section. *Annual Summaries to 1940*.
- Viereck, L. A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecol. Monogr.* **36**:181-199.
- Waggoner, P. E., and G. R. Stephens. 1970. Transition probabilities for a forest. *Nature* **225**:1160-1161.
- Walker, P. C., and R. T. Hartman. 1960. The forest sequence of the Hartstown Bog Area in Western Pennsylvania. *Ecology* **41**:461-474.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* **26**:1-80.
- . 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30**:279-338.
- Whittaker, R. H., and W. A. Niering. 1964. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology* **46**: 429-452.
- Zumberge, J. H., and J. E. Potzger. 1956. Late Wisconsin chronology of the Lake Michigan Basin correlated with pollen studies. *Geol. Soc. Am. Bull.* **67**: 271-282.