

The Hubbard Brook Ecosystem Study: Composition and Dynamics of the Tree Stratum



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Ecological Monographs, Vol. 40, No. 4 (Autumn, 1970), 373-388.

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THE HUBBARD BROOK ECOSYSTEM STUDY:
COMPOSITION AND DYNAMICS OF THE TREE STRATUM^{1,2}

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ABSTRACT

The synecology of tree species was studied in a mature second-growth forest in the Hubbard Brook ecosystem. The forest, on a 13-ha undisturbed watershed ecosystem covering a 245-m range of elevation, has a basal area of about 23 m²ha⁻¹. Dominance is shared by *Acer saccharum*, *Fagus grandifolia*, and *Betula alleghamiensis*. Direct gradient analysis and regression analysis indicated a strong response in both stand and species characteristics to an elevational complex gradient. Basal area per hectare, basal area per tree, deciduousness, and canopy height decreased with increasing elevation, whereas density, evergreenness, and species diversity increased. A lower rate of net primary productivity is correlated with higher elevations. Gradient analyses indicated that no two tree species have identical patterns of importance values over the elevational complex gradient. Sugar maple shows a decreasing trend; balsam fir, paper birch, and mountain ash show increasing trends. Beech, red spruce, mountain maple, and striped maple show intermediate patterns. Seedlings and saplings respond to the elevational gradient as do larger trees; however, the behavior of trees, seedlings, and saplings of the same species is clearly different. The Hubbard Brook ecosystem is located in relation to the vegetational zonation systems of earlier authors. The only generally agreed upon vegetational boundary, ca. 760 m (2,500 ft), is accounted for by a steepened rate of environmental change in the vicinity of that elevation. Various lines of evidence indicate that the present second-growth forest at Hubbard Brook approximates old-age mature northern hardwood forest. Therefore, the biogeochemical, productivity, and ecological data obtained from this study are representative of a mature ecosystem in dynamic balance with regional and local controlling factors, i.e., climate, geology, and topography.

INTRODUCTION

The Hubbard Brook ecosystem study is concerned with the biogeochemistry and ecology of

¹ This is contribution No. 15 of the Hubbard Brook Ecosystem Study. Financial support for this work was provided by NSF grants GB 1144, GB 4169, GB 6757, GB 6742, GB 14289, and GB 14325. We thank Lawrence Safford and James Gosz for critical comments and suggestions. This work was done through the cooperation of the N.E. Forest Experiment Station, Upper Darby, Pennsylvania. Published as a contribution to the U. S. Program of the International Hydrologic Decade and the International Biological Program.

² Received January 9, 1970; accepted July 6, 1970.

undisturbed and manipulated northern hardwood forest ecosystems. Small watersheds are used as units for study and comparison (Bormann and Likens 1967). Data on nutrient relationships have been reported by Likens et al. (1967) and Fisher et al. (1968), and Johnson et al. (1968) have published on weathering relationships of the undisturbed ecosystem. Theoretical models that relate stream water chemistry to hydrology and biology have been developed (Johnson et al. 1970). Data on the relationships of the biota to comparative losses of particulate matter and dissolved substances in undisturbed ecosystems have been

published by Bormann, Likens, and Eaton (1969). Other important aspects of the ecosystem which have been investigated include changes in chemistry following forest cutting and herbicide treatment (Bormann et al. 1968, Likens, Bormann, and Johnson 1969, Likens et al. 1970) and microbiological changes related to deforestation (Smith, Bormann, and Likens 1968).

This paper, the first on the synecological, nutrient, and energy relationships of the vegetation and biota (i.e., the intrasystem cycle) of the Hubbard Brook Experimental Forest, deals with tree-species populations in an undisturbed control watershed ecosystem. The major objectives of the study were threefold: (1) to characterize the synecological parameters of the watershed ecosystem and thus provide information on tree species to be used in combination with dimension-analysis data in estimating production and nutrient parameters of the ecosystem; (2) to determine the relationship of the distribution and reproduction of tree species to such site factors as elevation, slope inclination and aspect, and soil moisture; and (3) to establish the recent history of the ecosystem and the role of disturbance (cutting, grazing, fire, and windthrow) in its maintenance and development. The data gathered were used to test the applicability of continuum concepts to this vegetation; to characterize variations in reproduction of major tree species; to partially delimit niche requirements of major tree species; to establish, by comparison with published reports, the position of this ecosystem within the vegetation matrix of northern New England and New York; and to evaluate the biological stability of the ecosystem as it exists today.

HUBBARD BROOK EXPERIMENTAL FOREST

The Hubbard Brook ecosystem study is carried out with the cooperation of the Northeastern Forest Experiment Station at the Hubbard Brook Experimental Forest in West Thornton, New Hampshire. The forest ranges in altitude from 229 to 1,006 m and covers 3,076 ha of rugged terrain in the central part of the state. It is typified by an unbroken canopy of second-growth northern hardwoods with patches of spruce-fir, particularly at higher elevations. Climate of the experimental forest varies with altitude, but is generally classified as humid continental with short, cool summers and long, cold winters (Trewartha 1954). The average July air temperature is 19°C, and the January temperature averages -9°C (U. S. Forest Service 1964). Annual precipitation is about 123 cm with one-quarter to one-third falling as snow, and runoff is about 72 cm (Likens et al. 1970).

A number of small watersheds within the experimental forest are under intensive hydrologic study by the U. S. Forest Service. Six of these meet the specifications for the study of nutrient cycles by the small-watershed technique (Bormann and Likens 1967) and are under intensive biogeochemical study. One of these, watershed 6 (W-6), has been selected for detailed study of the biota and flow of nutrients and energy through an undisturbed forest-watershed ecosystem. Watershed 6 has an area of 13.23 ha and ranges in altitude from 546 m (1,790 ft) to 791 m (2,595 ft) above sea level. Slope inclination averages about 12°-13° and aspect is generally toward the south-east. The trench of the first-order stream is not pronounced; hence, the watershed may be characterized as a rather flat valley ascending a fairly steep slope. Variation in aspect is consequently limited over major portions of the watershed, but microaspect varies considerably (see pit and mound, Fig. 3).

The watershed is covered by a mantle of bouldery till with occasional outcrops of gneissic bedrock (Likens et al. 1967, Johnson et al. 1968) (Fig. 1). The predominant soil is a sandy loam podzol of the Hermon series with a thick H layer and a discontinuous but often well-developed A₂ (R. S. Pierce, *personal communication*). Locally the soil surface has been disturbed by windthrows, and pits and mounds are extensive. Large rocks are frequent (6% of the area is exposed rock). The soil surface is very permeable, and overland flow of surface water is minimal (Pierce 1967, 1969). Additional information on hydrology, biogeochemistry, geology, erosion, soil, and climate have been published elsewhere (Likens et al. 1967, Fisher et al. 1968, Johnson et al. 1968, Bormann et al. 1969, Hornbeck, Pierce, and Federer 1970).

The unbroken forest of watershed 6 is classified as spruce-northern hardwood by Braun (1950). Major species of overstory trees are *Acer saccharum*, sugar maple; *Fagus grandifolia*, beech; *Betula alleghaniensis* Britt., yellow birch; *Picea rubens*, red spruce; *Betula papyrifera*, white birch; and *Abies balsamea*, balsam fir. Plant names follow Fernald (1950), except where authorities are cited.

METHODS

A sampling procedure was designed to combine randomness in sample choice with systematic representation of all parts of the watershed. In the laboratory a grid of 25- by 25-m squares composed of 10 columns and 37 rows was marked on a map of the watershed. In the field a portion of this grid was surveyed on the watershed by running a base line up the center of the watershed

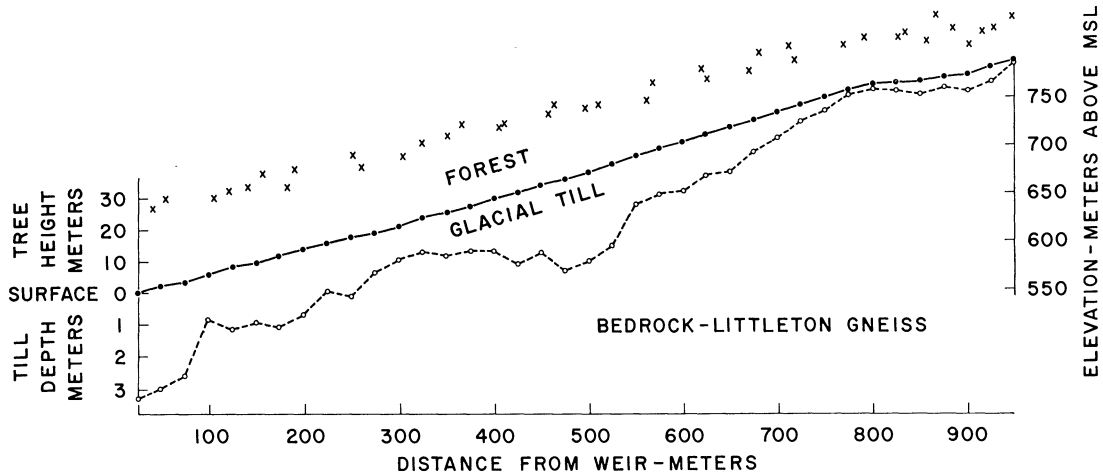


FIG. 1. A bisect of the watershed showing till depth, depth to bedrock, slope, and height of tallest trees in relation to distance from the weir and elevation.

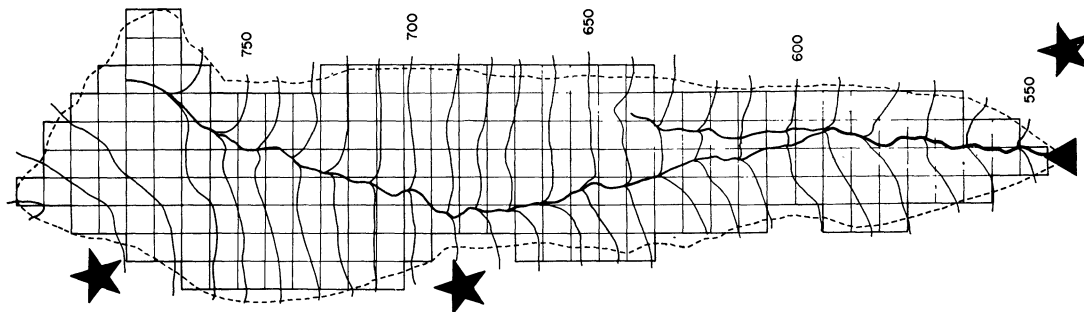


FIG. 2. Topographic map of watershed 6 (W-6) showing 10-m contour lines and the 208 25- by 25-m units. Each unit corner is marked with a stake showing row and column number and elevation. The solid triangle represents the weir, and stars represent precipitation-gauging stations.

with a transit and running perpendicular lines off at 25-m distances. These lines, in turn, were marked every 25 m by aluminum stakes, with one mark made beyond the boundary of the watershed. All measurements of distance were corrected for slope. The area of the watershed, 13.23 ha, was contained within 254 units, of which 169 were wholly within the watershed. Only those boundary units with 50% or more of their area within the watershed were subsampled. All subsequent sampling in watershed 6 was keyed into this grid system. The coordinate system thus established (Fig. 2) enabled us to print distribution maps of species, index values, environmental measures, or other values associated with the grid system with computer techniques.

Within each of the 208 25- by 25-m units available for sampling, a single 10- by 10-m quadrat was randomly chosen. This constituted a 16% sample of the total area, a sampling intensity great enough to allow estimation of the mean stand basal area within $\pm 10\%$ (Bormann 1953). Species and diameter at breast height of all trees 2 cm dbh

or greater were recorded on each 10- by 10-m plot. Tree saplings > 0.5 m high and < 2.0 cm dbh were recorded on four 2.5- by 2.5-m quadrats nested one in each corner of the larger quadrat. Tree seedlings, ≤ 0.5 m high, were counted on four 1- by 1-m quadrats similarly nested in the corners of the larger plot.

For each 10- by 10-m quadrat, elevation was measured at the center of the quadrat and average slope inclination and aspect were measured with an abney level and a compass, respectively. The percentage of the surface of the quadrat with boulders protruding was estimated, and the position of the plot on a soil-moisture scale was estimated. The moisture scale was based on the combination of three independent ratings: an estimate of the relative amount of water the plot received from higher elevations, an estimate of drainage from the plot, and a cover estimate of the density of the herbaceous vegetation. Scale ratings ranged from 3 (dry) to 12 (very moist). If a plot was swampy it was automatically rated 13. For each quadrat, overstory canopy cover was estimated

visually and recorded as 0%, 25%, 50%, 75%, or 100%. Heights of the two tallest trees were measured on every other row in the matrix system. Till depth was estimated on every unit by excavation and seismic measurements (Fig. 1, N. Johnson, *personal communication*). Estimates of environmental parameters on the larger surrounding 25-by-25-m unit were also made. The occurrence of pit and mound topography was rated 1 (none) to 4 (pronounced). The occurrence of one or more stumps relating to the cutting of the watershed about 50 years ago was noted, and evidence of deer or rabbit droppings or browsing was recorded (Fig. 3).

All quadrat data were punched on IBM cards, and data manipulation and statistical treatments were carried out with an IBM 7094 computer. Dominance-dynamics relationships for the watershed ecosystem were computed for the watershed as a whole (Table 1) and by elevation thirds (Table 2). Errors of the estimated parameters for the whole watershed and for one-third segments were calculated.

Stand characteristics (Fig. 4), that is, characters independent of species such as density, basal area, basal area/tree, importance value of conifer species, and tree height, were computed as running averages along altitudinal, slope-inclination, or aspect gradients. This is a form of direct gradient analysis (Whittaker 1967). Importance values for trees 2 cm and over were based on relative basal area, frequency, and density, and those for saplings and seedlings were based on relative frequency and density. Each form of importance values had a maximum of 100. Running averages were computed for 30.5-m (100-ft) segments of elevation with the segment moving upward by 7.6-m (25-ft) increments. Running averages along slope inclination were based on 9° (20%) segments with 2.2° (5%) increments and for aspect 30° segments and 5° increments. Means for stand and species characteristics were calculated for each of the soil-moisture categories.

Stand characteristics were analyzed by regression analysis with density and basal area per plot as dependent variables and elevation as the independent variable (Fig. 5). Stepwise regression was employed to analyze species characteristics such as density, basal area, and importance values of seedling, sapling, 2- to 10-cm, 11- to 70-cm, and 2- to 70-cm size classes of sugar maple, beech, and yellow birch. For the watershed as a whole, each of the above 15 dependent variables was regressed with elevation, slope, aspect, till depth, and pit and mound scale as independent variables. Use of the soil-moisture scale as an independent variable was

limited to the lower two-thirds of the watershed where these ratings seemed effective.

A computer technique which involves successively overprinting the same print with different characters has been employed to produce "tone density pictograms" to illustrate the relative distribution of quantitative data in three dimensions (Fig. 6). A computer matrix of 55 by 100 points is utilized. At systematic points within the matrix, measured values are entered. For example, in the construction of Fig. 6 importance values were entered into the computer representing each of 12 aspect-moisture rating classes. Aspect classes were 90°–120°, 121°–150°, 151°–180°, and 181°–210°, and soil-moisture classes were 3–5, 6–7, and 8–13. By a method of interpolation a value is computed for each of the 5,500 points in the matrix and the computer carries out the overprinting. This program permits the visual evaluation of large quantities of information rather readily and permits insight into relationships which might not be obvious in tabular presentation. For example, Fig. 6 illustrates the location of peaks of the response surface generated by plotting importance values against both aspect and soil-moisture variables simultaneously.

Species characteristics such as importance values, density, and basal area were computed as running averages along altitudinal, slope-inclination, and aspect gradients by methods described earlier.

Several methods were used to determine the history of the stand. Residents of the area with knowledge of the lumbering operation were interviewed. The extent of the former cutting was evaluated by the stump count previously mentioned (Fig. 3). Wood was collected from 30 widely scattered stumps and identified to species. Increment cores were removed from standing trees on watershed 6 and analyzed for release dates or dates of establishment. Particularly important was a ring analysis of 50 cross sections of trees obtained from nearby watershed 2 where all trees had been cut in an experiment designed to evaluate effects of cutting on nutrient cycling and hydrology (Bormann et al. 1968, Smith et al. 1968, Likens et al. 1969, 1970). Finally, numerous reconnaissances were made throughout the larger Hubbard Brook area to gain a more comprehensive understanding of the local vegetation of the basin.

RESULTS AND DISCUSSION

Recent history of the vegetation of watershed 6

Prior to 1895 most of the forest in and around the Hubbard Brook Valley was mature, old-age,

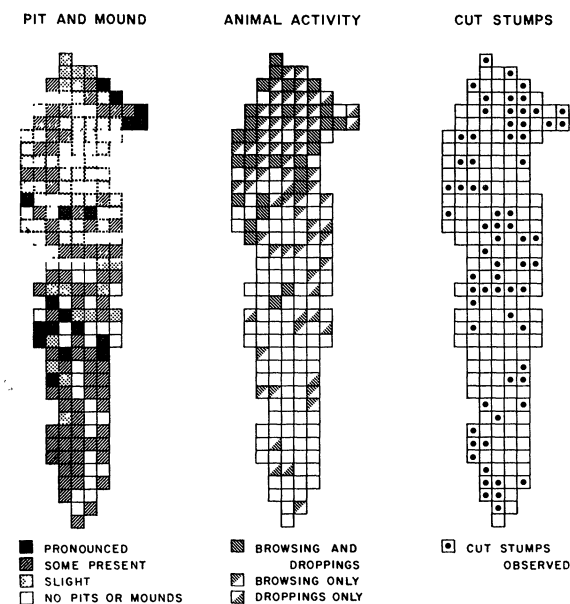


FIG. 3. Distribution of pit and mound topography, signs of animal browsing and droppings, and cut stumps on watershed 6.

virgin forest (Brown 1958, Gove 1968). Cutting began around the turn of the century and within a few decades the whole valley was cut over. Since the original cutting, no significant cutting has occurred, and no resident can recall a forest fire in the Hubbard Brook Valley.

Cutting of the Hubbard Brook Forest about 50 years ago raises questions as to the stability of the present forest and its relation to the mature forest that formerly inhabited the site. These questions are of importance, for the more closely the present ecosystem approaches the former ecosystem, the more closely will the results of the Hubbard Brook study reflect the steady-state relationships of the climax forest rather than the directional changes characteristic of successional ecosystems.

The stump survey in watershed 6 (Fig. 3) and supplementary observations indicate that the entire area of the watersheds was cut from the weirs to the ridge top. No evidence of fire—charcoal, burned stumps, or fire scars—was found in the area of watershed 6, which confirmed the local residents' reports. Patches of windthrown trees indicate some local wind damage subsequent to cutting.

Analyses of annual rings of standing trees on watershed 6 and 50 stumps on watershed 2 indicated that a scattering of ash (*Fraxinus americana*) trees began as open-grown seedlings in 1909 and many more ash and maple trees began as open-grown seedlings in 1917. This pattern can be explained by two separate cutting operations. The first was probably a spruce cut that reached the

watershed study area about 1909 and resulted in the removal of large spruce trees scattered through the hardwood forest. The spruce cut was probably much heavier in other sections of the valley, i.e., at higher elevations and on other aspects. The second cut occurred about 1916–17 when better hardwoods and remaining spruce were probably cut. The ring analyses indicated that the second cut left a forest of scattered large, cull hardwoods of beech, birch, and maple as well as smaller hardwoods. Shortly after cutting, additional seedlings of sugar maple, ash, and pin cherry became established. Pin cherry is presently represented by a few individuals, but its past importance in the forest is shown by many fallen and well-rotted trunks identified by their decay-resistant bark. A cutting pattern similar to this has been described for northern hardwood forest at Bartlett, New Hampshire, approximately 25 miles east-northeast from Hubbard Brook (Leak 1961).

Apparently cutting was done in the winter and logs were removed on sleds (Gove 1968). Since winter conditions would minimize soil disturbance, probably most soils in the watershed were relatively undisturbed by the cutting operation. Hart (1961) has shown that the humus layer in northern hardwood forests (for several years after cutting) decreases in proportion to the intensity of the cut. This is due to acceleration of nutrient turnover rates and nutrient loss from the ecosystem, an extreme case of which we have recently reported (Bormann et al. 1968, Likens et al. 1969, 1970). It seems probable, however, that revegetation brought both of these processes quickly under control (Marks and Bormann, *unpublished data*).

There is a question as to whether red spruce was a more important component of the old-age forest than it is at present. The podzol soil underlying the present forest may owe its origin to an earlier coniferous stand. The following evidence bears on the composition of the earlier forest. (1) Ring analyses indicated that the forest left after the second cutting was largely a hardwood forest. (2) Wood-anatomy studies indicated that 22 of 29 stumps still identifiable were hardwood (yellow birch) and seven were spruce. (3) The present vegetation of watershed 6 is predominantly northern hardwoods and shows no evidence of a shift toward spruce. (4) Spruce has succeeded in re-establishing itself in other areas of Hubbard Brook, suggesting that the southeast-facing slopes in the area of watersheds 6 and 2 are relatively unfavorable to its establishment. (5) An extensive study of cut-over spruce-hardwood forest indicated that spruce-fir reproduction is usually abundant on sites where a large volume of these

TABLE 1. Mean and standard deviation of density and basal area by size classes of trees in watershed 6, Hubbard Brook Forest

Size class	Density (number ha ⁻¹)	Basal area (m ² ha ⁻¹)
Seedling.....	232,350 ± 12,625	—
Sapling.....	4,732 ± 192	—
2-10 cm dbh.....	1,362 ± 49	3.36 ± 0.13
11-70 cm dbh.....	556 ± 18	20.23 ± 0.76

species was present before cutting (Westveld 1931). (6) Podzol soils are known to occur extensively under similar northern hardwood forests (Westveld et al. 1956).

We conclude that the composition of the present ecosystem approximates the old-age mature forest that preceded it, although the proportion of spruce may have decreased slightly. It is likely, however, that the present ecosystem has a somewhat lower biomass than the previous ecosystem and is still accumulating biomass (Bormann et al. 1968, Likens et al. 1969, 1970). The net accumulation of nitrogen in the undisturbed ecosystem supports this view. Slight directional shifts in species importance may be occurring. This will be discussed in more detail later.

The ecosystem as a whole

The population structure of the stand on the watershed ecosystem as a whole indicated an all-aged forest (Table 1). Importance values for trees ≥ 10 cm dbh showed dominance by *Acer saccharum* (I.V. 33), *Fagus grandifolia* (I.V. 28), and *Betula alleghaniensis* (I.V. 25) with an admixture of *Picea rubens* (I.V. 4), *Abies balsamea* (I.V. 3), and *Betula papyrifera* (I.V. 4). The understory, 2- to 10-cm dbh size class, contained the species listed above in about the same proportions, plus two common understory trees, *Acer spicatum* (I.V. 11) and *A. pensylvanicum* (I.V. 7).

Basal area for the stand as a whole averaged 23.60 ± 0.77 m²ha⁻¹ (102 ft²acre⁻¹). Barrett (1962) says 28.2 m²ha⁻¹ is fairly representative of old-growth hardwood stocking in the northeast. However, basal areas ranging from 30.6 to 47.1 m²ha⁻¹ have been reported for northern hardwood forests between 488 m (1,600 ft) and 732 m (2,400 ft) in Vermont (Bormann and Buell 1964, Siccama 1968). Stearns (1951) has reported a range of 56.4-64.9 m²ha⁻¹ for old-age sugar maple-hemlock-yellow birch stands in Wisconsin, and Whittaker (1966) a range of 53.2-64.0 for climax cove forest in the Southern Appalachians. Compared to the above stands, the basal area of watershed 6 is relatively modest.

Basal area in watershed 6 is probably influenced by three factors: (1) the forest is still accumulating biomass after the cutting about 50 years ago; (2) the stand includes sizeable areas where persistent environmental factors depress production; and (3) the forest as a whole is limited in production by a generally oligotrophic situation.

Response of stand characteristics to the elevational complex gradient

Our analyses, both direct gradient and regression, indicated that the vegetation of watershed 6 was not homogeneous, and that both stand and species characteristics exhibited considerable response to environmental gradients. By far the most important independent variable affecting this variation was elevation, indicating that both stand and species characteristics were responding to an elevational "complex gradient" (Whittaker 1967).

Basal area of the stand (trees ≥ 2 cm dbh) clearly declined with increasing elevation (Table 2). The difference between the lower and upper thirds of the watershed is statistically significant at the 1% level. Running averages indicated that the decline of basal area with elevation was somewhat irregular, but distinctly downward (Fig. 4). A plot of basal area per quadrat against elevation indicated a generally linear decrease in basal area with increasing elevation. This relationship is expressed in the equation $Y = 40.9 - 0.0254X$, where Y = basal area in square meters per hectare and X = elevation in meters (Fig. 5).

A plot of density per quadrat, 2- to 70-cm size class, against elevation showed, in contrast, a distinct curvilinear relationship (Fig. 4, 5), with a more or less linear response below 701 m (2,300 ft) to 732 m (2,400 ft) but with rapid increase in density above these elevations. This relationship is shown by the equation $Y = 57805 - 179.28X + 0.141X^2$, where Y = density in stems per hectare and X = altitude in meters.

The density relationships of the 2- to 70-cm class are explained by two opposing trends in the 2- to 20-cm and the 21- to 70-cm classes (Table 2). Density of the latter class declines with elevation showing a 16% drop between middle and lower thirds and a 51% drop between upper and lower thirds. Coincidentally, density in the 2- to 10-cm and 11- to 20-cm class increases approximately three- and twofold, respectively, between upper and lower thirds. Sapling density remains about the same over the whole range of elevations, whereas tree-seedling density drops markedly at upper elevations, where it is only 17% of the density represented at lower elevations. This drop in seedling density is coincident with rapid increases in herb cover (Siccama, Bormann, and

TABLE 2. Dominance-dynamics characteristics of the major tree species of the watershed-6 ecosystem at three elevation ranges (L = lower third of the watershed, 546-625 m; M = middle third, 625-709 m; U = upper third, 709-791 m)

Species*	Seedlings			Saplings			2-10 cm dbh			11-20 cm dbh			21-70 cm dbh		
	L	M	U	L	M	U	L	M	U	L	M	U	L	M	U
Density (number/ha)															
<i>Acer saccharum</i>	371,000	182,569	34,186	1,488	372	270	364	299	208	96	135	112	96	109	31
<i>Fagus grandifolia</i>	87,900	37,465	28,546	3,032	2,978	2,800	324	286	595	74	54	142	98	47	36
<i>Betula alleghaniensis</i>	2,250	12,500	5,552	16	117	112	26	54	207	70	51	86	64	62	47
<i>B. papyrifera</i>	—	—	261	—	—	47	—	—	172	—	—	65	—	—	2
<i>Picea rubens</i>	150	35	203	120	89	256	32	39	195	—	4	44	—	1	4
<i>Abies balsamea</i>	—	—	349	—	—	191	—	—	210	—	—	41	—	—	6
<i>Prunus pensylvanica</i>	—	—	—	—	—	—	—	1	22	2	10	15	—	—	—
<i>Acer pensylvanicum</i>	6,200	9,062	6,162	456	567	321	18	56	135	8	6	6	—	—	—
<i>A. spicatum</i>	6,250	3,993	5,145	360	239	572	10	76	363	2	—	—	—	—	—
<i>Pyrus americana</i>	—	—	116	—	—	33	—	—	38	—	—	—	—	—	—
Total.....	474,400	245,625	80,523	5,488	4,367	4,600	776	811	2,165	252	260	518	260	219	126
Frequency (%)															
<i>Acer saccharum</i>	100	100	85	74	40	27	96	83	60	52	61	53	56	65	24
<i>Fagus grandifolia</i>	94	96	81	96	90	77	88	81	81	47	39	55	48	32	29
<i>Betula alleghaniensis</i>	22	51	33	4	8	13	18	28	71	38	31	48	42	39	35
<i>B. papyrifera</i>	—	—	5	—	—	7	—	—	28	—	—	29	—	—	2
<i>Picea rubens</i>	2	1	7	24	18	29	18	24	49	—	3	24	—	1	5
<i>Abies balsamea</i>	—	—	9	—	—	10	—	—	30	—	—	14	—	—	5
<i>Prunus pensylvanica</i>	—	—	—	—	—	—	—	1	8	2	7	9	—	—	—
<i>Acer pensylvanicum</i>	76	88	71	38	58	36	14	25	33	8	6	6	—	—	—
<i>A. spicatum</i>	66	62	70	42	22	40	8	25	64	2	—	—	—	—	—
<i>Pyrus americana</i>	—	—	5	—	—	5	—	—	13	—	—	—	—	—	—
Basal area (m²/ha)															
<i>Acer saccharum</i>							0.94	0.82	0.60	1.79	2.46	1.83	6.53	7.03	2.27
<i>Fagus grandifolia</i>							0.80	0.50	1.40	1.27	1.00	2.38	8.57	4.53	2.49
<i>Betula alleghaniensis</i>							0.13	0.18	0.61	1.47	0.99	1.53	4.32	5.32	2.72
<i>B. papyrifera</i>							—	—	0.57	—	—	0.98	—	—	0.09
<i>Picea rubens</i>							0.10	0.15	0.54	—	0.04	0.64	—	0.05	0.27
<i>Abies balsamea</i>							—	—	0.44	—	—	0.75	—	—	0.31
<i>Prunus pensylvanica</i>							—	0.01	0.08	0.04	0.18	0.22	—	—	—
<i>Acer pensylvanicum</i>							0.04	0.17	0.36	0.10	0.07	0.07	—	—	—
<i>A. spicatum</i>							0.04	0.20	0.49	0.02	—	—	—	—	—
<i>Pyrus americana</i>							—	—	0.11	—	—	—	—	—	—
Total.....							2.05	2.03	5.20	4.69	4.74	8.40	19.42	16.93	8.15
Importance value															
<i>Acer saccharum</i>	53	50	33	26	13	8	44	36	12	37	49	22	36	46	26
<i>Fagus grandifolia</i>	22	20	29	44	53	46	39	30	24	29	23	26	38	24	29
<i>Betula alleghaniensis</i>	3	9	8	1	3	4	6	9	12	28	21	18	25	29	35
<i>B. papyrifera</i>	—	—	1	—	—	2	—	—	8	—	—	12	—	—	2
<i>Picea rubens</i>	X ^b	X	1	5	5	9	5	7	10	—	1	9	—	1	4
<i>Abies balsamea</i>	—	—	1	—	—	4	—	—	8	—	—	8	—	—	—
<i>Prunus pensylvanica</i>	—	—	—	—	—	—	—	X	1	1	4	3	—	—	—
<i>Acer pensylvanicum</i>	11	13	14	11	19	11	3	8	7	4	2	1	—	—	—
<i>A. spicatum</i>	10	9	13	11	7	14	2	10	14	1	—	—	—	—	—
<i>Pyrus americana</i>	—	—	1	—	—	1	—	—	2	—	—	—	—	—	—

*The first six species listed are capable of attaining large size; the remainder are understory species. *Frazinus americana*, *Prunus virginiana*, *Acer rubrum*, and *Tsuga canadensis* were insignificant components of the vegetation and are not included in the analysis.
^bX = <1

Likens 1970) and in evidence of browsing (Fig. 3).
 The curve of average basal area per tree shows an inverse relationship to that of density per hectare. Basal area per tree declines curvilinearly with increasing elevation (Fig. 4, 5). This relationship is shown in the equation $Y = -1890. + 6.973X - 0.00576X^2$, where Y = average basal area per tree in square centimeters and X = altitude in meters. The value of R , curvilinear, was only slightly better than R , linear; however, the

curvilinear equation seemed to better fit the situation over the lower two-thirds of the watershed.
 Height of the upper part of the canopy and percentage of evergreenness (i.e., percentage of spruce and fir) are strongly related to elevation, with height decreasing with elevation and evergreenness increasing (Fig. 4).
 Species diversity (average number of species per .01-ha quadrat) in the 2- to 70-cm size class was 52% higher in the upper third (6.09 spp./01 ha) than in the middle third (4.01 spp./01 ha),

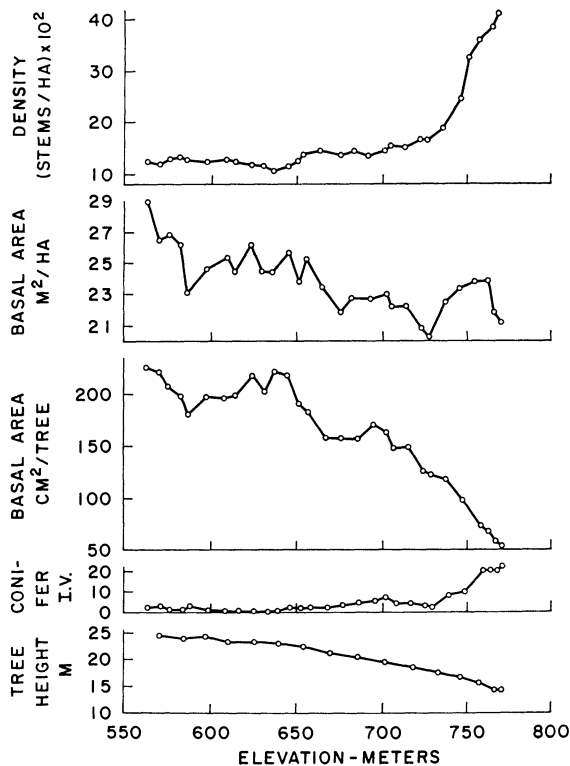


FIG. 4. Running averages of stand characteristics along the elevational gradient on watershed 6. Points in the average include 30.5-m bands with 7.6-m increments. All values based on stems ≥ 2 cm dbh on 10- by 10-m plots. Importance values are based on density, basal area, and frequency. The maximum importance value is 100%.

and the middle third was 10% higher than the lower (3.62 spp./0.01 ha). The 10- to 70-cm size class was more diverse than the 2- to 10-cm size class at all elevations. This may suggest that tree-species diversity, due to the presence of climax and pioneer species, will decrease as the forest matures and successional species die out.

In summation, basal area of the tree vegetation (i.e., all individuals ≥ 2 cm dbh), basal area per tree, deciduousness, and canopy height all decrease with increasing elevation, whereas density, evergreenness, and species diversity increase with increasing elevation. Over the 245-m span of elevation the character of the forest changes markedly from one with a well-defined overstory, understory, and shrub and herb layer to a lower forest with one overstory layer, an increased evergreenness, and a luxuriant herb layer. This change appears to be linear over the lower two-thirds of the range, but becomes curvilinear above about 732 m (2,400 ft).

If it is assumed that the whole watershed had the same cutting intensity and that it was rapidly and fully stocked with seedlings and sprouts, two trends in secondary succession would be expected

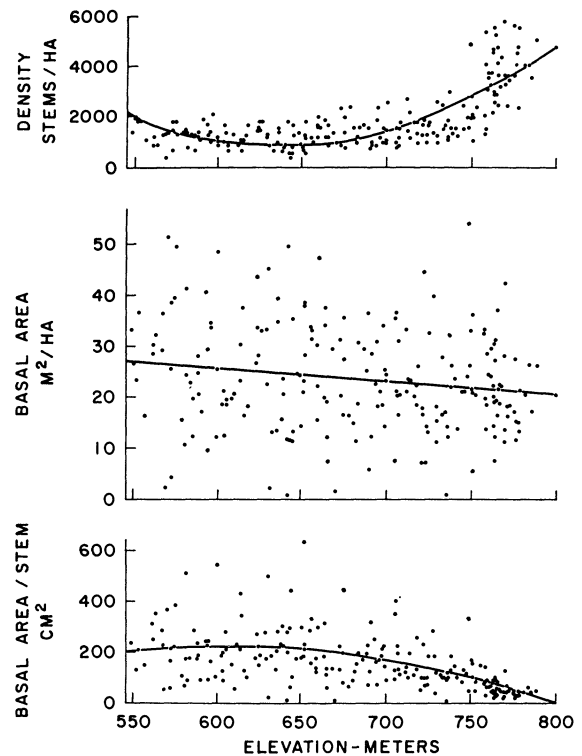


FIG. 5. Scatter diagrams of density, basal area, and basal area/stem vs elevation of 208 10- by 10-m plots on watershed 6 with fitted regression curves. The regression equations for these curves are as follows: density = $57805 - 179.28$ (meters elev) + 0.141 (meters elev)², with $R = 0.79$; basal area = $40.9 - 0.025$ (meters elev), with $R = 0.16$; and basal area/tree = $-1890 + 6.973$ (meters elev) - 0.00576 (meters elev)², with $R = 0.54$, R linear = 0.50.

among initial arboreal invaders: (1) successful individuals would grow larger, increasing their volumetric requirements, whereas less successful individuals would die; and (2) the density of the original invaders would decrease (Bormann 1966). With time, the forest would pass from a dense brushy stand to a well-layered stand with remnants of the original invaders forming overstory and understory and newer individuals forming lower layers (Marquis 1967). The lower elevations of the watershed conform to the more developed conditions described above. The forest is well layered, and scattered over the forest floor are rotting boles of less successful individuals, particularly *Prunus pensylvanica*, that have succumbed during the maturation process. On the other hand, the forest of the higher elevations is dense and composed of small trees and is still in a brushy state. Living *Prunus pensylvanica* and *P. virginiana* still constitute a measurable proportion of the stand at upper elevations (Table 2).

The rate at which a cut or leveled forest ecosystem redevelops is primarily dependent on the

rate at which the ecosystem accumulates biomass. The more rapidly the system accumulates biomass, the more rapidly will developing individuals come into conflict and the more rapidly will thinning occur. Thus, a lower rate of net primary productivity with higher elevation may account, in part, for the present differences in structure between upper and lower elevations.

Three lines of evidence support the idea that net primary productivity decreases with elevation. (1) Annual total basal-area increments measured by thirds of the watershed, based on regressions derived from approximately 600 increment cores taken at three elevations and applied to total populations, indicate that present rates of increase in total basal area are about 10% greater at lower elevations (lower $0.508 \text{ m}^2\text{ha}^{-1}$, middle $0.507 \text{ m}^2\text{ha}^{-1}$, upper $0.459 \text{ m}^2\text{ha}^{-1}$). These data do not include losses due to death. If we assume that present day basal-area relationships are at least a partial reflection of biomass accumulation since cutting, the differences between total basal areas found on each third of the watershed confirm lower productivity rates at the upper elevations. This is particularly so when it is recalled that not only is basal area lower at higher elevations, but tree height declines also (Figs. 1, 4). (3) Litter fall is a measure of productivity, and leaf-fall measurements indicate approximately 3,050, 2,749, and 2,265 kg ha^{-1} for lower, middle, and upper thirds of the watershed (Gosz, *personal communication*).

Differences in net productivity between the upper third and the lower two-thirds of the watershed may be explained by geologic and meteorologic factors. Rock outcrops, excavation, and seismic observations indicate that average till depths drop sharply above 732 m (Fig. 1). Most importantly, this implies shallower soils over the upper third of the watershed. Meteorologic factors over the upper third of the watershed are also less conducive to tree growth. A phenological study (Mahall and Bormann, *unpublished data*) shows a difference of approximately 5 days in leafing out between upper and lower elevations, indicating a shorter growing season above. In addition, the uppermost portion of the watershed is probably more fully subjected to northwest winds. Siccama (1968) has noted that in Vermont 732–762 m (2,400–2,500 ft) is the approximate lower limit of a vegetation zone characterized by extended periods of snow cover, sharply reduced length of frost-free period, and frequent cloud envelopment. These factors may also apply at Hubbard Brook.

Disturbance must also be taken into account. Mountainside vegetation, particularly on exposed peaks or ridges, is subject to recurrent distur-

bances especially by wind. For watershed 6, above 760 m strong northwest winds and ice storms are more frequent and severe and together cause extensive branch breakage (Gosz, *personal communication*). Such disturbance could contribute to the maintenance of patches of younger brushy forest. Browsing effects may also be more important at these higher elevations (Fig. 3). In the Green Mountains of Vermont, Siccama (1968) has noted frequent occurrence of brushy stands at elevations similar to the uppermost elevations of watershed 6. One aspect of the wind effect is wind-throwing shown by mound and pit topography (Lyford and MacLean 1966, Fig. 3). In our watershed, however, this is not particularly related to elevation.

Response of species to slope, aspect, and soil-moisture gradients

Statistical indicators showed significant relationships between species characteristics and elevation. However, no statistically significant relationships were found between density, basal area, and importance values for various size classes of sugar maple, beech, and yellow birch and slope and aspect for watershed 6 as a whole, or for slope, aspect, and soil moisture for elevations below 732 m (2,400 ft).

In this study three factors tended to obscure these relationships. (1) The response of species to the independent variable, elevation, was relatively strong and tended to cover the effect of the other measured variables. For example, in the stepwise regression of five size classes of sugar maple, beech, and yellow birch, in 13 of 15 cases elevation was the first variable extracted (i.e., accounted for the greatest percentage of the variance), and for the 15 dependent variables it accounted for, on the average, 66% of the total variation attributable to the measured variables. (2) The rather flattish nature of the valley ascending watershed 6 tended to minimize the effects of aspect. (3) The sampling design, although adequate to fulfill the major purposes of the study, was inadequate to define quantitatively the relationships with minor independent variables.

Species distribution and reproductive behavior with respect to the independent variables may be more complex than is ordinarily suspected. This was indicated by tone density pictograms for the distribution of importance values of several size classes of three major species with respect to four aspect classes and three moisture classes (Fig. 6).

The patterns shown in Fig. 6 provide an insight into the reproductive behavior of dominant tree species not usually evident from other kinds of analyses. The most striking feature is that sites

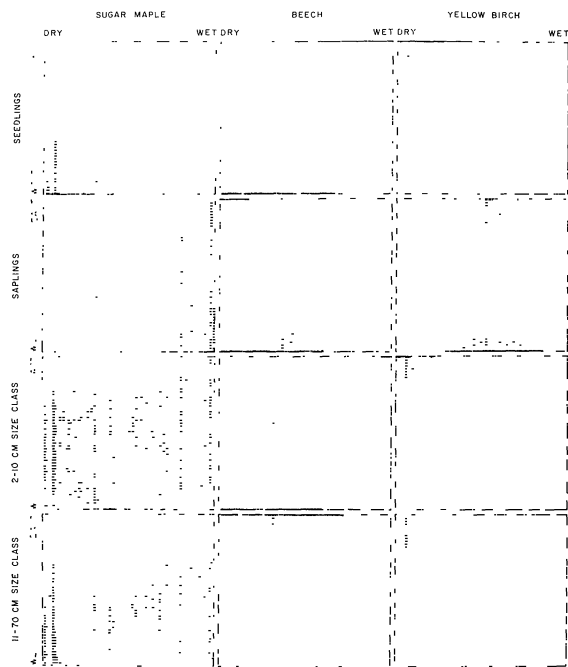


FIG. 6. Computer-drawn tone density pictograms showing the relationship of importance values to soil-moisture (dry = 3 to wet = 13) and aspect (east, 90°, then south to west, 210°) gradients. (See text for description of method.) Three ranges of importance are illustrated for each of the size classes of the three major tree species. On each pictogram the darkest areas represent the highest third of the response surface and the blank areas the lowest third. The pictograms are comparable to one another only in the location of the peaks and not with respect to quantitative equality between species or size classes (e.g., the range of importance values illustrated in yellow birch seedlings is 0-26, and the range for sugar maple seedlings is 29-41; each of these ranges is subdivided into three levels, so for yellow birch seedlings the darkest areas represent importance values between 17 and 26, and for sugar maple the darkest represent importance values between 37 and 41.)

of maximum abundance (where the pictogram shows the highest importance values) of a species in the lower layer of the community often do not coincide with sites of maximum abundance for the same species in the upper layers. This lack of coincidence suggests two fundamental observations. (1) The distribution of a species in the upper layer of the forest will change as individuals of the upper layer are replaced by individuals from the lower layers. This change may be of two kinds: (a) directional, where a species either directionally enlarges or contracts its role as a dominant in the stand, or (b) fluctuational, where the importance and spatial distribution of a dominant tree species changes in a cyclical or fortuitous manner through time. (2) The second observation is that the distribution of trees in the upper layers will remain as it currently is. This,

however, implies that there are differential survival rates in lower layers whose action through time will bring about a replacement pattern in the upper layers similar to the ones which exist today.

Graphs of species characteristics against other combinations of independent variables lead to the same conclusion as those in Fig. 6. These observations emphasize the need for more sophisticated studies of the mechanisms regulating the reproduction of the dominant tree stratum in the mature forest community.

Response of species characteristics to the elevational complex gradient

Larger trees.—The importance of dominant tree species, as measured by importance values (Fig. 7), shifts between species along the 245-m range of elevation. No two species show identical trends of importance value; rather, several types of trends are apparent in the data.

Sugar maple generally decreases with increased elevation. Below 700 m elevation its importance values show considerable fluctuation, but always the species is one of the two leading dominants in the stand. Above 700 m, however, its values show a steady decline. In the last 40 m of elevation, sugar maple declines from a major dominant (I.V. 31) to a relatively inconspicuous component of the vegetation (I.V. 6). The importance values of yellow birch, ranging from 14 to 25, indicate a

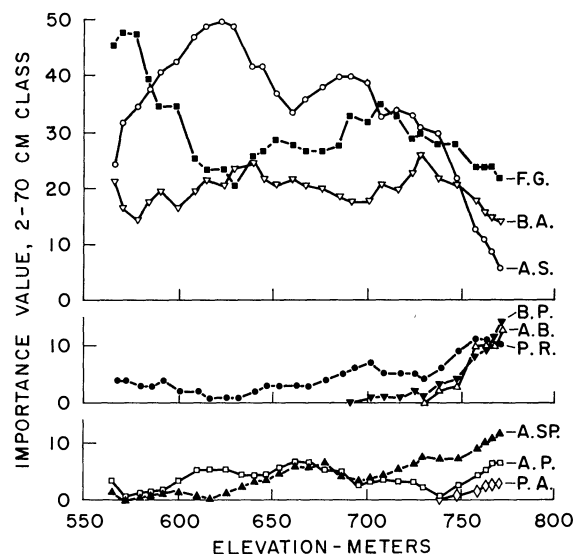


FIG. 7. Running averages of species importance values versus elevation on watershed 6. Points include 30.5-m elevation bands with a 7.6-m increment between points. Importance values based on density, basal area, and frequency in each elevation band. F.G. = *Fagus grandifolia*; B.A. = *Betula alleghaniensis*; A.S. = *Acer saccharum*; B.P. = *Betula papyrifera*; A.B. = *Abies balsamea*; P.R. = *Picea rubens*; A. SP. = *Acer spicatum*; A.P. = *Acer pensylvanicum*; P.A. = *Pyrus americana*.

considerable degree of steadiness over the whole elevational gradient. Beech has a pattern similar to that of yellow birch in that its importance values fluctuate between 20 and 48, but show no marked trend. Above 732 m beech is the major component of the forest.

Red spruce is a small but consistent component over the whole range of elevation, but begins to increase at about 632 m. This pattern of distribution is consistent with the widespread concept of spruce as a climax dominant in the lower elevation spruce-hardwood forest (Braun 1950) and as a major component of the boreal forest at higher elevations (Oosting and Billings 1951). Paper birch and balsam fir show clear trends of increase in importance value coupled with elevation. They are absent below about 690 m and 730 m, respectively, but above that point they show sharp increases.

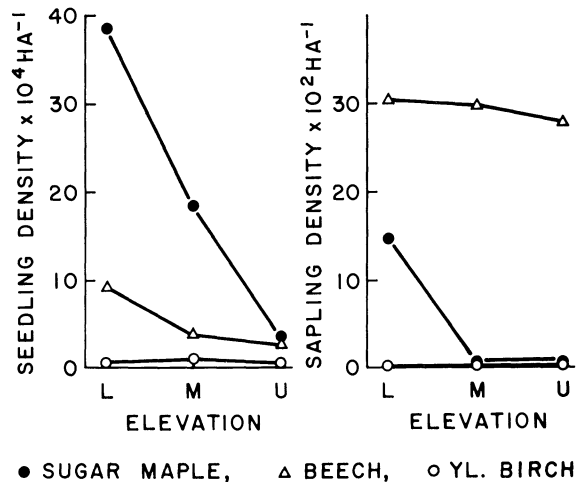
Trends in importance values in dominant trees are reflected in understory species. *Acer pensylvanicum* remains irregularly steady over the gradient. *Acer spicatum* has a trend similar to red spruce, i.e., generally increasing toward higher elevations. *Pyrus americana* shows a trend of strong increase above 740 m.

Seedlings and saplings.—Changes in the number of seedlings and saplings of a species along the elevational gradient parallel, in general, those of dominant members (2- to 70-cm size class) of the same species. However, the best development of seedlings and saplings probably occurs under somewhat different aspect and soil-moisture conditions than larger trees of the same species (Fig. 6).

Tree-seedling density shows a ratio of 6:3:1 between lower, middle, and upper thirds of the watershed (Table 2). The drop in tree-seedling density is particularly strong over the upper third of the watershed where it is accompanied by a threefold increase in cover and biomass of the herbs over that encountered in the lower two-thirds of the watershed (Siccama et al. 1970).

The drop in tree-seedling density is most marked for sugar maple, which shows a ratio of 11:5:1 over lower, middle, and upper thirds of the watershed (Table 2, Fig. 8). The drop in sugar maple seedling density is accompanied by a four- and fivefold decrease in sapling density between lower and middle and lower and upper elevations. These seedling and sapling trends support the conclusion based on importance values of the 2- to 70-cm class that sugar maple has a smaller role in the steady-state forest ecosystem at the highest elevations.

Beech seedlings show a similar but less severe decrease in density between lower and middle and



● SUGAR MAPLE, △ BEECH, ○ YL. BIRCH
 FIG. 8. Density of seedlings and saplings in relation to elevation (lower (L), middle (M), and upper (U) third) of the watershed.

upper thirds of the watershed, 3:1:1. Contrary to sugar maple, sapling density of beech is high throughout the watershed, 1:1:1. Apparently beech has the capacity to be and to remain a dominant component of the ecosystem throughout the elevational range of the watershed.

Although there are about four times fewer beech than sugar maple seedlings, beech saplings make up 74% of all saplings of overstorey species. This phenomenon is not uncommon in northern hardwood forests (Barrett 1962) and may signify a gradual increase through time of beech in the ecosystem. This realignment in species importance would be in line with (1) the greater importance of beech reported for pre-settlement forests of northern New England (Siccama 1963), (2) the observation that sugar maple tolerance is intermediate between beech and yellow birch in northern New York (Curtis and Rushmore 1958, Barrett, Farnsworth, and Rutherford 1962, Piusi 1966), (3) the knowledge that heavy cutting of stands results in less beech in the new stand than in the old (Rushmore 1961), and (4) the observation that beech reproduction has a near immunity to deer browsing (Barrett 1962). However, any tendency for beech to increase in present-day forests of northern New England must be balanced against the severe mortality that it may suffer from the so-called scale-*Nectria* complex (Zabel, Silverborg, and Fowler 1958).

The decline in beech seedling density with elevation while sapling density remains more or less uniform implies that root sprouting plays an important part in maintaining the species at the highest elevations. We have observed numerous instances throughout the watershed where large beech trees are surrounded by saplings of root

sprout origin. This is a common characteristic of the species (Rushmore 1961). Although the potential of root sprouts is questionable, in some cases they grow into dominant trees (Rushmore 1961). Possibly beech reproduction shifts from reliance on sexual reproduction toward reliance on vegetative reproduction in those portions of its range subject to severest environmental conditions.

Yellow birch seedlings and saplings constitute a small but regular part of the seedling and sapling layers throughout the watershed. Yellow birch regenerates poorly in thick litter of undisturbed forests (Gilbert 1960). Under these circumstances successful regeneration is limited to cracks in boulders, rotted logs, and stumps (Hough and Forbes 1943), or to patches of bare mineral soil on the sides of windthrow mounds, etc. Thus, data on seedlings and saplings similar to those in Table 2 and Fig. 8 are to be expected in mature forests. The less efficient reproduction of yellow birch does not necessarily signal a drop in the importance of this species through time; it may maintain itself through effective reproduction in localized disturbed sites (Marquis 1965) common to any mature forest. Whatever its reproductive behavior, the longevity of yellow birch (up to 300 years, Gilbert 1960) and its high representation in the present-day tree layers (Table 2) indicate that for a considerable period of time the species will continue to be an important component of this forest throughout the entire elevational range, barring unforeseen events.

Red spruce is a minor component of both the seedling and sapling layers. However, the density and frequency of both seedlings and saplings tend to increase at the uppermost elevations (Table 2).

The failure of red spruce to establish large populations of seedlings in northern hardwood forests has been widely reported and generally ascribed to the small energy reserves of the seeds and the very slow growth of the seedlings (Barrett 1962). Two-year seedlings are likely to be less than 2.5 cm tall with roots extending only to depths of < 5 cm. These small seedlings are very sensitive to drought in the organic horizons of the soil and to mechanical crushing by fresh hardwood litter. However, great shade tolerance (Place 1955) and an exceptional longevity, 400+ years, allow established seedlings to maintain themselves in the hardwood forest. The present distribution of smaller spruces and the capacity to respond to release (Place 1955) would seem to guarantee that red spruce will remain a component of the overstory of this ecosystem.

Seedlings and saplings of balsam fir and paper birch are absent at lower elevations, but in the upper third of the watershed these species together

make up 1% of the seedlings of overstory trees and about 6% of the saplings (Table 2).

Seedling and sapling patterns for understory species parallel those for overstory species. *Acer pensylvanicum* and *A. spicatum* have fairly regular populations throughout the watershed, but *Pyrus americana* has seedlings and saplings only at the highest elevation (Table 2).

In summary, the present distribution of seedling and sapling populations strongly suggests that conditions governing the establishment of tree species over the 245-m gradient undergo a marked directional change. The clearest indicators of directional change are (1) the strong negative trend with increasing elevation of *Acer saccharum*, (2) a somewhat weaker negative response of *Fagus* seedlings, and (3) a generally positive trend of populations of seedlings and saplings of *Picea rubens*, *Abies balsamea*, *Betula papyrifera*, and *Pyrus americana*. The population data for *Betula alleghaniensis*, *Acer spicatum*, *A. pensylvanicum*, and *Fagus* saplings did not reflect clear trends over the elevational gradient.

Relationship to regional vegetation

Intensive interdisciplinary studies on a variety of terrestrial ecosystems have been or are being launched throughout the world. One of the ultimate goals is the application of principles, generated by intensive study of local ecosystems, to larger regional and continental ecosystems. Application, in turn, rests on a firm comprehension of the relationships of ecosystems through space and time. It is on this point that strong interdependence of two vigorous branches of ecological research, ecosystem analyses and vegetation analyses, is established. Ecosystem analyses provide a clearer understanding of factors that determine relationships between species, whereas vegetation analyses provide a basis for classification which has predictive value through space and time.

Research on vegetational analysis has not yet provided a wide-ranging quantitative system of vegetation classification that applies to Hubbard Brook (McIntosh 1967, Whittaker 1967). Therefore, we will locate our study area within the various classical systems which have been proposed and briefly consider the application of continuum concepts to this vegetation.

Braun (1950) has reviewed the older literature pertinent to the vegetation of northern New Hampshire, which includes the Hubbard Brook area. Accordingly, our watershed study area belongs to the hemlock-white pine northern hardwood region which extends from Nova Scotia to Minnesota. Specifically, our watersheds would be classed as spruce-hardwoods of the New England Section of

the Northern Appalachian Highland Division. The spruce-hardwoods predominate in northern New England and grade imperceptibly into hemlock-northern hardwood to the south or at lower elevations and into the boreal forest to the north or at higher elevations. Along the elevational gradient the change from spruce-hardwoods to boreal forest in much of New England is rather abrupt.

Oosting and Billings (1951), in their study of higher elevation spruce-fir forest in northern New England, noted the change from deciduous to boreal forest at 762 m (2,500 ft) in the White Mountains. They also record the strong floristic similarity that characterizes the spruce-fir forests throughout its north-south extent on the higher elevations of the Appalachian Mountains.

Vegetational zonation in mountains of New England and New York was clearly recognized by students of vegetation and is reflected in many systems of classification (Chittenden 1905, Hawley and Hawes 1912, Bray 1915, Egler 1940, Oosting and Billings 1951, Westveld et al. 1956, Bormann and Nelson 1963, Harries 1965, Siccamo 1968). Some of these systems with zonal designations and altitudinal limits are illustrated in Fig. 9, and the relationship of the forest vegetation on the Hubbard Brook watershed ecosystems to these classifications is shown.

With the exception of the hardwood-boreal forest transition at about 762 m (2,500 ft), there is little agreement on zonal boundaries. This suggests that the zones and their boundaries, other than the hardwood-boreal forest transition, are rather arbitrarily drawn and do not represent well-defined community units. In fact, zones are often defined by the gradual loss or acquisition of species as one moves along a latitudinal or elevational gradient, rather than by abrupt transitions (Chittenden 1905, Hawley and Hawes 1912, Bray 1915, Westveld et al. 1956). These descriptions call to mind situations described by Whittaker (1967) in which species populations overlap broadly along a variety of gradients with gradual changes in population levels which result in gradual and continuous change in community composition.

To gain a larger perspective of the elevational distribution of major tree species in the White Mountains, we generalized from the literature (Chittenden 1905, Hawley and Hawes 1912, Harries 1965) the uppermost elevations at which various species have the potential to be a relatively major component of the vegetation (Table 3). Although these generalizations, supplemented by observations by the authors, are limited to areas underlain by acidic schists and granites in central New Hampshire, the pattern shown in Table 3

TABLE 3. Generalized upper elevational limit of tree species as a major component in the vegetation in central New Hampshire

Species	Meters	Feet
<i>Quercus alba</i>	152	500
<i>Juglans cinerea</i>	274	900
<i>Ulmus americana</i>	305	1,000
<i>Quercus rubra</i>	457	1,500
<i>Pinus strobus</i>	455	1,500
<i>Tsuga canadensis</i>	610	2,000
<i>Fraxinus americana</i>	610	2,000
<i>Acer saccharum</i>	762	2,500
<i>Acer rubrum</i>	762	2,500
<i>Fagus grandifolia</i>	792	2,600
<i>Betula alleghaniensis</i>	914	3,000
<i>Picea rubens</i>	1,280	4,200
<i>Abies balsamea</i>	1,707	5,600
<i>Betula papyrifera</i>	1,707	5,600
<i>Picea mariana</i>	1,707	5,600

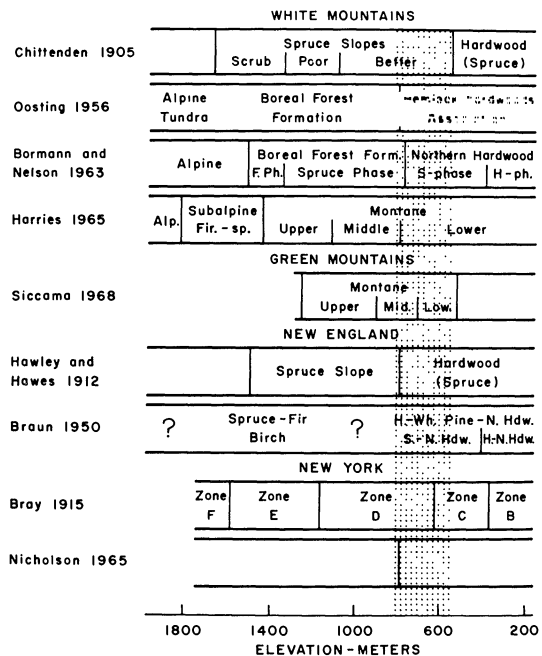


FIG. 9. Classification systems proposed by various workers for the vegetation of northern New England and adjacent New York. Zones are plotted against elevation in meters. Stippled area represents the portion of the elevation gradient encompassed by watershed 6.

holds reasonably well for northern Vermont (Siccamo 1968). It is apparent, on the other hand, that elevational limits are strongly influenced by latitude, slope inclination, aspect, and soil conditions and that the data in Table 3 and Fig. 9 do not account for this variation.

Nevertheless, Table 3 contains most of the major dominant tree species in the Boreal Forest Formation and the Hemlock-Hardwood Association of northern New England (Oosting 1956), and the dropping-out pattern suggests that these

species are more or less individualistically distributed over the elevational gradient. Some species may behave as couplets or triplets or as commodia (Whittaker 1956), but this is hard to assess because of incomplete information on the species behavior on different slope inclinations, aspects, soils, and so forth.

Observations on abandoned fields in north-central New England suggest that successional tree species are distributed according to an individualistic pattern. For example, on well-drained sites along the highway from Manchester, New Hampshire (ca. 152 m, 500 ft), to just north of Franconia Notch, New Hampshire (ca. 488 m, 1,600 ft), old-field dominants change gradually with increasing altitude and distance northward. At the lowest part of the gradient, *Betula populifolia*, *Pinus strobus*, and *P. rigida* are common. Northward and upward, *P. rigida* tends to drop out. Farther along, *P. strobus*, *B. populifolia*, *Picea rubens*, and *Abies balsamea* are found together in old fields. At still higher elevations, *B. populifolia* loses aggressiveness, and fields with *Picea rubens*, *A. balsamea*, *Larix laricina*, and *P. strobus* are found. Spruce, fir, and larch tend to behave as dominants in old fields at the higher elevations (> 457 m, 1,500 ft), and white pine loses its aggressiveness. *Populus tremuloides* is seen all along the transect. In the natural vegetation zones of New England (Westveld et al. 1956) a similar pattern in the distribution of successional trees is seen when pioneering species in adjacent zones typical of northern New England are compared.

Our data collected along a 245-m elevational gradient in watershed 6 also suggest that tree species are distributed individualistically along such a gradient. *Acer saccharum* declines rapidly in importance toward the highest elevations and appears to be nearing its altitudinal limit at the summit of the watershed (791 m). *Fagus grandifolia* shows a similar trend, but probably maintains itself as an important vegetational component even at somewhat higher elevations than 791 m. Our data on *Betula alleghaniensis* Brit., *Acer pensylvanicum*, *A. spicatum*, and *Picea rubens* yield little information on individualistic distributions along the elevational complex gradient except that their distributional ranges encompass the entire watershed, with the latter species more abundant at upper elevations. *Abies balsamea*, *Betula papyrifera*, and *Pyrus americana* become increasingly important toward the highest elevations both in the tree and in the reproductive layers. The few trees of *Fraxinus americana* and *Tsuga canadensis* reach their uppermost limit at about 600 m in watershed 6. Because of the limited range of these elevation studies, individual-

istic distributions cannot be confirmed for all species. A basic point is documented, however: that major deciduous components of forest do not simultaneously drop out as important components of the vegetation at the 762-m (2,500-ft) elevation recognized by most authors as the approximate transition from northern hardwood forest to boreal forest (Fig. 9). Ash and hemlock tend to drop out at elevations well below this altitude; beech and sugar maple at this altitude; and yellow birch and striped and mountain maple above this altitude. This order of relationships holds throughout the Hubbard Brook Valley.

In a gradient analysis of the vegetation over a range of elevations from 914 m (3,000 ft) to 1,372 m (4,500 ft) on Whiteface Mountain in New York, Nicholson (1965) concluded that peaks of species distribution of commodia did not coincide with the maximum expression of community types. For complex elevational gradients and slope-aspect gradients, Nicholson concluded that natural populations are distributed normally along complexes of gradients.

Siccama (1968), in a study of the vegetation of the west slope of the Green Mountains in Vermont between 549 m (1,800 ft) and 1,158 m (3,800 ft), found a distribution of tree species similar to that at Hubbard Brook and to others reported for New England and New York. Siccama found that the rate of change in forest composition and structure per unit of linear distance markedly increased between 762 m (2,500 ft) and 914 m (3,000 ft). The changes in forest characteristics in the Hubbard Brook watershed also are more or less linear between 546 m and 732 m, and the rate of change increases markedly above 732 m (Fig. 4, 5, 7). Siccama correlated the rather abrupt increase in rate of biological change between 762 m (2,500 ft) and 914 m (3,000 ft) with abrupt changes in meteorological phenomena: length of growing season, snow duration, hoar frost, and frequency of cloud envelopment. Siccama points out that these are not local, but phenomena that may act over a wide area in northern New England. These meteorological factors may be coupled with a geological factor, thinner glacial till which begins between 762 m (2,800 ft) and 945 m (3,100 ft) in the Green Mountains, to bring about a markedly steepened environmental gradient (Stewart 1961, Siccama 1968).

The steeply increasing rate of environmental change generates a tendency toward vegetational discontinuity along the elevational gradient in the range of about 762–914 m (Scott and Holway 1967, Siccama 1968). Vegetation of this zone is characterized by rapidly changing importance of tree species. As previously noted, the only gen-

erally agreed-upon elevation characterizing the zonations of earlier authors is about 762 m (Fig. 9).

The evidence currently available indicates that the vegetation of northern New England is composed of a system of interacting populations, and the balance among populations shifts with change in environment so that vegetation is a pattern of populations corresponding to the pattern of environmental gradients (Whittaker 1953). In New England the major environmental complex gradients, elevation and latitude, play an important role in shaping the regional vegetation pattern. The altitudinal effect is clearly seen in the mountainous regions where the loss and acquisition of species as one moves along elevational gradients of several hundred meters produce the zonal patterns described by various authors. These zones are characterized by changes in the composition or predominance of dominant species. This situation is clearly reflected in the nomenclature proposed by the Society of American Foresters Committee on Silviculture for the often contiguous vegetation zones of New England (Westveld et al. 1956): spruce-fir-intolerant hardwoods, spruce-fir-northern hardwoods, northern hardwoods-hemlock-white pine, transition hardwoods-white pine-hemlock, central hardwoods-hemlock-white pine, and central hardwoods-hemlock. Contrary to the findings of Wells (1960) in his study of the intergradation of vegetation at lower elevations in the mountains of southwestern Utah, our study and the general concept of regional vegetation in northern New England show extensive and intimate intergradation of physiognomically different life forms, i.e., needle-leaved evergreen and broad-leaved deciduous species.

The effect of latitude on the vegetation of New England is hard to separate from the effect of other variables, but it is probably important in determining the generally east-west arrangement of vegetation zones in the topographically lower regions of New England (Fig. 1 in Westveld et al. 1956) and in the elevation at which transitions between zones occur. Transitions between zones are found at progressively higher elevations toward the south. For example, the approximate lower limit of spruce-fir forest on Mt. Katahdin, Maine, is 152 m (500 ft); in the White Mountains it is 762 m (2,500 ft); and in the Catskills, New York, it is 1,067 m (3,500 ft) (Oosting 1956).

Emphasis on elevational and latitudinal effects does not imply that other factors do not also contribute to the regional vegetation pattern of New England. *Abies balsamea* exhibits an east-west morphological response associated with increasing aridity toward the interior of the continent (Myers

and Bormann 1963). Such a gradient may affect, in a more subtle way, the vegetation of New England. Other factors are responsible for the disjunct spruce-fir forest along the coast of central Maine, and there are numerous examples of the effects of topography, geology, and drainage.

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