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THE HUBBARD BROOK ECOSYSTEM STUDY: PRODUCTIVITY, NUTRIENTS, AND PHYTOSOCIOLOGY OF THE HERBACEOUS LAYER[1, 2]

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Abstract

The herb and shrub layers of the control northern hardwood forest ecosystem at Hubbard Brook contain 96 species of plants. This ecosystem, 13.2 ha in size, has a southeast-facing aspect, an average slope of 26%, and an altitudinal range of 545 to 791 m. Vascular cryptogams, woody saplings, shrubs, tree seedlings, and herbaceous phanerogams contributed 38%, 22%, 18%, 13%, and 8% respectively to the aboveground current growth in the herb-shrub layer. Ninety-three per cent of the current growth was localized in eight species in the 1966 summer growth aspect. *Dryopteris spinulosa, Viburnum alnifolium, Acer saccharum,* and *Fagus grandifolia* contributed 67% of the cover in the herb layer, and, respectively, made up 70% of the current growth of herbs, 83% of shrubs, 61% of tree seedlings, and 90% of saplings. For the ecosystem as a whole, the herbaceous layer contained 1.8 kg/ha K, 0.3 Mg, 0.3 Ca, 0.1 S, 0.09 Mn, 0.007 Fe, 0.008 Zn, 0.001 Na, and 0.001 Cu in the aboveground current growth. The herb-shrub layer responded in several ways to the elevational complex gradient. Species diversity increased by 50% and productivity tripled in the higher portions of the ecosystem coincident with a decrease in the productivity of the overstory. Increased productivity in the herb-shrub layer resulted from more luxuriant growth of species distributed throughout the ecosystem rather than from increased species diversity. Based on a phytosociological comparison of sites occurring at similar elevations but under different geological conditions, the Hubbard Brook ecosystem is placed near the oligotrophic end of a nutrient scale for northern hardwood forest ecosystems in the mountains of New England.

Introduction

The goal of the Hubbard Brook ecosystem study is the quantification of energy and nutrient relationships for both undisturbed and man-manipulated northern hardwood forest ecosystems (Bormann and Likens 1967, Bormann et al. 1968, 1970, Bormann, Likens, and Eaton 1969, Likens et al. 1967, 1970, Likens, Bormann, and Johnson 1969, Johnson et al. 1968, Fisher et al. 1968). The study centers around the use of the small watershed technique and the ecosystem concept (Bormann and Likens 1967).

The study has focused on six small, adjacent watershed ecosystems operated and maintained by the U. S. Forest Service. These are southeast-facing watersheds within the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. Watershed 6 (W-6) is used as a control watershed for the Hubbard Brook study. It is 13.23 ha in area, ranges in elevation from 546 to 791 m, and was cut over between 1909 and 1917.

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The lower two-thirds of watershed 6 are forested with uneven-aged northern hardwoods (*Acer saccharum,* sugar maple, *Fagus grandifolia,* beech, and *Betula alleghaniensis* Britt., yellow birch). The upper third, although still dominated by hardwoods, is somewhat more heterogeneous with species of the boreal forest (*Picea rubens,* red spruce, *Abies balsamea,* balsam fir, *Betula papyrifera,* paper birch, and *Pyrus americana,* mountain-ash) much more abundant (Bormann et al. 1970). The forest is typical in species composition and structure of northern hardwood forests in the altitude range of 500–900 m throughout the White Mountains of New Hampshire, Green Mountains of Vermont, and Adirondack Mountains in New York (Bormann et al. 1970).

Gradient analysis of the tree vegetation in watershed 6 indicated a strong response to the elevational gradient. The distribution and abundance of tree species shifted with elevation. Basal area, basal area per tree, deciduousness, and productivity decreased with increasing elevation while density, per cent evergreenness, and species diversity increased (Bormann et al. 1970). Phytosociologic analyses and comparisons with other forest stands, based on tree vegetation alone, indicate that the vegetation of watershed 6 is part of a vegetational gradient covering the upper part of the spruce-northern hardwood zone (Braun 1950) and the lowest part of the Boreal Forest Formation (Oosting 1956). The rate of vegetational change along this gradient is not linear, however, but is steepest over the upper third of the watershed.

This paper deals with the herb-shrub stratum of watershed 6, i.e., herbaceous vascular plants $\leqq 0.5$ m high plus shrubs and tree saplings. Although productivity and nutrient uptake of this stratum are small in comparison to the tree stratum, the herb-shrub stratum may be especially important in food chains for mammals and birds and is potentially subject to major modification by large grazing herbivores (Stearns 1951). Also, energy and nutrient conditions in this stratum determine the success or failure of the reproduction of potentially dominant tree species. Objectives of this paper are: (1) to characterize the biomass, nutrient, and phytosociologic parameters of the herb-shrub stratum; (2) to determine the effect of the elevational complex gradient (Bormann et al. 1970) on the behavior of herb, shrub, and tree species (seedlings and saplings) and on productivity-nutrient parameters; (3) to evaluate the effect of topographic variables such as aspect and slope inclination on phytosociological and biomass-nutrient parameters; and (4) to establish the position of Hubbard Brook in the regional vegetation matrix by a comparative evaluation of the herbaceous stratum from northern hardwood stands throughout northern New England.

The study was carried out in July and August of 1966 and 1967, hence these data represent the summer aspect of the herb layer. The strongly developed spring aspect has yet to be studied in terms of productivity and nutrient parameters. Details on climate, soil, geology, topography, and hydrology of the Hubbard Brook Experimental Forest may be found in Likens et al. (1967). Nomenclature follows Fernald (1950) unless authorities are given.

METHODS

Watershed 6 was surveyed into 208 25- by 25-m units (Bormann et al. 1970). One 1- by 1-m plot was randomly selected from each unit. Coverages of herbs and woody plant seedlings, individuals < 0.5 m in height, were estimated on each plot. Coverages of tree saplings, individuals $\geqq 0.5$ m in height and < 2 cm dbh, and taller shrubs were not estimated because of the difficulty in projecting the crown image onto the plot. On each plot the per cent cover of exposed rocks, open space in the herb layer, fallen tree trunks, non-vascular cryptogams, and exposed roots or tree stumps were estimated. The one to three tree species contributing most of the litter to the plot were recorded on the basis of overstory canopy projections on the area around the plot.

Elevation, slope inclination, and aspect of each plot were recorded and each plot was assigned a moisture rating from 3 (relatively dry) to 13 (relatively wet) according to a scalar described earlier (Bormann et al. 1970). Aspect (slope exposure azimuth) was measured on only 195 plots. Plots with less than 2.25° (5%) slope were not assigned an exposure angle.

Current growth of shoots of herbs, seedlings, saplings and shrubs on each plot was clipped and bagged by species. Species with $< 1\%$ cover were lumped and bagged together. Current growth of herbs included the whole shoot, whereas that of woody perennials included only leaves and current twigs. Thus estimates of productivity do not include root production and some production of wood and bark by perennial shoots. Studies of shrubs in the Great Smoky Mountains and the Long Island pine-oak forest estimate current twig and leaf production to be 34 to 70% of total aboveground production (Whittaker 1966, Whittaker and Woodwell 1968). A few hours after collection clippings were ovendried for 24 hr at 105°C. Dry weight was obtained to the nearest .01 g. Sampling was done during July 1966.

Since structure and composition of the vegetation on the watershed ecosystem are strongly influenced by elevation, plot data for some analyses were grouped in three contiguous elevational subdivisions approximately equivalent to those reported in the analyses of tree vegetation of watershed 6 (Bormann et al. 1970) and those used by R. H. Whittaker in dimension analyses of tree populations (*unpublished data*). The lower subdivision, 545–648 m, contained 70 plots, the middle subdivision, 648–721 m, contained 68 plots, while the upper subdivision, 721–791 m, had 70 plots. Subdivisions included about equal areas of the watershed.

Samples of herbs for chemical analyses were collected within each of the subdivisions on July 24 and 25, 1967. Samples were limited to 29 species (two of which had not been recorded on the plots) that yielded at least an estimated 30 g of ovendry weight within a maximum of 30 minutes of searching on any single subdivision. Abundant species such as *Dryopteris spinulosa* were collected by taking material irregularly through the subdivision. Less common species were collected in quantity where they could be found.

To obtain information on the variation in chemical concentrations in the various species and to allow a midsummer and late summer comparison, five replicate samples of six major herb species were collected from the lower subdivision on September 7, 1967.

Samples for chemical determinations were stored at a temperature of about —18°C in plastic bags immediately after collection. Approximately two months later, samples were removed and dried 48 hr at 80°C and ground in a Wiley Mill to pass a 20-mesh stainless steel sieve. Ground material was placed in chemically clean glass bottles, dried an additional 72 hr at 80°C, capped and stored in a refrigerator at about 2°C. Throughout the collection and grinding procedure plastic gloves were used to minimize chemical contamination. A representative 2-g sample of ovendry plant tissue was ashed at 500° ± 20°C for one hour in a silica crucible, dissolved in hot 6N HCl and filtered. Ca, Mg, K, Na, Cu, Mn, Zn, and Fe were determined on the filtrate with a Perkin-Elmer model 303 atomic absorption spectrophotometer. Orthophosphate was determined colorimetrically by the aminonaphtholsulfonic acid method with a Bausch and Lomb spectrophotometer. Nitrogen and S analyses were done on separate samples according to the methods given in the 10th edition of the Official Methods of the Association of Agricultural Chemists, 1965. A detailed description of the procedures used in the chemical analysis of plant tissues is in preparation by Likens and Bormann.

RESULTS AND DISCUSSION

Phytosociology and its relation to environmental variables on watershed 6

The vascular flora of watershed 6 contains 96 species (31 families): 71 herbs, 14 trees and 11 shrubs (Table 1). Thirty-seven of the herbs, all but hemlock of the tree species, and all but one of the shrub species occurred on at least one sample plot.

Dominant species in the herb layer were *Dryopteris spinulosa, Viburnum alnifolium, Acer saccharum* and *Fagus grandifolia* which together contributed 67% of the total cover. Total unoccupied space in the herb layer was 64% and total cover was 36%. Total projected cover in an older northern hardwood forest in Vermont at about the same elevation but on a mull soil was 49% (Bormann and Buell 1964). Importance values for herbaceous species, based on the sum of relative weight of current growth and relative cover percentage on the 185 plots where herbs occurred, indicated *Dryopteris spinulosa* to be the most important species on 95 plots. *Maianthemum canadense* was the second most important herbaceous species (dominant on 12 plots) with *Oxalis montana* (dominant on nine plots) the third ranking species.

Although slope inclination, aspect and canopy cover had various effects on species and stand characteristics of the herb layer, stand characteristics were most strongly correlated with the elevational complex gradient (Whittaker 1967). Although there were many trends in the responses of vegetation variables with respect to site factors other than elevation, the limited ranges of these conditions on watershed 6 and the small number of plots in some categories precluded effective separation of interactions between variables.

Slope inclination ranged from 0° to 28° (63% slope) with eight of the 208 plots on level ground (seven of these were in the upper subdivision). The average slope inclination of the watershed was 13° (29% slope) with a maximum of 15° (33% slope) in the middle subdivision and a minimum of 11° (26% slope) on the upper subdivision. Slope inclination was positively correlated with the per cent rock cover and the nonvascular cryptogam cover, but there were no significant correlations of slope inclination with herb, seedling, or sapling weight, cover, or number of species per plot.

Aspect was significantly and positively correlated with the per cent of unoccupied space in the herb layer and negatively with the cover percentage of the herbs and seedlings. Plots ranging in aspect from 50° to 150° (NE to SSE) had an

TABLE 1. Cover percentages, frequencies and biomass of aboveground current growth on watershed 6. Cover and frequencies are based on the herb layer only (i.e. < 0.5 m high). Biomass includes both the herb layer and shrub layer (i.e. < 2 cm dbh). Space unoccupied by the projected cover in the herb layer equals 64%. Data are given by elevational thirds and for the watershed as a whole

	Lower subdivision			Middle subdivision			Upper subdivision			Whole watershed		
	Cover	Freq.	Wt.	Cover	Freq.	Wt.	Cover	Freq.	Wt.	Cover	Freq.	Wt.
Species	(%)	(%)	kg/ha± SE	(%)	(%)	kg/ha± SE	(%)	(%)	kg/ha± SE	(%)	(%)	kg/ha± SE
Trees												
Acer pensylvanicum	1.4	77.1	2.4±0.6	1.1	79.4	2.4±0.9	0.5	44.3	0.4± 0.2	1.0	66.8	1.8±0.4
A. saccharum	10.5	92.9	25.6±4.3	3.8	80.9	7.9±1.8	0.6	30.0	2.9± 1.6	5.0	67.8	12.0±1.8
A. spicatum	1.0	28.6	1.5±0.7	0.8	35.3	1.4±0.8	1.1	48.6	3.6± 1.5	1.0	37.5	2.2±0.6
Fagus grandifolia	4.5	70.0	34.6±6.8	3.7	76.5	45.7±9.5	1.3	48.6	37.3±11.8	3.1	64.9	39.1±5.5
Shrubs												
Rubus spp.	0.6	7.1	1.3±0.8	0.4	8.8	1.2±0.8	2.1	17.1	9.9± 4.7	1.0	11.1	4.1±1.6
Viburnum alnifolium	7.3	32.9	23.0±7.2	5.6	36.8	20.5±7.4	6.3	37.1	33.1±11.1	6.4	35.6	25.5±5.1
Herbs												
Aster acuminatus	0.5	10.0	0.5±0.3	0.5	5.9	0.5±0.3	0.6	7.1	1.2± 0.7	0.5	7.7	0.7±0.3
Clintonia borealis	0.2	11.4	0.4±0.2	0.3	16.2	0.5±0.2	1.1	31.4	2.2± 0.7	0.5	19.7	1.1±0.3
Cornus canadensis	—	—	—	—	—	—	0.5	4.3	0.7± 0.5	0.2	1.4	0.2±0.2
Dennstaedtia punctilobula	1.6	5.7	2.7±1.5	0.7	8.8	0.9±0.4	3.7	12.9	15.5±11.0	2.0	9.1	6.4±3.8
Dryopteris noveboracensis	0.2	2.8	0.4±0.3	0.3	5.9	0.4±0.2	0.6	2.9	1.0± 0.8	0.4	3.8	0.6±0.3
D. spinulosa	8.0	60.0	26.8±6.6	8.9	55.9	35.4±7.8	21.7	74.3	92.0±13.3	12.9	63.5	51.6±5.9
Lycopodium lucidulum	0.8	27.1	2.1±0.7	0.2	19.1	0.7±0.4	0.4	22.9	2.4± 1.2	0.5	23.1	1.7±0.5
Maianthemum canadense	0.5	10.0	1.3±0.7	0.6	19.1	1.0±0.4	3.3	62.9	6.0± 1.0	1.1	30.8	2.8±0.5
Oxalis montana	1.2	34.3	1.7±0.5	1.1	25.0	1.4±0.7	3.4	51.4	3.7± 1.0	1.9	37.0	2.3±0.4
Solidago macrophylla	—	—	—	—	—	—	0.5	8.6	0.8± 0.5	0.2	2.9	0.3±0.2
Trientalis borealis	—	—	—	T	1.5	T	0.5	15.7	0.4± 0.2	0.1	5.8	0.2±0.1
Uvularia sessilifolia	0.7	7.1	1.4±0.9	0.3	7.4	0.4±0.4	1.3	7.1	1.7± 1.0	0.8	7.2	1.2±0.5
Total herb cover	16.2			15.3			40.2			24.0		
Total seedling cover	25.4			15.2			10.4			17.0		

Species present on the watershed with $<.05$ % cover in the herb-shrub layer:

Trees

Abies balsamea, Acer rubrum, Betula alleghaniensis, B. papyrifera, Fraxinus americana, Picea rubens, Prunus pensylvanica, P. virginiana, Pyrus americana, Tsuga canadensis.

Shrubs

Lonicera canadensis, Cornus alternifolia, Ribes glandulosum, Rubus alleghaniensis, R. canadensis, R. idaeus, R. pubescens, Sambucus canadensis, S. pubens.

Herbs

Actaea pachypoda, Agrostis alba, Aralia nudicaulis, A. spinosa, Arisaema atrorubens, Athyrium filix-femina, Carex annectens, C. arctata, C. blanda, C. brunnescens, C. commun[illegible]*nia caroliniana,* [illegible] *Galeopsis tetrahit,* [illegible] *uniflora, Osmund*[illegible] *norvegica, Prenanthes altissima, P*[illegible]*um viride, Viola incognita, V. rotundifolia.*

average cover of 47% while those ranging from 150° to 250° (SSE to WSW) had an average cover of 38%. (These values include the overlap of the foliage and therefore exceed the value given previously for total projected cover for the watershed as a whole.)

The correlation of species diversity (number of species/m^2) with increasing exposure angle was not significant at the 0.05 level, but the sign was negative for total number of species, number of herb species, and number of seedling species indicating at least that there may be a decreasing trend in species diversity on watershed 6 from east- to west-facing exposures. It has been noted that species diversity on southwesterly exposures in northern New England and New York is relatively lower than on northeasterly exposures at similar elevations (B. W. Post, *personal communication;* Nicholson 1965). Average exposure angle of watershed 6 was 156° and there were only a few degrees difference between the average exposure angle within the three subdivisions.

On 12 herb plots where tree canopy coverage over the plot was less than 75%, average weight of current growth was 27.8 g/m^2 and the number of species was 7.8 species /m^2 as compared to an average for the entire watershed of 7.7 g/m^2 and 6.1 species/m^2 respectively. This response might be expected as there is more light reaching the herb stratum and less competition with the trees for water and nutrients (Anderson, Loucks, and Swain 1969).

Exposed rock occurred on 85 plots and ranged from 1 to 90% in cover. On the average, exposed rock occupied about 6% of the surface area of the watershed with a range of 6 to 7.5% between the three subdivisions. Bormann and Buell (1964) also reported 6% rock cover in a similar forest in

Vermont. Fallen trees, exposed roots and tree stumps occupied about 8% of the area of the forest floor in watershed 6. There were striking differences between the upper subdivision and the lower two subdivisions with respect to the diversity of source of tree litter. Plots of the lower two subdivisions received litter almost wholly from beech, sugar maple and yellow birch. On the upper subdivision mountain maple (*Acer spicatum*), white birch and red spruce were recorded as contributors to the litter of the plots almost as many times as beech, maple and yellow birch.

The most striking vegetational variation was associated with the elevational complex gradient. Species diversity (number of spp./m^2) in the herb layer (seedlings, saplings, shrubs, herbs) averaged 6.1 for the whole watershed with shrub and tree seedling and sapling diversity more or less constant over the elevation range. However, herb diversity showed about a 50% increase in the upper third of the watershed (2.5 for each of the lower thirds vs. 3.8 for the upper third). Diversity of tree species in the overstory (spp./100 m^2) also increased from 3.6 to 6.1 (Bormann et al. 1970). Although total cover of all species in the herb layer was positively correlated with elevation, the correlation of tree seedling cover with elevation was negative. R. H. Whittaker (*personal communication*) reports increases in herb cover with elevation in the Siskiyou Mountains and in the Great Smoky Mountains. Total weight of current growth of herbs was positively correlated with elevation.

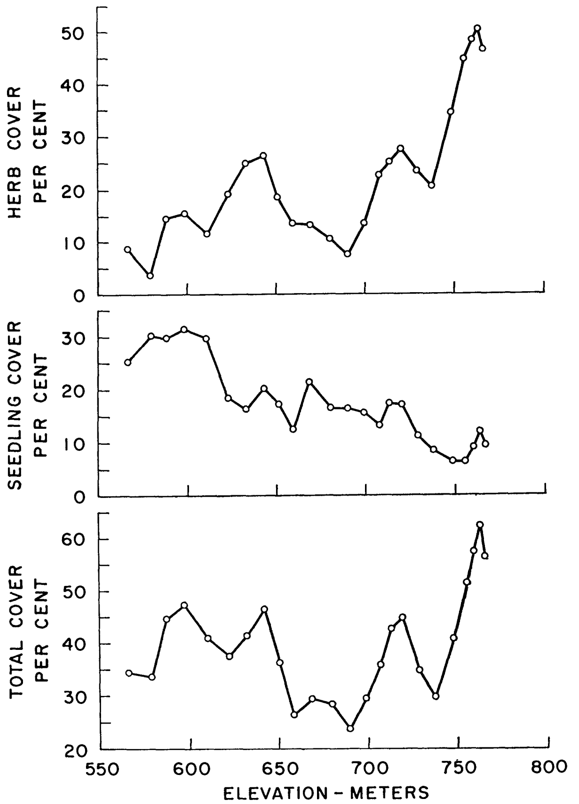

FIG. 2. Running averages of herb, seedling and total cover in the herb layer along the elevation gradient of watershed 6. Units of the running average are as in Fig. 1.

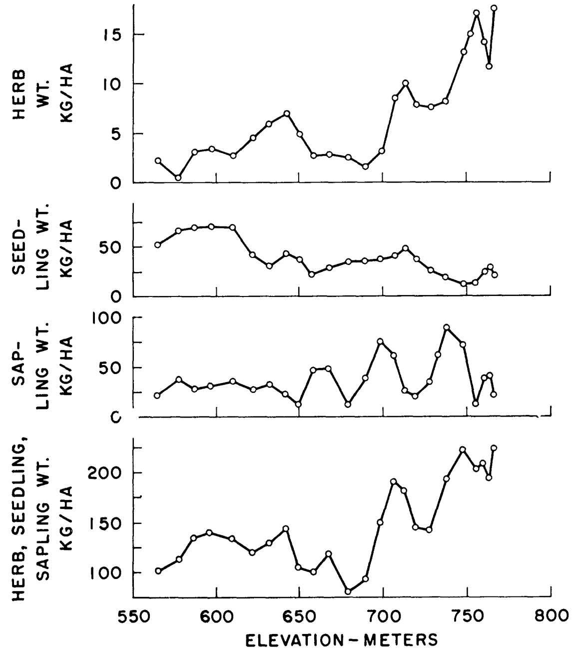

FIG. 1. Running averages of herb, seedling and sapling weight of aboveground current growth along the elevation gradient of watershed 6. The units of the running average are 30.5-m altitudinal bands with a 7.6-m increment.

Weight of current herb growth and herb cover along the elevational gradient show a rather abrupt increase associated with the shoulder of the ridge (Fig. 1, 2). Apparently this point, about 700 m, marks the beginning of a much-steepened environmental gradient. This elevation marks the transition from predominantly hardwood forest to evergreen boreal forest in many systems of vegetation classification applicable to New England (Siccama 1968, Bormann et al. 1970).

Herb species contributing significantly to the weight of current growth on watershed 6 may be most abundant at elevations equal to or above the elevational limits of watershed 6 (Siccama 1968). Thus the patterns seen in watershed 6 may represent the tails of distributions of herb species whose peaks occur at higher elevations in the mountains of the region.

Productivity

Of five growth-form groups present on the watershed, vascular cryptogams contributed 37%

TABLE 2. Summary of ovendry weight (kg/ha) of aboveground current growth by several growth-form groups in the combined herb-shrub layer on watershed 6

Elevation range	545–648	648–721	721–791	545–791
Number of plots	70 plots (m²)	68 plots (m²)	70 plots (m²)	208 plots (m²)
Herbs				
Cryptogams	32.4(7)*	37.8(6)	111.7(5)	60.8(8)
Phanerogams	8.4(18)	7.8(20)	21.4(20)	12.6(20)
Subtotal	40.8	45.6	133.1	73.4
Woody				
Shrubs	25.1(6)	22.6(6)	42.2(4)	30.0(10)
Seedlings	37.4(6)	18.7(6)	8.5(4)	21.6(13)
Saplings	28.5(5)	38.6(3)	41.1(7)	36.1(9)
Subtotal	91.1	79.9	92.2	87.7
Lumped weight category	0.9(13)	1.2(12)	0.7(16)	0.9(23)
Grand total	132.8	126.6	226.0	162.1

*Number of species on plots.

of the aboveground current growth in the combined herb-shrub layer. Woody saplings (22%), shrubs (18%), tree seedlings (13%), and herbaceous phanerogams (8%) followed in that order.

Productivity of the herb-shrub layer showed a marked increase with increasing elevation. The weight of current growth on the upper subdivision (226 kg/ha) was approximately double the weight on the lower and middle subdivisions (133 and 127 kg/ha respectively). Aboveground current growth production in the herb-shrub layer averaged, for the entire watershed, 162 kg/ha including 0.9 kg/ha for species in the lumped weight category (Table 2).

Herbaceous vascular cryptogams contributed about 27% of the total weight on the lower two subdivisions and about 50% on the upper subdivision (Table 2). *Dryopteris spinulosa* contributed 85% of the weight of current growth of the cryptogam group (which included eight species) and about 70% of the total weight of the herbs on the watershed (vascular cryptogam group plus herbaceous phanerogam group) (Tables 1, 2).

Herbaceous phanerogams (Table 2) contributed less than 10% of the total current growth in the herb-shrub layers of watershed 6 (6.4%, 6.2% and 9.5% in successively higher subdivisions). *Oxalis montana* made the greatest contribution to the current growth of the herbaceous phanerogam group in the lower two subdivisions of the watershed (1.7 and 1.4 kg/ha). In the upper subdivision, *Maianthemum canadense* was the largest contributor (6.0 kg/ha) and *Oxalis montana* was second (3.7 kg/ha). The three leading species (*Oxalis montana, Maianthemum canadense* and *Uvularia sessilifolia*) contributed about 50% of the herbaceous phanerogam weight with about equal percentages (51, 43 and 56%) in the successively higher subdivisions (Table 1).

A total of 73 kg/ha aboveground herb current growth at Hubbard Brook compares with 380 kg/ha in Great Smoky Mountain Cove Forest, 79 kg/ha in Great Smoky Mountain pine-oak forest, 170 kg/ha in Great Smoky Mountain pine heath, and 22 kg/ha for Long Island oak pine forest (Whittaker and Woodwell 1969). H. Art (*personal communication*) reports a total of 121 kg/ha for the Fire Island, N.Y., maritime forest.

Viburnum alnifolium contributed over 90% of the current growth of shrubs in the lower two subdivisions (23 kg/ha and 21 kg/ha respectively). In the upper subdivisions this was reduced to 78% with *Rubus* spp. contributing most of the remaining weight. Total shrub current growth of the lower two elevation subdivisions was rather similar (25 and 23 kg/ha) and only about half of the weight, 42 kg/ha, on the upper subdivision (Table 2).

There was a striking change in productivity of seedlings and saplings in relation to elevation. This group contributed about 50% of the total weight of all groups in the lower subdivisions (66 and 57 kg/ha respectively), but only 23% in the upper subdivision (Table 2). *Acer saccharum* was the leading seedling species in the lower subdivision (23 kg/ha or 61% of the seedling weight). In the middle and upper subdivision *Fagus grandifolia* had the largest weight in the seedling size group (8 kg/ha or 44% and 4 kg/ha or 43% respectively).

Fagus grandifolia contributed the largest proportion of the sapling current growth in each subdivision with 24, 38 and 34 kg/ha, accounting for about 90% of the total weight of this group. Many of the *Fagus grandifolia* stems included in this sample were root sprouts, probably still connected to the parent tree. The future success of these beech saplings is unknown, but if the current trends continue beech will become increasingly important in the stand (Bormann et al. 1970).

Weight of the current growth of the herbs (cryptogams and phanerogams) in the upper subdivision was greater by a factor of about three over the lower subdivisions (Table 2). However, herb species composition changed very little along the altitudinal gradient. Five herb species present in the plots of the lower subdivision were not recorded on the upper subdivision and eight species not recorded on the lower subdivision were found on the upper one. In all, 16 species were recorded in the lower and 20 in the upper subdivision. Changes in species composition involved species with small weights of current growth. Thus, differences in productivity on the upper subdivision are due primarily to the increased abundance and vigor of the same species which are dominant in the lower subdivisions.

The success of the herbs on the upper subdivision presents an interesting problem. The increase in herb productivity is correlated with a decrease in productivity of the overstory (Bormann et al. 1970). This suggests that environmental conditions at the higher elevation are relatively adverse to the growth of the largest growth forms, but favorable to the herbaceous growth form. Vegetation on the upper subdivision differed markedly from that on the lower two subdivisions which were rather similar. There was an obvious, rapid change in the canopy vegetation over a short distance of ground surface beginning at about 700 m elevation (Bormann et al. 1970). The causes of this steepened vegetation gradient have not been clearly defined, but are probably related to: (1) a steeper slope just below the shoulder of the ridge and reduced slope above the shoulder of the ridge; (2) reduced depth of till; (3) increased moisture due to absence of well-defined stream channels and reduced slope; and (4) wind effects on the overstory canopy (Gosz, *personal communication*). At similar elevations in the Green Mountains quite striking changes were noted in soil characteristics. These included increased soil acidity, lower total amounts of exchangeable soil nutrients, and greater amounts of soil organic matter (Siccama 1968).

Increased light intensity at the level of the herb layer may also occur in those portions of the upper subdivision dominated by deciduous species due to a lower and more irregular canopy cover (seven of the eight plots with less than 100% canopy cover occurred on the upper subdivision). Gosz (*personal communication*) reports increased branch and twig breakage at upper elevations due to more frequent ice storms. Herb productivity was observed to be much reduced beneath the dense conifer forest which occurs locally on the upper subdivision. Total current growth in the herb layer on the upper subdivision was negatively correlated to the combined importance value of sugar maple, beech, yellow birch, spruce and fir but positively correlated to the combined importance of tree species which commonly have a shrubby habit at these elevations (mountain ash, mountain maple, stripled maple and white birch).

The net effect of the above factors serves to restrict the productivity of the tree stratum at the upper elevations in watershed 6. The herb stratum, which is much less affected by climatic extremes found at tree-top levels, apparently has more available resources in terms of light, nutrients and water. This response parallels that observed by Anderson et al. (1969) in coniferous forests in Wisconsin.

Current growth in the herb and shrub strata of Hubbard Brook is below that reported for generally similar (mesic) forest stands in the Great Smoky Mountains (Whittaker 1966). Comparable southern stands, hemlock-mixed forest and gray beech forest in north- and south-facing gaps, had from two to seven times as much current growth of herbs as Hubbard Brook. It is of special interest that *Dryopteris spinulosa* comprised a major part of the weight of the current growth of herbs in the southern stands as it does in the northern stands.

A good correlation was found between the sum of the cover percentages of the herbs and seedlings on square-meter plots and the sum of the weight

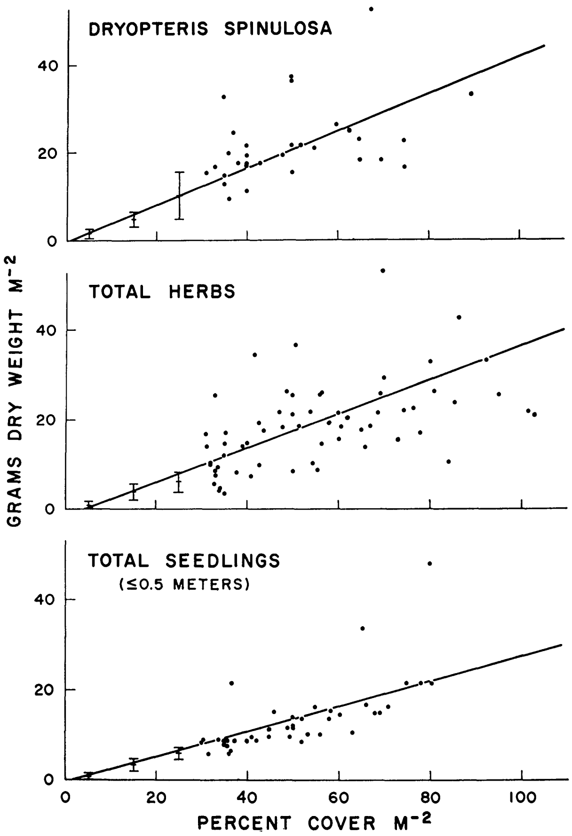

FIG. 3. Relationship between cover percentage and weight of aboveground current growth of *Dryopteris spinulosa,* total herbs, and total seedlings based on 1- by 1-m plots. Points in the 0–10, 10–20 and 20–30% cover range have been grouped and are illustrated by the mean ± SE. Equations for the lines are as follows: *Dryopteris spinulosa* $Y = -0.423 + 0.420X$ ($R = 0.87$); total herbs $Y = -1.766 + 0.386X$ ($R = 0.83$); seedlings $Y = -0.572 + 0.280X$ ($R = 0.89$), where Y = grams of dry weight/m^2 and X = per cent cover on m^2 plots. Where more than one species is involved, cover is the sum of the cover percentages of the individual species.

of their current growth. Since cover percentages in the herbaceous layer may be estimated relatively easily in field studies (in comparison to measuring weight of current growth), the relationship may be used to gain a rough estimate of the weight of the herbs or seedlings from the sum of their cover percentage on square-meter plots (Whittaker 1966). Cover-weight relationships are shown for seedlings (185 points), herbs (177 points), and for the leading herb, *Dryopteris spinulosa* (Fig. 3). These equations are probably applicable for use in the spruce-northern hardwood forests of the uplands and mountain slopes of New England, New York, and adjacent Canada.

Whittaker (1966) developed a regression, based on 16 forest stands in the Great Smoky Mountains, expressing the relationship between herb cover and herb weight. This equation was $Y = 0.082 + 0.360X$, where Y = clipping weight in grams per square meter and X = total cover of herbs on a square meter plot.

Our equation for predicting herbaceous productivity from cover (Fig. 3) was compared to the one for the Great Smoky Mountains. Whittaker's equation applied to Hubbard Brook cover data overestimated the herb weight by 12% while the equation derived at Hubbard Brook and applied to herb cover data from the Great Smoky Mountains underestimated herb weight in the southern stands by 3%. The closeness of the reciprocal predictions suggests that current growth production of the herb layer beneath a variety of forest types in the Appalachian region is predictable (within 10 to 20%) from the herb cover.

TABLE 3. Concentrations of elements in herbaceous species from watershed 6, based on July 1967 samples. Data from Wisconsin[a] and Canada[b] are included for comparison

Species	K (%)	N (%)	Mg (%)	Ca (%)	S (%)	P (%)	Mn (ppm)	Fe (ppm)	Zn (ppm)	Na (ppm)	Cu (ppm)
Athyrium filix-femina	3.04	2.53	0.38	0.81	0.19	0.18	221	179	44	20	14
" " (Wisc.)	3.06	1.43	0.39	0.88	0.08	0.38	82	274	31	—	6
Dennstaedtia punctilobula	2.03	2.82	0.24	0.21	0.22	0.18	1340	114	63	11	9
Dryopteris noveboracensis	2.78	2.38	0.42	0.54	0.31	0.17	1090	117	41	16	13
D. phegopteris	2.81	2.25	0.43	0.61	0.33	0.15	357	163	51	57	12
D. spinulosa	2.58	2.47	0.43	0.37	0.22	0.20	1370	81	104	16	14
Lycopodium lucidulum	1.41	2.01	0.12	0.06	0.17	0.10	296	218	36	22	8
Osmunda claytoniana	2.88	2.41	0.13	0.29	0.21	0.18	1050	54	64	12	8
Cryptogam mean[c]	2.44	2.43	0.33	0.43	0.22	0.16	764	148	57	24	11
Aralia nudicaulis	1.71	2.32	0.28	0.80	0.19	0.22	2668	105	74	12	9
" " (Wisc.)	2.25	1.90	0.34	0.97	0.11	0.30	601	149	37	—	63
Arisaema atrorubens	1.78	—	0.24	0.92	0.22	0.21	255	242	199	26	7
Aster acuminatus	2.92	2.14	0.30	0.67	0.18	0.19	2414	278	214	22	16
Carex intumescens	1.90	2.84	0.14	0.18	0.29	0.22	1037	122	77	13	19
C. leptonervia	3.23	2.86	0.15	0.26	0.22	0.15	666	272	93	14	27
Clintonia borealis	4.47	2.29	0.35	1.10	0.14	0.16	1159	271	48	26	20
" " (Wisc.)	5.54	1.76	0.28	1.19	0.09	0.31	320	426	429	—	5
Cornus canadensis	1.35	1.79	0.45	3.09	0.22	0.25	529	101	46	9	5
" " (Wisc.)	1.14	1.52	0.68	0.85	0.24	0.25	149	117	30	—	2
" " (Canada)	0.38	—	0.27	0.98	—	0.19	101	68	—	—	—
Galium triflorum	2.14	2.83	0.27	1.70	0.31	0.20	318	109	294	20	12
Maianthemum canadense	4.99	2.40	0.30	0.86	0.17	0.22	1444	136	88	11	8
Medeola virginiana	2.24	2.30	0.34	0.46	0.22	0.13	234	186	88	18	16
Mitchella repens	1.15	—	0.35	1.14	0.15	0.11	656	128	60	15	8
Oxalis montana	2.92	—	0.40	0.60	0.33	0.25	1330	302	84	29	10
" " (Canada)	0.79	—	0.19	0.44	—	0.21	869	170	—	—	—
Polygonatum pubescens	5.45	—	0.14	0.52	—	0.32	1558	117	64	17	17
Smilacina racemosa	2.73	2.26	0.20	0.99	0.17	0.13	620	136	44	9	8
" " (Wisc.)	3.57	1.82	0.22	1.32	0.13	0.33	146	229	22	—	5
Solidago macrophylla	5.38	2.58	0.41	0.98	0.18	0.31	3488	120	86	26	17
Streptopus roseus	3.39	2.00	0.28	0.81	0.15	0.15	1069	164	233	16	9
" " (Wisc.)	3.94	1.56	0.30	1.58	0.08	0.27	128	327	49	—	9
Trientalis borealis	3.03	2.02	0.44	1.16	0.13	0.17	485	129	36	13	8
Trillium erectum	3.21	2.47	0.22	0.77	0.15	0.15	764	119	75	10	9
T. undulatum	7.41	—	0.47	1.31	0.32	0.16	156	132	22	13	5
Uvularia sessilfolia	2.22	2.54	0.24	0.85	0.18	0.20	434	114	31	9	11
Viola incognita	3.68	3.22	0.83	0.78	0.26	0.22	1316	142	302	21	8
V. rotundifolia	4.69	2.76	0.47	0.64	0.23	0.12	526	514	398	40	9
Phanerogam mean[c]	3.41	2.37	0.33	0.84	0.20	0.19	1143	187	114	17	12

[a] Gerloff, Moore, and Curtis 1964.

[b] Gagnon et al. 1958.

[c] Mean based on individual samples which varied in number between species, thus the value given is not the mean of the column of figures given in the table. Mean based on Hubbard Brook data only.

Chemical analyses of the herbs

The quantitative data on the concentrations of elements in the aboveground tissues of 29 herbaceous species are summarized in Table 3.

Concentrations of each element per unit dry weight of herbaceous tissue (all species averaged) were very similar in the lower two subdivisions. However, for some elements there were marked differences between the lowest two subdivisions and the upper one. Phosphorus, Ca, Mg, and Mn occurred in higher concentrations in the tissues on the upper subdivision, while concentrations of Zn and Fe were lower above. These differences were large (at least 20%), but lack of replicate sampling prevented tests of statistical significance. These differences may reflect differences in soil chemistry at the different elevations, since in other regions concentrations of nutrients in herb tissues have been correlated with nutrient content of the A horizon (Gagnon, Lafond, and Amiot 1958). No striking differences between elevations were evident for the other elements (K, Ca, Na, S).

Comparison of the chemical analyses of material collected in July with September collections suggested either no significant change in chemical concentrations or a slight increase in September. Sampling procedures allowed establishment of confidence intervals for the September collections, but not for the July collections. Therefore, direct statistical comparisons were not possible. However, values for July collections were within the 95% confidence interval of September means 44 times whereas 15 of the July values were below the comparable September confidence limit and six were higher. Data for *Dryopteris spinulosa* are presented in Table 4. Similar data for *Aster acuminatus, Clintonia borealis, Dennstaedtia punctilobula, Lycopodium lucidulum,* and *Smilacina racemosa* are on file at Yale University and Cornell University. These comparisons suggest that material collected from midsummer through mid-September yield similar results and may be used to characterize the chemistry of the herbaceous layer adequately.

Relative to the cryptogams, tissues of phanerogams were found to have higher concentrations of P, Ca, K, Mn, Zn and Fe (at least 19% greater), whereas they were lower in Na (39%). There were no appreciable differences in Cu, Mg, S or N.

The greater abundance and diversity of flowering herbs on richer soils, plus the generally lower nutrient concentrations in the tissues of cryptogams, suggest that the success of cryptogams on the acid soils of New England mountain slopes may be due in part to lower nutrient requirements.

Table 4. Comparison of concentrations of elements in current growth of *Dryopteris spinulosa* collected on July 24 and September 7, 1967, on the lower subdivisions of watershed 6. September collections were replicated to allow computation of 95% confidence intervals (five replications)

Element	September		July
	Mean	±CI(95%)	
Potassium (%)	2.41	0.76	2.78
Nitrogen (%)	2.28	0.10	2.53
Magnesium (%)	0.36	0.11	0.46
Calcium (%)	0.34	0.12	0.38
Sulphur (%)	0.22	0.03	0.24
Phosphorus (%)	0.22	0.02	0.19
Manganese (ppm)	1830	206	1250
Iron (ppm)	107	10	56
Zinc (ppm)	106	17	85
Sodium (ppm)	18	2	15
Copper (ppm)	14	2	14

The large percentage of K in the herb tissues relative to other elements suggests selective absorption of this element or relatively more available K. Similar occurrences of large amounts of K were found in the herbaceous plants in Wisconsin (Table 3). The intrasystem cycle for K in the Hubbard Brook watershed ecosystem is complicated (Likens et al. 1967, Johnson et al. 1968). Input-output relationships indicate that during some years small amounts of K may accumulate in the ecosystem, but over longer periods the K budget is nearly balanced. The importance of various homeostatic mechanisms in maintaining this delicate balance is illustrated by comparison of the average annual amount of K^+ lost from the ecosystem in streamwater, 0.1 kg/ha (Johnson et al. 1968), and the amount annually cycled by the herbs alone (1.5 kg/ha).

A comparison of the nutrient content (kg/ha) of the herbaceous flora by elevational subdivisions indicates a marked increase at the highest subdivision (Table 5). Current growth of herbs at the upper subdivision contained about three times the amounts found in the lower subdivisions for all the elements. The middle elevation contained more than the lowest elevation, but was appreciably less than the upper elevation. Increased weight of current growth at the upper elevations (Table 2, 3) plus higher concentrations of some elements in herb tissues at the highest elevation, account for this trend.

Major herb species found on watershed 6

Eight major herb species, *Dryopteris spinulosa, Oxalis montana, Maianthemum canadense, Dennstaedtia punctilobula, Clintonia borealis, Lycopodium lucidulum, Aster acuminatus,* and *Smilacina racemosa* contributed 91% (67.3 kg/ha) of the

TABLE 5. Chemical content (g/ha) in the net annual productivity of the herbaceous layer (aboveground growth of herbs only) in watershed 6. Data based on July sample

Element	Lower third	Middle third	Upper third	Whole watershed[a]
	545–648m	648–721m	721–791m	545–791m
Potassium	1047	1226	3010	1766
Nitrogen	895	955	3124	1667
Magnesium	155	140	598	299
Calcium	161	177	541	294
Sulphur	80	95	208	149
Phosphorus	70	88	257	139
Manganese	45	66	164	92
Iron	4	5	13	7
Zinc	3	4	15	8
Sodium	1	1	2	1
Copper	1	1	2	1

[a] weighted average.

estimated aboveground current growth of herbs on the watershed. These species have a wide ecologic amplitude and are common throughout the Appalachian Mountains. While the morphology and geographic distribution of most of the tree species found on watershed 6 are familiar and easily pictured, this is less true of the common herbs. The following discussion provides an equivalent perspective, relative to the northern hardwood forest, for the reproductive habits, size and geographic distribution of the more common herbs on watershed 6.

Dryopteris spinulosa var. *americana,* a summer green fern, and var. *intermedia,* an evergreen fern, were both present on the watershed. *Dryopteris spinulosa,* disregarding varieties, often contributes well over half the total biomass of the herb stratum throughout the mountains of northern New England and northern New York. On many sites, especially at the upper elevation limits of the hardwood forest in New England, this species often forms a continuous cover 0.25 to 0.75 m high, over large areas. *Dryopteris spinulosa* fronds tend to occur in clumps of 5–10 per rhizome and the plants commonly spread vegetatively by a rather thick rhizome. The species occurred on 132 of the 1- by 1-m plots on watershed 6 and was the leading dominant on 95 of these with an average weight of 52 kg/ha and an average cover of 13%. A strong positive correlation was found with respect to elevation on the watershed, but other site characteristics such as aspect and slope were uncorrelated.

In the Adirondacks and Green Mountains *D. spinulosa* was most abundant in the altitudinal range between 750 m and 1,200 m. In hardwood forests below 800 m on four mountains in northern Vermont, *D. spinulosa* cover ranged from 11 to 31% and was strongly positively correlated with elevation. Much higher cover percentages were found in the spruce and fir forests between 900 and 1,150 m on the Green Mountains (Nicholson 1965, Siccama 1968). Thus, the watershed 6 ecosystem is on the lower end of the altitudinal distribution of *D. spinulosa* in the mountains of New York, Vermont, and New Hampshire.

Dryopteris spinulosa is not a major component of the early or mid-seral stages of succession on the slopes of the White Mountains, being found on only six of 22 revegetating landslide sites (Flaccus 1958). The importance of this species in the mature stands in the Appalachian Mountains is reflected by a presence of 100% in the White Mountains, Great Smoky Mountains, Adirondack Mountains, Catskill Mountains and Green Mountains (Crandall 1958, Nicholson 1965, Siccama 1968). In the boreal-hardwood transition forest in the vicinity of the Great Lakes it had a presence of about 60% and it was also reported from some of 55 stands in northern New Jersey (Maycock and Curtis 1960, Davidson and Buell 1967).

Oxalis montana is an evergreen flowering plant. Plants are 1 to 4 cm tall and usually form colonies on the forest floor which may be as extensive as those of *Dryopteris spinulosa,* especially in the spruce-fir forests on the mountains of the northeast. In the hardwood forest the colonies seldom become more than several meters in diameter. *Oxalis montana* occurred on 77 plots on watershed 6 and was the leading dominant on nine. Average weight of this species was 2 kg/ha and cover averaged 2%. *Oxalis montana* was not significantly correlated with any of the site features measured on watershed 6.

Generally the distribution of *O. montana* along the altitudinal gradient of the mountains of the region is similar to that of *Dryopteris spinulosa* with a maximum abundance between 800 and 1,200 m (Nicholson 1965, Siccama 1968). *Oxalis montana* is not especially characteristic of the early or mid-seral stages of succession in the region, occurring on only seven of 22 landslide sites (Flaccus 1958).

Maianthemum canadense is a summer-green flowering species of wider ecologic amplitude than the preceding two species, being found along the entire gradient from maritime forest on barrier beaches on Long Island (Art, *personal communication*) to the subalpine meadows of the higher mountains of New England. Plants are usually 4 to 10 cm tall and form perceptible colonies in some instances that are seldom as extensive as the colonies of the preceding species. *Maianthemum* occurred on 65 plots on watershed 6 and was the dominant herb on 12 of these. Frequency and cover of this species increased along the altitudinal gradient on the watershed. Average weight of current growth of *Maianthemum* was 3 kg/ha and average cover was 1%, whereas in Vermont over a similar range in elevation *Maianthemum* cover averaged 3% (Siccama 1968).

On Whiteface Mountain in New York the species reached a peak frequency at about 1,375 m whereas in the Green Mountains a maximum was reported at 800 m (Nicholson 1965, Siccama 1968). The species was sufficiently abundant in 55 stands in northern New Jersey to warrant its use as a species in establishing adaptation numbers (Davidson and Buell 1967). In the boreal-northern hardwoods transition forests around the Great Lakes *Maianthemum* had a presence of 100% (Maycock and Curtis 1960) and it had presence values ranging from 63 to 100% in the White Mountains, Adirondack Mountains, and Catskill Mountains (Nicholson 1965). It was not reported in the forests of the Great Smoky Mountains although it was present in the grassy balds (Whittaker 1966). *Maianthemum* was uncommon on early and mid-seral stages of succession on the White Mountains, occurring on three of 22 landslide sites (Flaccus 1958).

Dennstaedita punctilobula is a summer-green fern which is characteristically best developed in disturbed areas in the forest. The species is quite similar to *Dryopteris spinulosa* in size of fronds and tendency to form colonies, but within the forest these are seldom as extensive as colonies of *Dryopteris*. On watershed 6 *Dennstaedtia* occurred on 19 plots and was the dominant herb on 10 of these. Average current growth was 6 kg/ha and average cover 2%. There was a slight increase in frequency of this species with increasing elevation on the watershed. *Dennstaedtia* was positively correlated with the occurrence of exposed roots, stumps, and with the occurrence of *Aster acuminatus*. These relationships reflect the tendency of the species to occupy disturbed areas, especially exposed soil characteristic of pit and mound topography, and soil thrown out of animal burrows. The early successional role of *Dennstaedtia* is also shown by its occurrence on 15 of 22 landslide sites in the White Mountains (Flaccus 1958). There was no specific altitude at which this species reached maximum abundance or frequency in the Green Mountains, probably due to its opportunistic success in forest openings over a wide range of habitats up to the krummholz. It was present in 24% of the stands in the Catskills and was noted as being very abundant in disturbed areas in the Great Smoky Mountains (Crandall 1958).

Clintonia borealis, a summer-green herb, is characteristically found at mesic spots on the forest floor and is most abundant in the lower portion of the spruce and fir forest on the mountains of the northeast. Plants are commonly 5 to 15 cm tall when erect, but often the leaves are flattened on the surface of the litter. *Clintonia* spreads vegetatively by branching rhizomes and is often colonial, with colonies of about the same order of size as those of *Oxalis montana*. On watershed 6, *Clintonia* occurred on 41 plots and was the dominant herb on eight of these. The species averaged about 1 kg/ha in weight of current growth and covered about 0.5% of the forest floor. In the Green Mountains at elevations similar to those of watershed 6, *Clintonia* averaged 3% coverage (Siccama 1968). *Clintonia* was positively correlated with elevation and negatively correlated with slope. The latter feature probably reflects the affinity of the species for mesic habitats which may be expected in areas of reduced slope.

Species presence ranged from 75 to 100% in forests of the White Mountains, Great Smoky Mountains, Catskill Mountains and in the boreal-northern hardwood transition forest in the vicinity of the Great Lakes (Nicholson 1965, Maycock and Curtis 1960). *Clintonia* is not a characteristic component of the vegetation in the early or mid-seral stages of succession in the region, occurring on only eight of 22 revegetating landslide sites in the White Mountains (Flaccus 1958).

Lycopodium lucidulum is an evergreen herb which spreads by layering and by specialized vegetative reproductive structures (bulblets) produced on the upper branches. The species forms small, dense colonies (seldom over a meter across) and is one of the common lycopods in the mountain forests of the northeast. On watershed 6, it occurred on 48 plots and was dominant on eight of these. *Lycopodium lucidulum* averaged about 2 kg/ha in weight of current growth and covered about 0.5% of the forest floor.

The preceding species generally are more abundant at elevations higher than watershed 6. In contrast, the elevation of watershed 6 is about at the midpoint of the abundance distribution of *L. lucidulum* along the altitudinal gradient in the northeast. This was shown in the similarity of the frequency in the three subdivisions of watershed 6 (27, 19 and 23%). On Whiteface Mountain in New York a broad zone of maximum importance of this species occurred between 100 and 900 m while in the Green Mountains a similar zone was recognized between 800 and 900 m (Nicholson 1965, Siccama 1968).

Lycopodium lucidulum ranged in presence from 25% to 75% in the White Mountains, Adirondack Mountains, Catskill Mountains, Great Smoky Mountains, and in the boreal-hardwood transition forest in the vicinity of the Great Lakes (Nicholson 1965, Maycock and Curtis 1960). The species is distinctly characteristic of the mature forest as it occurred on only one of 22 revegetating landslide sites in the White Mountains (Flaccus 1958).

Aster acuminatus, a summer-green herb, is characteristic of disturbed areas in the forest. The species tends to be colonial, spreading by branching rhizomes. Plants are commonly 10 to 50 cm tall and almost predictably may be found on windthrow mounds, at entrances to animal burrows and in the vicinity of rocks and rock outcrops.

On watershed 6, *A. acuminatus* occurred on 16 plots and was the dominant herb on three of these. Current growth averaged 1 kg/ha and the species covered about 0.5% of the forest floor. The species was positively correlated with elevation on the watershed, but no significant correlations were noted with other physical site factors.

The species reached a maximum abundance between 900 and 1,000 m in the Adirondack and Green Mountains, and ranged in presence from 38 to 100% in the White Mountains, Green Mountains and Great Smoky Mountains (Nicholson 1965, Siccama 1968). The species was not reported from the boreal-hardwood transition forest in the vicinity of the Great Lakes (Maycock and Curtis 1960). *Aster acuminatus* is distinctly a species of early successional stages in the region, occurring on 19 of 22 landslides in the White Mountains (Flaccus 1958).

Smilacina racemosa, another summer-green herb, is of widespread and common occurrence in the forests of New England, but in contrast to the preceding species, reaches its maximum development in the forests below the elevation range of watershed 6. Plants of *S. racemosa* are commonly 10 to 75 cm tall in the forest, may form barely perceptible colonies, and spread by rhizomes. On watershed 6, *S. racemosa* occurred on 18 plots and was the dominant herb on 10 of these. Current growth averaged about 1 kg/ha and its coverage was about 3%. There were no significant correlations of this species with site factors.

Smilacina racemosa was reported from Whiteface Mountain in New York, the Great Smoky Mountains, northern New Jersey, and from the boreal-hardwood transition forest in the vicinity of the Great Lakes but not in the spruce-fir forest of the Catskill Mountains nor from spruce-fir stands in the White Mountains (Nicholson 1965, Siccama 1968, Maycock and Curtis 1960, Whittaker 1966, Davidson and Buell 1967). *Smilacina racemosa* occurred on only two of the 22 revegetating landslides studied by Flaccus (1958) indicating its late successional status.

The relationship of the Hubbard Brook ecosystem to other forests of northern New England

The northern hardwood forest ecosystem of New England is strongly affected by an elevational complex gradient to which it responds by the waxing and waning of populations of tree species. At higher elevations, the northern hardwood forest grades into the boreal spruce-fir forest (Bormann et al. 1970).

Our watershed ecosystem, dominated by sugar maple-beech-yellow birch forest, occurs over an elevational range just below the marked transition to spruce-fir forest. In basal area, 24 m^2ha^{-1}, and species composition it is typical of many second growth forest ecosystems in the northeastern U.S. (Barrett 1962).

Here we propose to establish, through comparative herb phytosociology, the relationship of the watershed 6 ecosystem to other northern hardwood ecosystems occurring in the same altitudinal range (480 m–670 m), but over a range of geologic sites in northern New England.

Data comparable to Hubbard Brook are available for two forested areas in the Green Mountains of Vermont at similar elevations and on similar topography, Gifford Woods and Camels Hump. At Gifford Woods 37 families and 111 species were recorded and on Camels Hump 39 families and 131 species (Bormann and Buell 1964, Siccama 1968). The major species composition of the three areas was similar in that about half of the species (44% at Hubbard Brook, 50% at Gifford Woods and 50% at Camels Hump) occurred in the same seven families: Polypodiaceae (7.9%, 13.7%, 7.6%), Liliaceae (13.5%, 9.2%, 10.7%), Compositae (6.7%, 6.4%, 11.4%), Cyperaceae (11.5%, 6.4%, 9.2%), Ranunculaceae (2.1%, 5.5%, 4.6%), Violaceae (2.2%, 4.6%, 5.3%), and Labiatae (1.1%, 4.6%, 1.5%).

Dryopteris spinulosa, Maianthemum canadense, Oxalis montana and *Dennstaedtia punctilobula* are the most important herbaceous species at Hubbard Brook. Generally, the first three appear to be characteristic dominants of comparable mountain forests throughout New England and New York (Flaccus 1958, 1959, Scott and Nicholson 1964). In a study of 16 hardwood stands at comparable altitudes in Vermont, *D. spinulosa* ranked first among the cryptogams and *Oxalis* first among the phanerogams. *Maianthemum* was not one of the leading elements of the herbaceous vegetation on the Green Mountains (Siccama 1968).

Phytosociologic data are available for seven areas on the mountain slopes of northern New England at altitudes from 480 to 670 m, comparable to Hubbard Brook. Comparison is justi-

TABLE 6. Frequencies of some herbaceous species beneath northern hardwood forest stands in Vermont and New Hampshire. Stands arranged according to a hypothetical sequence from more eutrophic (left) to more oligotrophic (right)

Species	Gifford Woods (Vt.)	Camels Hump (Vt.)	Jay Peak (Vt.)	Bolton Mt. (Vt.)	Mt. Abraham (Vt.)	Hubbard Brook (N.H.)	White Mts. (N.H.)
Mean sample elevation	480m	670m	670m	670m	670m	670m	—
Adiantum pedatum	32.0	—	—	—	—	—	—
Aster divaricatus	8.1	1.0	—	—	—	—	—
Asarum canadense	6.0	0.7	—	—	—	—	—
Hydrophyllum virginianum	4.0	6.7	—	—	—	—	—
Solidago flexicaulis	2.0	2.7	—	—	—	—	—
Mitchella repens	—	1.3	—	—	—	—	—
Botrychium virginianum	2.0	0.7	0.7	—	—	—	—
Impatiens spp.	6.0	10.7	5.3	—	—	—	—
Allium tricoccum	8.0	0.3	—	3.3	—	—	—
Carex plantaginea	8.0	2.7	—	1.3	—	—	—
Laportea canadensis	16.0	28.0	9.3	10.7	—	—	—
Polystichum acrostichoides	4.0	1.7	2.0	6.0	—	—	—
Viola canadensis	14.0	10.3	6.0	4.7	—	—	—
Thalictrum spp.	4.0	—	2.7	—	0.7	—	—
Athyrium thelypteroides	46.0	11.0	4.7	4.7	2.7	—	—
Carex laxiflora	6.0	9.7	3.3	9.3	3.3	—	—
Caulophyllum thalictroides	24.0	4.0	1.3	0.7	0.7	—	—
Tiarella cordifolia	8.0	31.7	30.7	8.0	6.7	—	—
Solidago macrophylla	—	14.3	20.7	9.3	2.7	—	—
Arisaema atrorubens	72.0	1.7	7.3	2.7	3.3	4.3	—
Viola incognita	56.0	—	—	—	—	11.1	—
Actaea spp.	4.0	1.0	—	—	—	0.5	—
Smilacina racemosa	16.0	10.3	18.0	3.3	7.3	8.7	—
Viola rotundifolia	16.0	2.7	1.3	16.7	2.0	3.4	—
Oxalis montana	4.0	50.7	60.0	34.0	27.0	57.3	—
Coptis groenlandica	—	—	2.7	—	1.3	0.5	—
Carex intumescens	—	17.0	13.3	13.3	2.0	2.9	—
Streptopus roseus	—	31.0	36.0	6.7	8.6	3.4	—
Trillium undulatum	—	0.7	—	—	—	6.7	—
Athyrium filix-femina	14.0	1.3	6.0	—	—	1.0	9.0
Galium triflorum	2.0	2.3	4.7	—	—	—	3.0
Prenanthes altissima	—	4.0	16.0	0.7	0.7	—	8.0
Viola spp.	—	39.7	26.0	19.3	14.0	—	30.0
Uvularia sessilifolia	—	6.0	—	3.3	8.7	7.2	23.0
Dryopteris spinulosa	36.0	72.0	71.3	68.7	79.3	63.5	28.0
Lycopodium lucidulum	8.0	34.3	54.7	28.7	58.7	23.1	21.0
Maianthemum canadense	6.0	37.7	24.3	13.3	37.3	30.8	6.0
Trillium erectum	2.0	48.0	30.0	16.0	22.7	8.2	18.0
Aralia nudicaulis	—	9.3	2.7	6.7	11.3	6.7	6.0
Aster acuminatus	—	10.3	5.3	9.3	11.4	7.7	30.0
Clintonia borealis	—	30.7	20.7	16.7	45.3	19.7	25.0
Trientalis borealis	—	2.3	6.0	3.3	2.0	5.8	15.0

fied since all stands are located at approximately the same elevations on mountain slopes, data were collected from herb strata beneath mature forests, and all were sampled with a large number of plots of equal size. Soils of these areas reflect a range of till conditions from granite and gneiss to fairly calcareous material.

Frequency data from all seven areas (Table 6) indicate that the herbaceous stratum of the Hubbard Brook watershed includes most of the major species commonly found beneath mature forests at similar elevations throughout the region. Eight herb species, *Aster acuminatus, Aralia nudicaulis, Clintonia borealis, Dryopteris spinulosa, Lycopodium lucidulum, Maianthemum canadense, Oxalis montana* and *Trillium erectum,* had sizeable frequencies in most stands and were found in all seven locations, whereas eight other species occurred at Hubbard Brook and in at least five other locations.

These data presented an opportunity to determine where Hubbard Brook was located on a scale of decreasing base saturation of the soil (more eutrophic to more oligotrophic). Three categories of evidence were used to arrange the stands in Table 6. First, stands were arranged on the basis of frequency of taxa characteristic of mesic, lower elevation stands in the region (*Athyrium thelypteroides, Arisaema atrorubens, Asarum canadense, Adiatum pedatum, Caulophyllum thalictroides, Hydrophyllum virginianum,* and *Laportea canadensis*) and of taxa more common on higher elevation, acidic humus soils (*Aster acuminatus, Oxalis montana, Dryopteris spinulosa,* *Coptis groenlandica, Clintonia borealis, Lycopodium lucidulum,* and *Trillium undulatum.* These species groupings are very similar to the mesic herb union and mesic high-elevation herb union described in the Great Smoky Mountains along the altitudinal gradient (Whittaker 1956). Whereas the altitudinal gradient often infers a climatic gradient, a response of these herbs along the soil richness gradient infers an edaphic controlled distribution rather than a climatic one. Second, the two stands at the extreme left are underlain by mull soils indicative of higher base saturation than is normally expected at these elevations in New England (Bormann and Buell 1964). All other stands were underlaid by mor. Third, chemical concentrations in stream water from undisturbed first order watersheds reflect soil chemistry and amount of available nutrients (Likens et al. 1967). Calcium concentrations from first order streams on Camels Hump averaged 4.5 ppm, while those from Hubbard Brook averaged 1.5 ppm. Well water from Gifford Woods contained 10 ppm calcium. Species diversity (number of species/m^2) among stands in Table 6 decreased irregularly with increasing oligotrophy of the soil.

Species, soil conditions, and stream water chemistry suggest that Hubbard Brook lies at or near the oligotrophic end of a scale of northern hardwood forests characteristic of midslope elevations in the mountains of New England.

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