

THE HUBBARD BROOK ECOSYSTEM STUDY: FOREST BIOMASS AND PRODUCTION¹

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Abstract. A small watershed in the White Mountains of New Hampshire bearing mesophytic, cool-temperate, broadleaf-deciduous forests was studied. *Acer saccharum*, *Betula lutea*, and *Fagus grandifolia* are dominant, but toward higher elevations *Picea rubens* and *Abies balsamea* also occur and indicate the transition toward subalpine climate. The stands are young (following cutting in 1909–17) but contain older trees; stand composition is thought reasonably representative of the climax. For application of the Brookhaven system of forest dimension analysis, 93 sample trees of major species were cut and roots excavated. Mean dimensions of sample trees, and the constants for the system of logarithmic regressions relating volume, surface, mass, and growth to diameter at breast height and other independent variables, show decrease in tree sizes and height/diameter ratios toward higher elevations. Stand characteristics, based on application of the regressions to forest samples, show trends of decrease for the elevation belts from low to high: stem basal area 26.3, 23.7, and 22.0 m²/ha, weighted mean tree height 16.9, 16.7, and 10.8 m, weighted mean age 124, 95, and 83 yr, stem wood volume 176, 155, and 103 m³/ha, aboveground biomass (dry matter) 162, 152, and 102 t/ha, estimated volume increment 379, 365, and 223 cm³/m²/yr, aboveground net primary productivity (1956–60) 1127, 1041, and 790 g/m²/yr, and leaf area ratio 6.2, 5.7, and 5.5 m²/m². Biomass (and, presumably, production) of root systems is 18%–21% of that aboveground. Different estimations suggest that a mean climax biomass for the watershed may be around 350 t/ha, aboveground. Net ecosystem production (i.e., addition to the pool of woody biomass in the community) is estimated as 350 g/m²/yr aboveground and 85 belowground for 1956–60, 238 and 52 g/m²/yr for 1961–65. Analysis of stem wood volume increments reveals an abrupt and striking (18%) decrease in volume growth and productivity from 1956–60 to 1961–65. The net primary productivity of the former period, with a weighted mean for the watershed of 1110 g/m²/yr above and below the ground, is thought more nearly normal for the forest. Both drought and effects of increasing air pollution (notably increasing acidity of rainfall) may be responsible for the recent decrease in productivity.

Key words: Allometry; area, leaf and branch; biomass; dimension analysis; ecosystem study; forest; Hubbard Brook; productivity; regressions, forest dimensions.

INTRODUCTION

A series of watersheds at Hubbard Brook, New Hampshire, are being studied as ecosystems, with special concern for nutrient cycling. The present paper applies the Brookhaven system of forest dimension analysis (Whittaker and Woodwell 1968, 1969, 1971) to one of the forested watersheds. Its purposes include (1) analysis of the dimensional relations of deciduous forest trees; (2) determination of forest productivity and biomass, together with volume and surface dimensions for the watershed; (3) characterization of the forest dynamics—particularly whether productivity may be at a steady-state level and how closely the present forest biomass may approach the climax level; and (4) establishment thereby of the basis for study of nutrient circulation in the forest community.

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STUDY AREA

The Hubbard Brook Experimental Forest is at low elevations in the White Mountains, in the Township of West Thornton 22 km north of Plymouth, New Hampshire. A number of small watersheds with weirs are under intensive hydrologic study by the U. S. Forest Service; and some of these are also being used for studies of nutrient circulation and ecosystem function (Bormann and Likens 1967, Likens & Bormann 1972). A series of papers on the area discuss the geology and hydrology (Likens et al. 1967, Johnson et al. 1968, 1970, Hornbeck et al. 1970), the nutrient balance between precipitation and outflow (Fisher et al. 1968, Bormann et al. 1969, Likens et al. 1967, 1972, Hobbie and Likens 1973), the effects of forest cutting (Bormann et al. 1968, Likens et al. 1969, 1970, Smith et al. 1968, Pierce et al. 1970, Hornbeck et al. 1970), composition of the forest stands (Bormann et al. 1970), and composition and nutrient turnover of the undergrowth (Siccama et al. 1970).

Watershed 6 is 13.23 ha, with elevations from 546 to 791 m. Exposure is generally toward the southeast, with slope inclinations averaging 12°–13°.

Bedrock is the Littleton gneiss, but apart from local outcrops this is overlain by bouldery glacial till generally increasing in depth toward lower elevations (Likens et al. 1967, Johnson et al. 1968, Bormann et al. 1970). Climate is cool temperate, humid continental with mean July and January air temperatures of 17.5°C and -12°C at 450 m elevation, mean annual precipitation about 125 cm with one-fourth to one-third of this falling as snow (U. S. Forest Service 1964, Federer 1973). The forest is of northern hardwoods, dominated by *Acer saccharum*, *Fagus grandifolia*, and *Betula lutea* (or *B. alleghaniensis*), but it is close to the transition to boreal or subalpine forest dominated by *Picea rubens* and *Abies balsamea*. The latter two species form 13% of basal area and 10% of stem volume in the upper third of the watershed. Tree composition and change with elevation are described by Bormann et al. (1970), and undergrowth composition by Siccama et al. (1970).

Thornton township began to be settled by farmers in 1770, and the population thereafter increased to a peak somewhat over 1,000 by 1830. No record exists of the extent of cutting in the watershed; but in 1830 there was a sawmill on Mirror Lake, 5.5 km and 400 m elevation below the study site; it burned probably between 1856 and 1860 and was replaced by another in 1860 (Likens 1972). A railroad was completed to nearby North Woodstock in 1883-1884, and more intensive logging became possible thereafter (Brown 1958, Gove 1968, Bormann et al. 1970). Some time after the turn of the century the entire watershed area was logged; Bormann et al. (1970) suggest that spruces were removed in a first cutting around 1909, and all merchantable trees in a second completed by 1917. The cutting left largely intact the forest soils and the smaller trees, and the forest has been undisturbed since 1917. No evidences of fire have been found in the watershed. The present forest, though younger and smaller than the climax, is believed to be similar in species composition (Bormann et al. 1970).

METHODS

Sample tree choice

For the study the watershed was divided into three elevation belts, 550-630 m (3.24 ha), 630-710 m (4.58 ha), and 710-785 m (5.41 ha). Ninety-three trees representing the range of elevations and major species were subjected to dimension analysis. These included nine sets of 7 trees each for all combinations of the three dominant species (*Acer saccharum* = sugar maple, *Betula lutea* or *B. alleghaniensis* = yellow birch, and *Fagus grandifolia* = beech) and the three elevation belts, plus 15 trees

each of two species (*Picea rubens* = red spruce, and *Acer spicatum* = mountain maple) taken from the high-elevation belt. Trees of each set of 7 or 15 were selected to represent the range of stem sizes of that species in the forest. For the sets of 7 one tree was sought for each of seven size classes between 1 and 63 cm dbh (diameter at breast height), and the sets of 15 were chosen to represent evenly classes within the size ranges for those species (3-38 cm for *Picea*, 1-10 cm for *A. spicatum*). No trees with forked stems were taken, and an effort was made to select trees of average rather than maximum vigor.

Measurements on sample trees

Measurements and calculations followed those of Whittaker and Woodwell (1968, 1971) and employed the Brookhaven dimension analysis forms and computer programs. Trees were felled and a tape laid along the stem axis from tip to base. The distances of all living and dead branches were tallied from the tip downward, along with basal diameters and ages of living branches. Branch ages were determined for younger branches by bud-scale scars on both branches and stem, and for older branches by wood rings of branches and age of the stem where they emerged. In many slower growing, older branches, branch wood rings that could be counted under the microscope were far short of the stem age where the branch emerged. It was assumed that wood rings were missing in these branches, and they were assigned the ages of the stems where they emerged.

The tree crown was divided along the tape into five height ranges, in each of which a living branch was chosen at random and information recorded on branch length, number of current twigs, and fresh and dry weights of fractions (living wood, dead wood, current twigs with leaves, and older leaves and fruits if any). Samples were oven-dried at 105°C. Dry weights were in most cases based on fresh/dry weight ratios obtained from subsamples, and for large branches twig numbers were based on counts for twig subsamples. Fruits were collected from all branches other than the sample branches and weighed, and in some cases (primarily *Picea*) wood of dead branches was also collected and weighed for the whole tree. Three to five twigs with leaves were taken from each of the crown height ranges and frozen for later determination of leaf number, blade area, insect loss, twig diameter and length, and distribution of dry weight among twig, leaf blades, and petioles. Leaf blade area was read with a photoelectric device developed at Brookhaven National Laboratory; leaf consumption by insects was estimated as a percent of blade area.

Chlorophyll was extracted from fresh leaf discs in 80% acetone and read at 652 m μ for the Arnon (1949) formula.

Stems were cut into logs or bolts usually 2 m long, but shorter logs (to give at least five logs above the stump) were used for small trees. The first log for a given tree was the stump from just above ground level or root flare to the height of the cut that felled the tree; the second log was from the same cut to breast height (1.35 m). Fresh weights and dimensions of logs were recorded; and sample discs 5 or 10 cm thick were cut from the base of each log, weighed fresh, measured, and returned to the laboratory for determination of dry weight, dry wood diameter and bark thickness, apparent sapwood age and thickness, wood radial increment thicknesses by 5-yr periods from the current ring to the center of the disc, and disc age. For three trees of each set of 7, and five of each set of 15, bark was separated from wood of the discs, and more detailed measurements were made to permit determination of wood and bark volumes and weight/volume relations.

Root systems were excavated with the encouragement of dynamite sticks set under and around the root crowns. The dynamite also broke the largest crowns into pieces of manageable size. Parts of some root crowns were lost, but complete enough ones were obtained for 81 trees, including at least 5 for each of the sets of 7. Roots were cut off the crowns and combined with additional roots excavated from the craters; fresh weights were obtained for these roots and the crowns, and samples were taken to obtain fresh/dry ratios. Broken and cut ends of roots were recorded by millimeter-size classes to permit correction for root loss. Intact sample roots were excavated by hand and measured for basal diameter, length, and fresh and dry weights.

Calculations on sample trees

Dry weights of logs were calculated from log fresh weights and disc fresh/dry ratios. Fresh and dry volumes were calculated for bark, sapwood, and heartwood if any and used to obtain first dry-weight values for each of these for the logs. Wood and bark densities (dry weight/fresh volume) were computed from the sample discs for which the wood and bark had been separated, and mean density values were used to correct the first calculations of wood and bark weights. Five-year volume increments, computed from the current period (1961-65) to the center of the log, were used to determine wood dry-weight growth for the current and preceding 5-yr period and to estimate bark growth (from bark weight times wood growth/wood weight). Surface areas were computed for the wood (cam-

bium) and bark (treated as a smooth cylinder). Volume, weight, growth, and surface values were summed for all logs of a tree.

The sets of sample branches (for each species and elevation belt combination) were used to compute various regressions; the most important of these used the logarithms of branch basal diameter as independent variable and related to it the logarithms of several dependent variables (dry weights of live wood, of live wood plus dead wood, of current twigs with leaves, and of older leaves in *Picea*; number of current twigs; and branch bark surface). Branch surface was computed as described by Whittaker and Woodwell (1967, 1968). We estimated these dependent variables for each live branch of a tree by applying the regression to the recorded basal diameter, and summed the estimates for all branches of a tree. We estimated branch wood production from the relation $\Delta W_b = BW_b/a$, in which ΔW_b is annual growth of branch wood and bark, W_b is branch wood and bark dry weight estimated from the regression on basal diameter, a is branch basal age, and B is a growth-rate slope computed from the regression of branch wood and bark dry weight on branch age, $\log W_b = A + B \log a$ (Whittaker 1962, 1965). The whole-tree collections, rather than the regressions on branch diameters, were used to obtain values for fruit dry weight, and dead branch weight in *Picea*. Given the estimate for total dry weight of current twigs with leaves for a tree, mean ratios for sample twigs were used to obtain (1) the distribution of this dry weight among twigs, petioles, and leaf blades, (2) the surface area of leaf blades from blade area/weight ratios, and (3) a correction of the blade weight for per cent loss to herbivores.

Dry weights of root crowns and excavated roots were determined from the field fresh weights and fresh/dry ratios of subsamples. The sample roots were used to compute logarithmic regressions of root dry weight on root basal diameter for each set of trees. We applied these regressions to the root broken ends of each tree to estimate dry weight of roots lost, and added this estimate to the weight of roots excavated.

The calculations to this point were compiled, checked, and corrected if necessary; then the resulting values for whole trees and their fractions were used to obtain a wide range of logarithmic and linear regressions. The most important independent variables for these whole-tree regressions are (1) dbh, (2) parabolic volume (one-half stem cross section area at breast height times tree height), (3) estimated volume increment (one-half current wood growth in cross section area at breast height times tree height), and (4) conic surface (one-half stem circumference at breast height times tree height).

The most important dependent variables are (1) volumes of stem wood and of bark, (2) dry weights of stem sapwood, stem heartwood if any, stem bark, living branch wood and bark, dead branch wood and bark, current twigs with leaves, older leaves if any, fruits, root crown, and roots, (3) surface areas of stem wood, stem bark, branch bark, and leaves, (4) current annual growths of stem wood, stem bark, branch wood and bark, current twigs and leaves, and fruits, and (5) volume growth of stem wood for the current and all preceding 5-yr periods.

Forest samples

The forest stand was sampled by Bormann et al. (1970). The watershed was first surveyed and divided into a grid of 25- by 25-m squares; 169 of these squares lay wholly and an additional 39 more than half within the watershed. In each of these 208 squares a single 10- by 10-m quadrat was randomly chosen, and species and dbh were recorded for all trees 2 cm or more in diameter. Tree seedlings more than 0.5 m tall but less than 2 cm diameter were recorded in four 2.5 × 2.5-m quadrats in the corners of the 10 × 10-m plot, and tree seedlings less than 0.5 m tall were counted in four 1-m² plots in the same corners. Increment borings were taken separately, with tree diameters and heights recorded, from 497 trees along transect lines across the watershed; and the increment cores were read to obtain bark thickness and radial wood increments for the last two 5-yr periods.

Undergrowth composition and production were studied by Siccama et al. (1970). In each of the 25 × 25-m squares a random 1-m² quadrat was chosen. In these quadrats coverages of herbs and woody plant seedlings were recorded, and current aboveground growth of herbs and current twigs with leaves of shrubs, seedlings, and saplings were clipped to obtain their fresh and dry weights.

Leaf litter fall was collected in 45 traps 0.53 m in diameter systematically distributed through the watershed (Gosz et al. 1972). Branch litter fall was collected also in fifteen 2 × 2-m plots. Leaf and branch litter was sorted by species, and dry weights recorded. We calculated shrub leaf litter using the living leaf biomasses determined from 1-m² plots by Siccama et al. (1970) and live/dry ratios; herb litter was determined from Siccama's living biomass data and a study of weight loss in the herb species from the summer green to the autumn brown condition (Gosz et al. 1972). We estimated fall of tree trunks and large branches by sampling the entire watershed. All fallen stems and large branches were marked with paint in September 1968, and a year later newly fallen trees and large branches were weighed fresh in the field and subsamples taken for fresh/dry weight ratios. Leaf

consumption by insects was sampled with 50 frass traps, 20 cm in diameter, and measurements were made of herbivore assimilation by common insect larvae to determine leaf dry weight consumed for a given weight of frass (Gosz et al. 1972).

Forest dimension computations

From the increment boring data logarithmic regressions were computed for each species and elevation belt, relating dbh (independent variable) to tree height, bark thickness, and wood radial increments for 1961–65 and 1956–60 as dependent variables. Regressions of age on diameter were computed for the sets of sample trees. The stand counts from the 25 × 25 m quadrats were combined by elevation belts (50 quadrats at low, 72 at middle, and 86 at high elevations), and the regressions were used to estimate values of the other variables from diameters for the trees of the combined samples. From dbh and the other variables parabolic volume, conic surface, and estimated volume increments for 1961–65 and 1956–60 were calculated for each tree. With these in turn as independent variables, the various dependent variables for tree volume, dry weight, growth, and surface given under "Calculations on sample trees" were computed from the whole-tree logarithmic regressions. Regressions for major species thought most appropriate were applied to minor species: *Acer saccharum* regressions to *Acer rubrum*; *Betula lutea* to *Betula papyrifera*, *Prunus virginiana*, and *P. pensylvanica*; *Fagus grandifolia* to *Fraxinus americana*; *Picea rubens* to *Abies balsamea*; and *Acer spicatum* to *A. pensylvanicum* and *Pyrus americana*.

These estimates were summed by species and divided by quadrat areas for elevation belts to obtain forest dimensions—volume, biomass, production, and surface area. All these were calculated more than once, making alternative estimates of each dimension available by means of dbh and one or more of the other independent variables. Among the estimates those thought dimensionally most appropriate were used (Whittaker and Woodwell 1969). The values in the tables use volume and biomass estimates from parabolic volume as independent variable, surface estimates are from conic surface, current twig and leaf production from parabolic volume, and other production estimates from estimated volume increment. Regressions on dbh were used for the period volume increments.

Root production was separately estimated for each species and elevation belt, as the sum of (1) the biomass of root crowns, times the ratio of stem production to stem biomass, and (2) the biomass of roots (excluding crowns), times the ratio of branch wood and bark plus current twig production to branch wood and bark biomass. The results, a

TABLE 1. Mean dimensions of sample trees in the Hubbard Brook forest

Dimensions	Major species, low and mid. elev.			By elev., major spp. combined			Minor species	
	<i>Acer saccharum</i>	<i>Betula lutea</i>	<i>Fagus grandifolia</i>	Low elev. 550–630 m	Mid. elev. 630–710 m	High elev. 710–785 m	<i>Acer spicatum</i>	<i>Picea rubens</i>
A. Mean tree dimensions:								
Number of trees averaged	14	14	14	21	21	21	15	15
Dbh, cm	25.9	24.6	23.3	24.5	24.7	22.9	4.8	14.5
Diameter at ground level, cm	36.8	38.6	32.2	35.0	36.8	34.4	7.5	20.0
Height, m	17.9	16.2	16.0	17.5	15.9	11.9	6.3	9.1
Age, yr	79.	66.	106.	88.	79.	90.	24.	87.
Breast-height bark thickness, mm	6.3	4.9	3.5	4.9	4.8	4.9	1.6	2.8
Breast-height wood increment, ^a mm/yr	1.13	1.36	.89	1.07	1.19	1.29	0.53	0.72
Basal area increment ^a	11.30	13.59	7.45	10.72	10.84	9.67	0.77	4.28
Aboveground dry weight, kg	723.	654.	624.	766.	568.	428.	8.72	87.5
Aboveground production, dry, kg/yr	30.9	37.7	21.3	32.7	27.2	19.3	0.86	3.38
B. Volume, dm ³ :								
Parabolic volume estimate ^b	980.	726.	679.	920.	669.	455.	10.52	152.
True stem volume	780.	573.	625.	756.	562.	418.	11.68	144.
Stem wood volume	689.	515	582.	682.	509.	394.	10.08	128.
Heartwood volume	56.	65.	157.	114.	71.	130.	—	—
Estimated volume increment ^a	13.23	13.85	7.60	12.8	10.34	6.82	.311	2.74
True volume increment ^a	12.88	13.90	8.66	13.0	10.60	7.79	.476	4.41
C. Surface, m ² :								
Conic stem surface estimate ^c	9.14	7.65	7.35	8.83	7.26	5.04	.586	2.62
Parabolic surface estimate ^c	12.58	10.58	10.15	12.14	10.06	7.08	.836	3.74
Stem bark surface	10.16	8.19	8.70	9.88	8.17	6.05	.717	3.29
Stem wood surface	9.51	7.73	8.38	9.34	7.74	5.69	.657	3.09
Branch bark surface estimate ^d	42.3	101.5	65.0	2.2	67.1	53.2	1.49	19.0
Leaf blade surface ^e	193.	214.	156.	209.	168.	157.	4.91	60.
D. Shoot dry weight: distribution, ^f %								
Stem wood	59.6	43.1	56.5	52.3	53.7	51.4	54.1	57.0
Stem bark	7.5	5.0	3.7	5.5	5.3	5.7	8.0	8.0
Branch wood and bark	30.6	48.1	34.2	38.6	36.8	35.7	29.7	19.6
Dead branch wood	.8	2.2	4.5	2.2	2.8	5.4	5.3	8.2
Current twigs and leaves	1.5	1.6	1.1	1.4	1.4	1.8	2.9	.8
Older leaves								6.3
E. Root/shoot relations:								
Root system dry weight, kg	121.0	128.3	104.7	120.2	115.8	82.9	2.543	31.42
Root/woody shoot ratio, ^g mean	.187	.201	.190	.166	.219	.205	.305	.417
Largest trees ^h	.177	.145	.154	.149	.168	.186	.289	.406
Smallest trees	.467	.370	.465	.378	.489	.352	.313	.535
Mean woody mass ^f % in—								
Stem	57.2	40.8	51.3	50.5	49.6	48.3	53.6	49.5
Branches	28.5	42.6	34.2	36.0	33.5	35.1	22.9	21.1
Root crown	5.2	6.4	4.2	4.7	6.0	8.4	14.1	10.6
Roots	9.1	10.2	10.3	8.8	11.0	8.2	9.4	18.8
F. Aboveground net production ^f :								
% in—								
Stem wood	26.5	20.8	24.4	23.7	23.4	23.8	27.2	53.0
Stem bark	3.3	2.2	1.7	2.5	2.4	2.5	4.2	6.3
Branch wood and bark	33.5	45.6	37.5	38.4	41.0	32.5	38.0	14.2
Current twigs and leaves	35.	27.6	31.4	32.0	30.4	39.1	29.1	22.6
Fruits	1.2	3.7	5.0	3.4	2.8	2.1	1.5	3.9
G. Leaf and twig relations:								
Current twig diameter, mm	2.32	2.36	2.12	2.25	2.31	2.26	2.54	1.08
Leaf number/twig	4.52	2.52	3.52	3.63	3.40	3.70	4.69	
Dry weight, current twig and leaves								
g	1.041	.289	.526	.548	.690	.617	.802	
Percent ^f in twigs	3.8	4.8	6.1	5.3	4.5	5.0	6.3	
" petioles	10.1	5.7	2.3	5.9	6.1	6.0	12.7	
" blades	86.1	89.5	91.6	88.8	89.4	89.0	81.0	

^a Increment measurements are for the 1961–65 period of lower growth. Estimated volume increment is one-half basal area increment times height.

^b One-half basal area times height.

^c Conic stem surface is $\pi D \cdot H/2$, parabolic stem surface is $[\pi/6k^2][(4kH + 1)^{3/2} - 1]$, $k = (H - 135 \text{ cm})/R^2$; R is dbh/2 and H is tree height.

^d Calculation described by Whittaker and Woodwell (1967).

^e One surface of deciduous leaves; full surface of spruce needles, based on a ratio of 9.2 dry mg/cm² surface (Burger 1953).

^f Ratios of means. Because of the curvilinear relations the various means and ratios cannot be computed from one another.

^g Ratio of belowground dry weight to that of stem and branch wood and bark.

^h Means for sets of three largest or smallest trees.

TABLE 1. (continued)

Dimensions	Major species, low and mid. elev.			By elev., major spp. combined			Minor species	
	<i>Acer saccharum</i>	<i>Betula lutea</i>	<i>Fagus grandifolia</i>	Low elev.	Mid. elev.	High elev.	<i>Acer spicatum</i>	<i>Picea rubens</i>
				550–630 m	630–710 m	710–785 m		
Leaf blade area, cm ² /leaf	197.	85.	122.	133.	136.	143.	160.	
Blade dry weight/area, mg/cm ²	4.88	4.35	3.96	4.44	4.40	4.28	4.12	
Leaf blade chlorophyll, mg/cm ²	49.2	54.5	53.3	52.4	52.2	50.0	54.9	
H. Interrelations:								
Biomass accumulation ratio ^f	23.4	17.3	29.2	23.5	20.8	22.2	10.2	25.8
Basal area increment/basal area ^f %	9.57	9.32	6.86	9.25	7.96	8.90	14.86	5.94
Wood density, ⁱ dry g/fresh cm ³	0.62	0.55	0.60	0.59	0.59	0.59	0.46	0.42
Bark density ^j	0.60	0.58	0.53	0.56	0.57	0.55	0.44	0.49
Stem volume/parabolic volume ⁱ	0.936	1.022	1.038	1.029	0.969	1.072	1.457	1.301
Woody biomass/parab. volume, ⁱ g/cm ³	0.905	1.027	1.129	1.008	1.033	1.120	1.359	1.225
Shoot production ratios to—								
Estimated volume increment ⁱ	3.031	2.998	3.731	3.117	3.386	3.382	2.666	2.028
Leaf dry weight ^f g/g	2.92	3.80	3.40	3.31	3.44	2.70	3.67	0.77
Leaf surface area ^f g/m ²	160.	176.	137.	156.	162.	123.	174.	70.
Leaf blade chlorophyll, g/g	326.	354.	256.	299.	310.	246.	317.	205.
Volume incr. ratio, 1956–60/ 1961–65		1.297	1.268	1.241	1.222	1.271	1.186	1.162
								1.602

^f Means of ratios. See ⁱ.

slight refinement on direct root/shoot ratios (Whittaker 1962, Lieth 1968, Newbould 1967, 1968), are close to the conventional 1:5 estimate of forest root production from shoot production. Fruit production estimates based on foliage production and mean fruit/foliage ratios for the sample trees were preferred to those from the regressions; the former estimates converge with fruit weights in litter collections by Gosz et al. (1972). Flower and bud-scale production data are taken directly from the litter collections of Gosz et al. (1972).

RESULTS

Dimension analysis of trees: Mean tree dimensions

In Table 1 mean dimensions of the sample trees are summarized. To reduce the number of columns in the table and facilitate comparisons, we grouped the nine sets of sample trees for major species. The first three columns combine for each species the 14 trees from lower and middle elevations. These mean values are thought more widely applicable than those also including the shorter, near-subalpine, high-elevation trees. The following three columns combine 21 trees, 7 for each of the three major species (*Acer saccharum*, *Betula lutea*, and *Fagus grandifolia*) from a given elevation belt. The values in the table are arithmetic means by which trees of different species and elevation belts may be compared (though means of linear, square, and cubic or mass dimensions cannot be compared within a species or belt).

In most respects dimensions of the three major species are not significantly different. These dominants represent, in three species rather than the many of a tropical forest, a community paradox: the conspicuous convergence in structural characteristics of dominant species in contrast to the differences in functional characteristics that are assumed to permit their coexistence. Certain minor differences appear, however, resulting from the thin bark of *Fagus* and the heavier branches of *Betula* (Table 1D, E, F). *Picea rubens* trees in this forest are mostly young and small. *Acer spicatum* is a small-tree species, with stem dbh seldom exceeding 10 cm and several shoots often growing from a common root crown. The sample trees of *Picea* and *A. spicatum* average smaller by one and two orders of magnitude than those of the three major species in their cubic dimensions (volume and dry weight). A number of other dimensional trends are correlated with tree size, notably the root/shoot ratios (Table 1E, also data on intraspecies trends with tree size in Andersson 1970), basal area increments (1A), estimated volume increments (1B), biomass accumulation ratios (1H), and ratios of true stem to parabolic volume (1H).

The three major species at Hubbard Brook have shoots that average smaller and younger than the *Quercus robur* for which parallel data are given by Andersson (1970, 1971), but larger and older than the Brookhaven forest trees of Whittaker and Woodwell (1968). Mean aboveground dry weights are an order of magnitude larger for the three species than for *Quercus coccinea* and *Q. alba* at Brook-

haven. The Hubbard Brook trees have lower bark/stem ratios, root/shoot ratios, and foliage/shoot ratios than the Brookhaven trees. It should be noted, however, that the fraction of dry weight and growth in branch wood and bark in the Hubbard Brook trees is even higher than that of the Brookhaven trees. The latter are growing in a relatively open and well-lighted stand in which heavy branches would be expected. Not only do the trees at Hubbard Brook have the high branch/stem ratios of open-growth trees, these ratios increase from the smaller to the larger trees (Fig. 1).

Mean heights of the major species (Table 1A) decrease from low to high elevations, and other dimensional relations of which height is a component consequently decrease. Mean aboveground weight of trees (Table 1A), for example, decreases in the three elevation belts by ratios of 1.0, 0.74, 0.56 despite similar mean stem diameters. Apart from effects related to tree height, differences with elevation seem minor or lacking; in particular there are no obvious trends with elevation in root/shoot and branch/stem ratios. There may, however, be some increase in dead branch wood toward the more rigorous climate of the high elevation belt, and some increase in percent of dry weight in root crowns toward higher elevation.

Regressions

Tables 2 and 3 summarize dimensional relations in a less easily interpreted, but generally more useful form. The regressions, like the mean dimensions, are very similar for the three major tree species. Differences between these and the minor species, and between elevation belts in the major species, appear in the regression constants as well as in mean dimensions. The decreases in slope constants B toward higher elevations, for dimensions of which height is a component, may in particular be noted. Also, the slope constants B are higher for branch dimensions than for corresponding stem dimensions in the three major species. Such a relation (cf. Fig. 1) is the reverse of that expected in a climax forest and suggests open-growth history of the larger trees at Hubbard Brook.

The regressions are thus not appropriate to the trees of a climax forest. Many forests on which research is done in the eastern United States and Western Europe are, however, second-growth stands with dimensions comparable to those of the Hubbard Brook or Brookhaven forests. With care in application, considering the height and growth characteristics of particular stands, the Hubbard Brook regressions should be suitable for estimation of dimensions of some deciduous forests for which no sample tree analyses are available. Experience suggests that interspecies regressions (such as those for

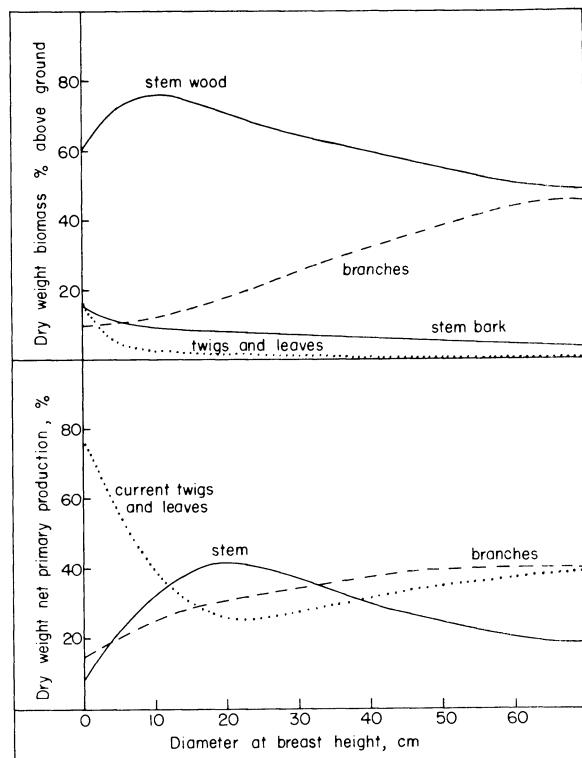


FIG. 1. Trends in biomass and production percentages, aboveground, in relation to dbh for the Hubbard Brook forest. The curves are smoothed by eye from data for the 63 sample trees of three major species (*Acer saccharum*, *Betula lutea*, and *Fagus grandifolia*).

the elevation belts in Tables 2 and 3), combining data for several species of similar growth form, are in some cases as useful as regressions for particular species (Ogawa et al. 1965, Whittaker and Woodwell 1968). Biomass, volume, and surface regressions can in general be applied to stands other than those from which they were derived with more confidence than can production regressions. Regressions on independent variables of which height is a component (i.e., parabolic volume and conic surface area) may give somewhat better results than those on diameter. Production regressions on estimated volume increment should, when applied to a different stand, give better production estimates than would regressions on the other independent variables. A further caution is in order if the Hubbard Brook regressions are used to estimate production elsewhere. The trees were analyzed during a period when both wood and leaf growth were below normal. The regressions of production on diameter and parabolic volume will consequently give low estimates. (This need not be true of the regressions on estimated volume increment, which includes a growth index.) Possible corrections for a period of better growth are given as ratios of wood volume

TABLE 2. Regressions on diameter for sets of sample trees in the Hubbard Brook forest. Estimates of constants A and B in the regression equation, $\log_{10}y = A + B \log_{10}x$ for different dependent variables on breast height diameter (DBH) in cm (x) are given, with coefficients of correlation (r) and estimates of relative error (E), for different tree species and elevation groups of trees. The trees were analyzed in a period of low growth, and regressions of production on diameter give low estimates; Table 1-H, volume increment ratio, shows a possible correction for these.

<i>Acer</i> <i>sac-</i> <i>charum</i>	<i>Betula</i> <i>lutea</i>	<i>Fagus</i> <i>grandi-</i> <i>folia</i>	Low eleva-	Middle eleva-	High eleva-	<i>Acer</i> <i>spi-</i> <i>catum</i>	<i>Picea</i> <i>rubens</i>	<i>Acer</i> <i>sac-</i> <i>charum</i>	<i>Betula</i> <i>lutea</i>	<i>Fagus</i> <i>grandi-</i> <i>folia</i>	Low eleva-	Middle eleva-	High eleva-	<i>Acer</i> <i>spi-</i> <i>catum</i>	<i>Picea</i> <i>rubens</i>		
Numbers of trees in samples								Numbers of trees in samples									
14	14	14	21	21	21	15	15	14	14	14	21	21	21	15	15		
Regressions on \log_{10} DBH in cm (x)																	
Tree height, cm (y):																	
<i>A</i>	2.5370	2.5085	2.4511	2.4803	2.5250	2.5855	2.3735	2.1159	<i>A</i>	0.6266	1.0535	1.4182	1.0823	1.0094	0.9950	0.8976	0.9115
<i>B</i>	0.5317	0.5273	0.5753	0.5796	0.5053	0.3842	0.6527	0.7408	<i>B</i>	2.9740	2.7995	2.5509	2.7276	2.8039	2.7899	3.1640	2.5428
<i>r</i>	0.966	0.956	0.954	0.974	0.940	0.932	0.988	0.978	<i>r</i>	0.987	0.977	0.990	0.977	0.980	0.980	0.982	0.975
<i>E</i>	1.168	1.204	1.228	1.176	1.195	1.167	1.079	1.138	<i>E</i>	1.708	1.997	1.515	2.052	1.735	1.805	1.585	1.610
Stem volume, cm ³ :																	
<i>A</i>	2.2971	2.4315	2.2681	2.3283	2.3423	2.3857	2.3343	2.2203	<i>A</i>	0.0444	-0.3437	-0.1289	-0.1063	-0.1667	-0.3401	0.4642	1.1710
<i>B</i>	2.3692	2.2437	2.3906	2.3571	2.3081	2.2300	2.2661	2.3357	<i>B</i>	2.2803	2.7373	2.9859	2.5451	2.7646	3.0635	2.7880	2.0936
<i>r</i>	0.999	0.998	0.998	0.999	0.997	0.998	0.998	0.998	<i>r</i>	0.914	0.960	0.994	0.917	0.957	0.981	0.982	0.884
<i>E</i>	1.143	1.197	1.186	1.165	1.189	1.163	1.129	1.141	<i>E</i>	3.034	2.500	1.460	3.797	2.261	1.869	1.492	2.489
Stem wood volume, cm ³ :																	
<i>A</i>	2.2228	2.3488	2.1850	2.2342	2.2860	2.3322	2.2423	2.1212	<i>A</i>	2.2151	2.2264	2.2916	2.2380	2.2622	2.2953	2.3096	2.3151
<i>B</i>	2.3839	2.2685	2.4276	2.3905	2.3180	2.2345	2.2961	2.3732	<i>B</i>	2.4209	2.4150	2.3916	2.4223	2.3881	2.3171	2.2524	2.1830
<i>r</i>	0.998	0.998	0.998	0.998	0.997	0.998	0.998	0.998	<i>r</i>	0.999	0.997	0.997	0.997	0.997	0.995	0.995	0.991
<i>E</i>	1.161	1.195	1.197	1.182	1.194	1.158	1.120	1.143	<i>E</i>	1.147	1.256	1.227	1.234	1.187	1.285	1.185	1.278
Stem surface, cm ² :																	
<i>A</i>	2.9394	2.9761	2.8588	2.9115	2.9448	3.0001	2.8991	2.6670	<i>A</i>	1.7368	1.6000	1.8547	1.7161	1.7597	1.7230	2.0309	1.7583
<i>B</i>	1.4293	1.3651	1.4766	1.4551	1.3879	1.2862	1.3497	1.5389	<i>B</i>	2.2006	2.3156	2.1478	2.2230	2.2088	2.1832	1.7992	2.1514
<i>r</i>	0.996	0.993	0.994	0.996	0.992	0.993	0.987	0.997	<i>r</i>	0.996	0.991	0.994	0.996	0.988	0.993	0.965	0.986
<i>E</i>	1.153	1.204	1.193	1.159	1.191	1.167	1.181	1.107	<i>E</i>	1.248	1.430	1.300	1.272	1.403	1.307	1.446	1.359
Branch surface, cm ² :																	
<i>A</i>	2.4134	3.2692	3.3673	3.0569	3.0150	2.6937	2.5052	2.9252	<i>A</i>	0.7547	0.5460	0.7557	0.6732	0.6964	0.9594	1.0594	0.1608
<i>B</i>	2.3455	2.0191	1.7718	2.0065	2.0588	2.3271	2.5713	2.0170	<i>B</i>	2.1301	2.2716	2.0692	2.1760	2.1410	1.9180	1.7602	2.4391
<i>r</i>	0.988	0.979	0.994	0.972	0.946	0.953	0.958	0.976	<i>r</i>	0.978	0.991	0.975	0.988	0.970	0.936	0.980	0.953
<i>E</i>	1.498	1.622	1.259	1.786	1.989	2.155	1.791	1.450	<i>E</i>	1.640	1.416	1.708	1.506	1.680	2.101	1.305	1.889
Leaf surface, cm ² :																	
<i>A</i>	3.3016	3.3434	3.8393	3.4569	3.5698	3.6030	3.3632	3.6898	<i>A</i>	0.0172	-0.1228	-0.0417	0.0108	-0.1741	0.1313	0.4197	-0.4409
<i>B</i>	1.9329	1.9443	1.6169	1.8618	1.7789	1.8086	1.7983	1.6359	<i>B</i>	2.0127	2.0713	1.8274	1.9504	2.0436	1.8022	1.5626	2.2053
<i>r</i>	0.988	0.977	0.993	0.983	0.979	0.978	0.967	0.973	<i>r</i>	0.977	0.990	0.979	0.979	0.967	0.924	0.974	0.963
<i>E</i>	1.385	1.629	1.250	1.522	1.438	1.484	1.432	1.391	<i>E</i>	1.619	1.398	1.543	1.638	1.681	2.168	1.316	1.668
Stem dry weight, g:																	
<i>A</i>	2.0877	2.1413	2.0280	2.0769	2.0997	2.1843	1.9667	1.9906	<i>A</i>	0.3609	0.6097	0.8486	0.6369	0.5805	0.7138	0.3108	-0.2893
<i>B</i>	2.3718	2.2683	2.3981	2.3713	2.3176	2.1992	2.3040	2.2046	<i>B</i>	2.4044	2.3556	2.0653	2.2343	2.3143	2.1400	2.8242	2.3234
<i>r</i>	0.998	0.997	0.998	0.998	0.996	0.996	0.996	0.996	<i>r</i>	0.985	0.983	0.986	0.981	0.978	0.968	0.974	0.948
<i>E</i>	1.162	1.222	1.200	1.191	1.224	1.212	1.156	1.174	<i>E</i>	1.591	1.662	1.478	1.701	1.610	1.778	1.635	1.905
Stem wood dry weight, g:																	
<i>A</i>	1.2537	1.4021	1.0289	1.2543	1.1601	1.2164	1.2469	1.3543	<i>A</i>	1.0975	1.0295	1.4738	1.1669	1.2688	1.2812	1.0687	0.8703
<i>B</i>	2.2838	2.1083	2.2450	2.2292	2.2303	2.1520	2.1133	1.9961	<i>B</i>	1.9329	1.9443	1.6169	1.8618	1.7789	1.8086	1.7983	1.6359
<i>r</i>	0.996	0.994	0.997	0.991	0.988	0.982	0.994	0.997	<i>r</i>	0.988	0.977	0.993	0.983	0.979	0.978	0.967	0.971
<i>E</i>	1.238	1.291	1.230	1.432	1.407	1.530	1.198	1.130	<i>E</i>	1.385	1.436	1.326	1.411	1.410	1.599	1.220	1.659
Aboveground net production, g/yr:																	
<i>A</i>	1.3298	1.2763	1.6156	1.4008	1.4008	1.4008	1.4289	1.5646	<i>A</i>	1.0975	1.0295	1.4738	1.1669	1.2688	1.2812	1.0687	0.8703
<i>B</i>	2.1033	2.1745	1.8677	2.0520	2.0358	1.9115	1.9844	2.1158	<i>B</i>	2.1033	2.1745	1.8677	2.0520	2.0358	1.9115	1.9844	2.1158
<i>r</i>	0.991	0.990	0.991	0.990	0.990	0.990	0.985	0.973	<i>r</i>	0.991	0.990	0.991	0.990	0.985	0.973	0.991	0.960
<i>E</i>	1.356	1.436	1.326	1.411	1.410	1.599	1.220	1.659	<i>E</i>	1.356	1.436	1.326	1.411	1.410	1.599	1.220	1.659

growth in a more favorable period (1956–60) to that in the study period (1961–65) in the last row of Table 1H.

Coefficients of correlation, r , for the regressions of Tables 2 and 3 are mostly in excess of 0.95; for many of the tighter relations they are above 0.998. The high coefficients result from the wide range of tree sizes in the samples and have little value for interpreting the regressions (Whittaker and Woodwell 1968). More useful expressions of dispersions of values from the regression lines are given as “estimates

of relative error,” E and e (Whittaker and Woodwell 1968), computed from the standard error of estimate ($\text{SEE} = [\sum d^2/(n-1)]^{1/2}$), in which d is the difference between an actual value of y and one estimated from the regression equation for a given value of x , and n is the number of individuals for which x and y are measured). For a linear regression e is the SEE divided by the mean value of y ; a value of 0.10 for e suggests an expected error (or range including 68% of values, assuming these have normal distribution for a given value x)

Notes and Comments

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CORRECTIONS TO ALLOMETRIC EQUATIONS AND PLANT TISSUE CHEMISTRY FOR HUBBARD BROOK EXPERIMENTAL FOREST

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The allometric equations (Whittaker et al. 1974) and plant tissue chemistry (Likens and Bormann 1970, Whittaker et al. 1979) reported for the Hubbard Brook Experimental Forest (HBEF) in New Hampshire have proven valuable, not only for our own long-term studies of forest productivity and nutrient cycling (Likens et al. 1977, Bormann and Likens 1979, Likens 1985), but also to other researchers in similar forests (Morrison 1990, Aber et al. 1991, Burton et al. 1991) and to those making comparisons (Hogan and Morrison 1988). However, there are several errors in and additions to the published allometric equations and nutrient concentrations. It is important for anyone using these equations and concentrations to be aware of these errors and additions. In some cases, these errors have led to incorrect use of the equations (Martin 1977, Eickmeier 1988, Onega and Eickmeier 1991).

The recent whole-tree harvest at the HBEF (1983–1984) provided an opportunity to validate these allometric equations. When applied in the manner designed and intended by Whittaker et al. (1974), we found that they closely predict measured biomass. Although these equations have been used most often with diameter at breast height (dbh) as the only independent variable (Johannes et al. 1986, Cronan et al. 1987, Melancon and Lechowicz 1987), we found that equations based on parabolic volume (PV), which take tree height into account, are much better predictors than dbh alone.

Allometric Equations (Whittaker et al. 1974)

There are errors in column headings of tables in Whittaker et al. (1974) that will result in the equations

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being used inappropriately. The dependent variables, **Aboveground dry weight, g**; and **Log, aboveground dry weight, g**; in Tables 2 and 3 (Whittaker et al. 1974) are mislabeled. They should read *Total dry mass in grams*; and *Log, total dry mass in grams*; representing in reality the sum of aboveground plus belowground dry mass. The belowground mass of the species referred to in the tables is 14–20% of the total dry mass; thus use of the mislabeled equations leads to an overestimate of aboveground biomass of a northern hardwood forest by that amount. Correct equations for aboveground biomass for the four species are as follows:

Sugar maple (*Acer saccharum*)

$$\begin{aligned}\log_{10}(\text{aboveground dry mass in grams}) \\ = 2.0537 + 2.4793 \log_{10}(\text{dbh in centimetres}) \\ \log_{10}(\text{aboveground dry mass in grams}) \\ = -0.0201 + 0.9768 \log_{10}(\text{PV in cubic centimetres})\end{aligned}$$

Beech (*Fagus grandifolia*)

$$\begin{aligned}\log_{10}(\text{aboveground dry mass in grams}) \\ = 2.1112 + 2.4620 \log_{10}(\text{dbh in centimetres}) \\ \log_{10}(\text{aboveground dry mass in grams}) \\ = 0.1733 + 0.9526 \log_{10}(\text{PV in cubic centimetres})\end{aligned}$$

Yellow birch (*Betula alleghaniensis*); (referred to as *B. lutea* in Whittaker et al. 1974)

$$\begin{aligned}\log_{10}(\text{aboveground dry mass in grams}) \\ = 2.1047 + 2.4417 \log_{10}(\text{dbh in centimetres}) \\ \log_{10}(\text{aboveground dry mass in grams}) \\ = 0.0974 + 0.9615 \log_{10}(\text{PV in cubic centimetres})\end{aligned}$$

Red spruce (*Picea rubens*)

$$\begin{aligned}\log_{10}(\text{aboveground dry mass in grams}) \\ = 2.1735 + 2.1936 \log_{10}(\text{dbh in centimetres}) \\ \log_{10}(\text{aboveground dry mass in grams}) \\ = 0.8219 + 0.7966 \log_{10}(\text{PV in cubic centimetres}).\end{aligned}$$

We have reviewed the original data from which the allometric equations presented by Whittaker et al. (1974) were developed. The coefficients are correct as published; the problem is limited to mislabeling in the publishing of the tables. The published biomass and nutrient estimates for watershed six (W 6) of the HBEF (Whittaker et al. 1974, 1979) were not affected by this error.

The heading in Table 4, subsection F (Whittaker et al. 1974) **Regression predictions: Biomass aboveground, t/ha** [i.e., Mg/ha], is the projected maximum standing crop biomass at steady state for W 6 as determined by the current productivity. These values are not the biomass on the watershed in 1965. The 1965 biomass on W 6 is given in subsection D of Table 4.

Biomass of Spruce Needles (Whittaker et al. 1974)

Although not an error as such, the equations in Tables 2 and 3 for biomass of red spruce needles (**current twig and leaf production, g/yr:** and **Log current twig and leaf production g/yr:**) are for current needles and twigs only (Whittaker et al. 1974). No equations for older needles were presented, although the mass of older needles was determined in the original dimension analysis. Because of the recent interest in red spruce decline in the northeastern U.S. (e.g., Friedland et al. 1991) it is important to remind users that the published equations are for current twigs and needles only. The equations for older needles, based on both dbh and parabolic volume (PV), are given below:

$$\begin{aligned}\log_{10}(\text{older needle mass in grams}) \\ = 1.6119 + 1.6991 \log_{10}(\text{dbh in centimetres}) \\ \log_{10}(\text{older needle mass in grams}) \\ = 0.5764 + 0.6164 \log_{10}(\text{PV in cubic centimetres}).\end{aligned}$$

Either one of these equations, together with the published equations for current twigs and needles (Whittaker et al. 1974) will give the total needle mass plus twig mass for red spruce in the northern hardwood forest. Current needle/twig ratios were not given in Table 1 of Whittaker et al. (1974). We have calculated current needles alone to be 79% of the dry mass of the needle plus twig masses estimated by the equation.

Mountain Maple (Whittaker et al. 1974)

We believe that the equations for mountain maple (*Acer spicatum*) as reported in Tables 2 and 3 of Whittaker et al. (1974) instead may be for striped maple (*Acer pensylvanicum*). Our support for this conclusion is that the original dimension analysis data include stems of unreasonable diameters and heights for mountain maple. Mountain maple is a shrub, usually 2 or 3 m tall with commonly occurring diameters of 4–5 cm (although certainly larger sizes are known at the HBEF). In the original dimension analysis data for this species Whittaker et al. (1974) analyzed stems 10 cm in dbh and 10 m tall. Thus, it is our opinion that these equations should be used with caution. At the HBEF these species are of very minor abundance and contribute very little (<1%) to the total biomass. Thus we have not provided a corrected aboveground biomass estimator equation for this species.

Plant Tissue Chemistry

The concentration of phosphorus in roots (0.37%) recorded for sugar maple by Whittaker et al. (1979), and Likens and Bormann (1970), appears high in comparison with P concentrations in the other parts of this species and with other species, including the congener, mountain maple. More recent analyses (Fahey et al. 1988, Yanai 1990) indicate that P concentrations are

≈1/10 of the Whittaker et al. (1979) values. Thus, we suggest that 0.04% is more representative of P concentrations in sugar maple roots for the HBEF (Fahey et al. 1988, Yanai 1990). Recalculation of the phosphorus content in the biomass of sugar maple roots on W 6 in 1965 using the lower value results in a reduction of estimated P content of sugar maple roots from 34.7 kg/ha to 4.1 kg/ha, and for the total biomass of all species the reported phosphorus value of 88 kg/ha in Whittaker et al. (1979) should be 56 kg/ha.

Comparison of Two Estimates of Forest Biomass at the HBEF

The harvesting of watershed 5 in 1983–1984 as part of an experimental whole-tree harvest treatment provided an opportunity to compare estimates of biomass using allometry with results of actual weighing of total aboveground biomass. Total forest living biomass was estimated on three 0.25-ha plots using a total stem inventory (≥10 cm dbh) and the allometric equations (Whittaker et al. 1974) based on parabolic volume (PV). Tree heights in 1983, needed to calculate PV, were obtained from standing and felled trees at the time of the cut (winter of 1983–1984). Tree diameter to height relationships had changed significantly since the original tree height measurements in 1965, with trees of a given diameter being much taller (3–4 m) in 1983 than a tree of the same diameter in 1965.

Trees from the three 0.25-ha plots were felled, chipped into semi-trailer vans and weighed separately for each plot. Chips blown into vans were sampled (Hornbeck and Kropelin 1983) for wet/dry mass conversion and the vans were weighed to get total biomass. Logs selected for timber were sampled from freshly cut ends for wet/dry mass conversion and weighed on the trucks.

Slash remaining on the watershed after the cut was sampled by size classes on $N = 27$ 10 × 10 m plots, and on $N = 108$ 2 × 2 m and 1 × 1 m plots to estimate amounts of material present on the plots that would have been included in the allometry estimates, but which was not weighed in the harvesting process; 19 ± 2.4 Mg/ha of tree debris (mostly broken-off branches of various sizes) were left on the watershed. Since the plots harvested for biomass comparison were monitored carefully during clearing and skidding, less than the watershed average of 19 Mg/ha was left on these plots, but these plots were not sampled separately for slash.

The comparative results for the three plots are summarized in Table 1. Estimates based on allometry were ≈12 Mg/ha higher than the weighed amount. However when the weighed amounts are corrected for slash, that is increased by ≈50–75% of what was the average slash for the watershed as a whole (50–75% because of the care with which the biomass plots were harvested), the

TABLE 1. Weighed aboveground biomass on each of three 0.25-ha plots, in comparison with aboveground biomass estimated by allometry, in the northern hardwood forest at Hubbard Brook Experimental Forest (HBEF) in 1983–1984.

Plot	Biomass (Mg/ha)			Estimate by allometry	
	Measured value				
	Chips	Logs	Total		
Blue	120.5	28.5	149	176	
White	167.2	28.0	195	215	
Green	164.1	32.9	197	186	
Mean			180	192	
Estimated slash (Mg/ha)			9–14		
Total (Mg/ha)			189–194		

comparison shows an excellent predictability of the Hubbard Brook allometric equations when linked to changing tree diameter to height ratios. These results provide a strong verification of the use of allometric equations developed by Whittaker et al. (1974) in the northern hardwood forest.

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of $\pm 10\%$. In the logarithmic regressions the SEE is itself a logarithm to be added to or subtracted from $\log y$; its antilog is consequently a factor (E) by which a given value of y is to be divided or multiplied. A value for E of 1.10 thus suggests an expected error range (including 68% of values, assuming these have lognormal distribution for a given value of x) from $1.10y$ to $y/1.10$. In Tables 2 and 3 values of E are 1.10–1.20 for some of the tighter relationships, but range upward to 1.5–2.0 for looser relationships (particularly of branch dimensions to stem dimensions) (cf. Whittaker and Woodwell 1968, Andersson 1970, 1971, Reiners 1972).

Estimates of biomass and production from these regressions are affected by the high dispersions, a systematic error of underestimation from the logarithmic calculations (Baskerville 1972, Westman 1971), and a tendency to overestimate values for large trees and therefore of stands (Ogawa et al. 1965, Whittaker and Woodwell 1968). We have sought to reduce the effects of these by our choice of regressions, by selection of large trees of average condition for the sample sets, and by prediction of production from estimated volume increments using actual radial increments of large trees, rather than regressions on diameter. The problem of confidence limits for treatment of forest samples by logarithmic regressions is unsolved. As one check on the nature and size of errors the regressions for sets of sample trees have been used to predict, by means of the various independent variables, the mass and production values of trees for which these have been measured. The predictions are not consistently low or high; direction and size of the error for the sum of given set of trees is largely determined by the error for the one or few largest trees in the set.

Forest characteristics

Volume and area.—Table 4 summarizes various dimensions for forests in the three elevation belts at Hubbard Brook, together with the Brookhaven forest and five stands from the Great Smoky Mountains (Whittaker 1966, Olson 1971). Values for the latter are based on stand measurements and application of estimative ratios and regressions from the literature; no dimension analyses were undertaken. The Great Smoky Mountains samples include a rather open, red oak-white oak (*Quercus borealis-Q. alba*) forest (sample number 28) at 1,390 m on an open SW-facing slope of 15° inclination, a gray-beech (*Fagus grandifolia*) gap forest (25) at 1,580 m on an open N-25° slope, a beech gap forest (26) on the S-32° slope opposite the preceding, a mixed deciduous cove forest (23) at 1,310 m on a concave NNW-25° slope, and a young tulip tree (*Liriodendron tulipifera*) forest (22) on a lower NE-10°

slope at 700 m. We chose these stands in order to compare Hubbard Brook with mature but small broadleaf forests of high elevations (28, 25, 26), a young forest of high productivity (22), and a mature, large climax forest (23).

In many of their dimensions the Hubbard Brook forests are similar to the two beech gap stands (25, 26). Parabolic and stem wood volumes (Table 4C) at Hubbard Brook are similar at low elevations to those of the south-slope beech gap, smaller at high elevations than those of the north-slope beech gap. Basal areas (Table 4A, also Bormann et al. 1970) are in the same range for Hubbard Brook and the beech gap samples, but the low-elevation trees at Hubbard Brook are taller (weighted mean heights). Means weighted by tree sizes (Table 4 footnote) permit more effective comparison of stand ages, heights, and radial increments than do simple arithmetic means. Weighted mean height, computed by dividing stand parabolic volume by basal area, has the effect of weighting heights by basal area. Weighted mean ages also are in the same range as those of the beech forests. The Hubbard Brook forests are, however, faster growing and more productive stands than the beech forests, as indicated by their weighted mean radial increments at breast height (Table 4A) and their estimated volume increments (Table 4A). Leaf surface area indices (Table 3B) at Hubbard Brook, 5.5–6.2 m^2/m^2 , compare with 4.4–6.2 in the beech and cove forests; stem surface areas are smaller than in these stands. Branch surface area estimates at Hubbard Brook are higher than any estimates for high-elevation forests. The computations overestimate branch surface (Whittaker and Woodwell 1967), but high values should be expected because of both the heavy branches of the Hubbard Brook trees and the finely divided twigs of *Betula*, *Picea*, and *Abies*.

Biomass.—Biomass values for the Hubbard Brook forests are summarized in Table 5. As shown by Bormann et al. (1970) the proportion of the forest stand that the three major species make up together decreases from the low and middle to the high elevation belt. *Fagus* biomass decreases from low elevations to high; *Acer saccharum* and *Betula lutea* have their highest biomasses at middle elevations. Total stand biomass, and percent of that biomass in stem wood, decrease toward higher elevations; leaf and dead branch wood biomass, in contrast, increase. (The older leaves of *Picea* and *Abies* are responsible for the higher leaf biomass in the high-elevation sample.) Total aboveground biomasses are in the same range as those of high-elevation broadleaf forests in the Great Smoky Mountains (Table 4D). As in other closed forests the fraction of stand biomass in shrubs and herbs is less than 1%

TABLE 3. Regressions for sets of sample trees in the Hubbard Brook forest. Estimates of constants a and b in the linear regression equation $y = a + bx$, and A and B in the logarithmic regression equation $\log_{10}y = A + B\log_{10}x$, are given for different dependent variables on parabolic volume (VPO), conic surface (SC), and estimated volume increment (EVI) as independent variables; r is the coefficient of correlation, e and E are estimates of relative error. See Table 2 for numbers of trees in samples.

<i>Acer saccharum</i>	<i>Betula lutea</i>	<i>Fagus grandifolia</i>	Low elevations	Mid elevations	High elevations	<i>Acer spicatum</i>	<i>Picea rubens</i>
A. Regressions on parabolic volume (VPO), cm³ (x)							
Linear, bark volume, cm ³ (y):							
<i>a</i>	9588.3	3755.4	-1288.5	3301.8	-1821.5	3725.6	166.17
<i>b</i>	0.0828	0.0739	0.0639	0.0764	0.0823	0.0909	0.1362
<i>r</i>	0.959	0.983	0.990	0.964	0.941	0.875	0.972
<i>e</i>	0.389	0.205	0.196	0.364	0.443	0.653	0.257
Linear, wood volume, cm ³ :							
<i>a</i>	38158.	14379.	-17476.	33100.	15923.	-1418.9	134.33
<i>b</i>	0.6637	0.6908	0.8837	0.7052	0.7367	0.8701	0.9458
<i>r</i>	0.997	0.996	0.995	0.985	0.990	0.995	0.998
<i>e</i>	0.104	0.101	0.132	0.231	0.160	0.129	0.071
Linear, stem dry weight, g:							
<i>a</i>	34859.	11330.	-8796.2	15006.	9461.1	16901.	104.99
<i>b</i>	0.4594	0.4185	0.5580	0.4691	0.4839	0.4966	0.5045
<i>r</i>	0.997	0.998	0.997	0.990	0.990	0.966	0.999
<i>e</i>	0.105	0.080	0.107	0.192	0.165	0.321	0.056
Linear, branch wood and bark dry weight, g:							
<i>a</i>	-25584.	-114410.	-65051.	-22674.	-38985.	13225.	-51.33
<i>b</i>	0.2520	0.5915	0.4209	0.3420	0.3756	0.3069	0.2511
<i>r</i>	0.978	0.916	0.903	0.839	0.871	0.767	0.909
<i>e</i>	0.347	0.709	0.808	0.973	0.794	0.984	0.553
Log, stem dry weight, g:							
<i>A</i>	0.0936	0.2550	0.1329	0.1733	0.1428	0.1784	0.2601
<i>B</i>	0.9364	0.8974	0.9294	0.9186	0.9244	0.9215	0.8679
<i>r</i>	0.999	0.999	0.998	0.999	0.998	0.997	0.996
<i>E</i>	1.095	1.130	1.175	1.150	1.156	1.180	1.157
Log, stem wood dry weight, g:							
<i>A</i>	0.0100	0.1442	0.0755	0.0798	0.0810	0.1217	0.1465
<i>B</i>	0.9420	0.9081	0.9346	0.9270	0.9281	0.9242	0.8801
<i>r</i>	0.999	0.999	0.998	0.999	0.998	0.998	0.996
<i>E</i>	1.098	1.117	1.168	1.151	1.156	1.171	1.159
Log, stem bark dry weight, g:							
<i>A</i>	-0.6596	-0.3493	-0.7342	-0.5300	-0.7182	-0.7499	-0.3176
<i>B</i>	0.9004	0.8337	0.8679	0.8625	0.8887	0.9024	0.7958
<i>r</i>	0.996	0.996	0.995	0.991	0.989	0.984	0.993
<i>E</i>	1.252	1.246	1.300	1.447	1.389	1.499	1.204
Log, branch wood and bark dry weight, g:							
<i>A</i>	-1.8222	-1.1969	-0.5738	-1.0608	-1.2826	-1.5444	-1.4382
<i>B</i>	1.1644	1.0926	0.9839	1.0476	1.1041	1.1680	1.1896
<i>r</i>	0.980	0.966	0.986	0.969	0.969	0.980	0.967
<i>E</i>	1.944	2.329	1.639	2.291	1.975	1.804	1.622
Log, current twig and leaf dry weight, g:							
<i>A</i>	-0.4933	-0.5391	0.2062	-0.2975	-0.1963	-0.3770	-0.2574
<i>B</i>	0.7566	0.7599	0.6246	0.7153	0.7026	0.7595	0.6757
<i>r</i>	0.981	0.967	0.990	0.976	0.971	0.982	0.964
<i>E</i>	1.516	1.789	1.299	1.652	1.526	1.442	1.451
Log, aboveground dry weight, g:							
<i>A</i>	0.1912	0.2440	0.4122	0.3070	0.2700	0.1869	0.6436
<i>B</i>	0.9536	0.9504	0.9248	0.9357	0.9479	0.9699	0.8478
<i>r</i>	0.997	0.993	0.995	0.995	0.994	0.994	0.994
<i>E</i>	1.210	1.378	1.298	1.329	1.278	1.287	1.201
Log, root system dry weight, g:							
<i>A</i>	-0.1007	-0.2873	0.1748	-0.0537	-0.0679	-0.2566	0.7017
<i>B</i>	0.8664	0.9087	0.8290	0.8583	0.8739	0.9125	0.6767
<i>r</i>	0.994	0.985	0.991	0.993	0.982	0.991	0.963
<i>E</i>	1.301	1.588	1.400	1.364	1.511	1.346	1.457
Log, aboveground net production, g/yr:							
<i>A</i>	-0.4261	-0.4930	-0.1340	-0.2295	-0.2732	-0.2048	-0.0193
<i>B</i>	0.8280	0.8528	0.7249	0.7916	0.8088	0.8061	0.7461
<i>r</i>	0.990	0.983	0.993	0.987	0.983	0.980	0.989
<i>E</i>	1.398	1.590	1.282	1.494	1.442	1.496	1.246

TABLE 3. (continued)

<i>Acer saccharum</i>	<i>Betula lutea</i>	<i>Fagus grandifolia</i>	Low elevations	Mid elevations	High elevations	<i>Acer spicatum</i>	<i>Picea rubens</i>
B. Regressions on conic stem surface (SC), cm² (x)							
Linear, stem bark surface, cm ² (y):							
<i>a</i>	5136.7	3911.9	-1300.1	3084.3	2492.2	892.60	1240.6
<i>b</i>	1.0572	1.0195	1.2030	1.0839	1.0909	1.1809	1.0123
<i>r</i>	0.998	0.996	0.997	0.995	0.992	0.992	0.920
<i>e</i>	0.057	0.078	0.071	0.096	0.098	0.105	0.318
Linear, stem wood surface, cm ² :							
<i>a</i>	5038.2	3457.7	-1358.6	2965.0	2775.2	784.53	323.4
<i>b</i>	0.9860	0.9649	1.1600	1.0245	1.0282	1.1132	1.1794
<i>r</i>	0.998	0.996	0.997	0.993	0.991	0.994	0.998
<i>e</i>	0.060	0.074	0.073	0.111	0.105	0.091	0.054
Linear, branch bark surface, cm ² :							
<i>a</i>	-434910.	-866540.	-319490.	-407780.	-479720.	-266080.	-10014.
<i>b</i>	16.756	40.318	16.796	21.227	25.241	31.722	7.7147
<i>r</i>	0.966	0.901	0.945	0.817	0.764	0.824	0.921
<i>e</i>	0.365	0.582	0.436	0.880	0.929	0.70	0.493
C. Regressions on estimated volume increment (EVI), cm³/yr (x)							
Linear, stem wood production, g/yr (y):							
<i>a</i>	1076.3	3.0234	89.449	628.53	646.79	377.16	15.204
<i>b</i>	0.5638	0.5659	0.6710	0.5599	0.5519	0.6158	0.6965
<i>r</i>	0.982	0.980	0.994	0.981	0.977	0.956	0.987
<i>e</i>	0.185	0.207	0.101	0.209	0.186	0.243	0.166
Linear, stem bark production, g/yr:							
<i>a</i>	130.88	6.9536	11.703	19.592	-8.4375	56.605	6.9432
<i>b</i>	0.0668	0.0603	0.0468	0.0633	0.0642	0.0627	0.0924
<i>r</i>	0.967	0.984	0.986	0.958	0.968	0.851	0.969
<i>e</i>	0.255	0.179	0.152	0.334	0.249	0.468	0.223
Linear, branch production, g/yr:							
<i>a</i>	561.36	-2946.3	-2639.2	5.9570	-3307.4	319.29	-20.531
<i>b</i>	0.7399	1.4530	1.3999	0.9832	1.3945	0.8727	1.1122
<i>r</i>	0.869	0.785	0.770	0.697	0.886	0.743	0.936
<i>e</i>	0.603	0.932	1.012	1.167	0.644	0.735	0.432
Linear, current twig and leaf production, g/yr:							
<i>a</i>	-287.74	-1737.0	-1322.7	-542.59	-952.01	956.55	40.249
<i>b</i>	0.8512	0.8768	1.0549	0.8614	0.8898	0.9627	0.6705
<i>r</i>	0.894	0.772	0.859	0.815	0.867	0.701	0.940
<i>e</i>	0.576	0.970	0.657	0.849	0.608	0.762	0.329
Log, stem wood production, g/yr:							
<i>A</i>	0.1935	-0.0041	0.1056	0.00234	0.2342	0.0280	-0.0862
<i>B</i>	0.9098	0.9417	0.9293	0.9488	0.8943	0.9504	0.9859
<i>r</i>	0.989	0.999	0.998	0.996	0.994	0.994	0.983
<i>E</i>	1.416	1.139	1.139	1.251	1.252	1.272	1.155
Log, stem bark production, g/yr:							
<i>A</i>	-0.5274	-0.6220	-0.5939	-0.5974	-0.6071	-0.7485	-0.5916
<i>B</i>	0.8637	0.8580	0.8142	0.8524	0.8513	0.8943	0.8726
<i>r</i>	0.993	0.997	0.994	0.989	0.989	0.981	0.985
<i>E</i>	1.314	1.205	1.251	1.418	1.356	1.475	1.235
Log, branch wood and bark production, g/yr:							
<i>A</i>	-0.1587	0.1075	0.2928	0.0444	0.1494	-0.0929	-1.3586
<i>B</i>	0.9947	0.9572	0.8998	0.9461	0.9473	0.9921	1.5052
<i>r</i>	0.965	0.971	0.980	0.961	0.983	0.961	0.940
<i>E</i>	2.027	1.931	1.608	2.140	1.531	1.889	2.104
Log, current twig and leaf production, g/yr:							
<i>A</i>	0.7154	0.6370	1.0982	0.6803	1.0287	0.6971	0.0141
<i>B</i>	0.7896	0.7838	0.6868	0.7863	0.7022	0.8098	0.9547
<i>r</i>	0.956	0.957	0.961	0.960	0.948	0.938	0.929
<i>E</i>	1.879	1.931	1.667	1.894	1.752	1.941	1.680

(Table 4D, estimated from data of Siccamo et al. 1970).

Production.—A summary of production estimates (for 1956–60) for the Hubbard Brook forests is given in Table 5. Total production decreases to-

ward higher elevations; and in productivity, as in other dimensions, the two lower elevation belts are more like each other than either is like the high-elevation belt. The percentages show change of emphasis in production with change in elevation. In

TABLE 4. Forest comparisons: Hubbard Brook, New Hampshire; Brookhaven National Laboratory, New York; and Great Smoky Mountains National Park, Tennessee. The first four columns are based on dimension analyses, the last five columns on estimative ratios and regressions applied to forest samples

Sample number and forest dimensions	Hubbard Brook, elevation belts			Brookhaven		Great Smoky Mountains			
	Low	Mid	High	Oak-pine young	Red oak-white oak	Gray beech, north	Gray beech, south	Upper cove forest	Tulip tree, young
Sample number	71	72	73	60	28	25	26	23	22
A. Stand characteristics:									
Stems (>1 cm)/0.1 ha	129.	129.	242.	185.	260.	217.	214.	145.	182.
Stem basal area, m ² /ha	26.3	23.7	22.0	15.6	22.0	22.0	27.7	54.2	34.2
Bark/stem basal area, %	8.2	10.2	9.7	27.2	13.1	5.9	5.7	7.5	9.9
Canopy height, m	20.	20.	15.	9.	9.	16.	16.	36.	27.
Weighted mean height, ^a m	16.9	16.7	10.8	7.6	7.5	13.4	15.6	34.0	22.4
Weighted mean radial increment, ^a mm/yr	1.118	1.234	.745	.86	.79	.46	.62	.73	2.28
Increment/wood basal area, %	1.93	2.15	2.19	2.88	2.20	1.35	1.50	.89	4.29
Weighted mean age ^a	124.	95.	83.	43.	146.	84.	135.	222.	29.
B. Surface:									
Conic stem wood surface, m ² /m ²	.339	.296	.298	.21	.16	.50	.40	.50	.51
Stem wood surface, m ² /m ²	.397	.351	.371	.29	.2	.6	.5	.6	.6
Branch surface est., m ² /m ²	1.98	2.37	1.64	1.2	1.3	1.4	1.5	1.6	2.2
Leaf surface, m ² /m ²	6.2	5.7	5.5	3.8	3.5	4.4	5.2	6.2	7.4
C. Volume:									
Parabolic wood volume, m ³ /ha	204.	179.	108.	70.	72.	135.	204.	851.	346.
Stem volume, m ³ /ha	194.	172.	121.	75.4	65.	120.	185.	720.	310.
Stem wood volume, m ³ /ha	176.	155.	103.	59.4	58.	110.	170.	650.	275.
Estimated volume increment, cm ³ /m ² /yr	379.	365.	223.	159.	116.	162.	277.	547.	1444.
D. Biomass aboveground:									
Trees, ^b t/ha	161.5	151.3	101.8	64.	86.	130.	170.	500.	220.
Percent in stem wood	65.0	61.7	59.5	55.0	53.6	66.6	69.3	80.0	68.2
" stem bark	6.8	6.2	6.9	12.8	7.1	4.4	4.6	7.4	7.6
" branches	26.3	30.0	30.0	24.9	35.5	26.8	23.4	11.9	22.0
" twigs and leaves	1.9	2.1	3.6	7.3	3.8	2.2	2.7	.7	2.2
Shrubs, t/ha	.15	.13	.25	1.58	1.7	.01	.1	.07	.2
Herbs, t/ha	.04	.05	.13	.02	.1	.5	.2	.4	.02
Total, t/ha	161.7	151.5	102.3	65.6	88.	130.	170.	500.	220.
Biomass accumulation ratio	14.4	14.5	13.0	7.7	15.5	19.5	18.8	45.6	9.1
E. Net production, aboveground:									
Trees, ^c g/m ² /yr	1118.6	1032.5	769.1	796.	500.	600.	875.	1050.	2400.
Percent in stem wood	28.5	28.8	26.6	18.7	20.3	24.5	29.7	42.0	41.4
" stem bark	3.0	3.1	3.1	3.3	3.2	2.6	2.4	4.7	5.1
" branches	29.7	29.1	27.2	24.3	17.7	18.3	19.1	16.5	30.8
" twigs and leaves	35.7	36.3	39.7	50.9	58.8	54.6	48.8	36.8	22.7
" fruits, etc. ^d	3.1	2.7	3.4	2.8	—	—	—	—	—
Shrubs, g/m ² /yr	4.3	3.8	7.2	60.7	57.	.2	4.	1.5	7.
Herbs, g/m ² /yr	4.1	4.6	13.3	2.2	10.6	47.6	17.2	37.5	1.5
Total, g/m ² /yr	1127.0	1040.9	789.6	859.	568.	668.	906.	1097.	2408.
Production/leaf area, g/m ²	180.	181.	140.	226.	159.	143.	166.	170.	324.
F. Regression predictions:									
Biomass, aboveground, t/ha	411.	386.	365.	161.	85.	216.	146.	386.	358.
Production, aboveground, g/m ² /yr	1062.	1027.	995.	964.	710.	823.	751.	1029.	1077.

^a For weighted means ages of trees are weighted by their parabolic volumes, heights by basal areas, and radial increments by conic surfaces. The mean radial increment is for the low (1961-65) growth period at Hubbard Brook; corresponding increments for 1956-60 are 1,343, 1,526, and 0.912 mm/yr.

^b Includes tree biomasses (Table 4) plus estimates for saplings and tree seedlings.

^c Include tree productions (Table 5) plus estimates for saplings and tree seedlings, and values for flowers and bud scales based on litter collections.

^d Fruits plus flowers and bud scales.

particular, stem wood production decreases relative to leaf production toward higher elevations; such a shift would be expected toward a more rigorous environment. Aboveground net production and foliage production values are in the same range as those for the high-elevation beech forests (Table 4E, Whittaker 1966, Olson 1971). Aboveground productivities of undergrowth plants have been estimated from the data of Siccama et al. (1970), applying ratios (Whittaker 1962) to the clipping data for seedlings, saplings, and shrubs.

The litter collections of Gosz et al. (1972) supplement the results from dimension analysis. Gosz' data (for somewhat different elevation belts) suggest bud-scale productions of 10.0, 9.0, and 7.4 g/m²/yr and flower productions of 3.3, 3.2, and 1.4 g/m²/yr for the three belts from low to high elevation. These values have been included in the total production estimates in Table 4E. Gosz' data for leaf litter production are reasonably consistent with the results of the dimension analysis; his values, uncorrected, of 288, 282, and 255 g/m²/yr of leaves

TABLE 5. Biomass summary for the Hubbard Brook forests, tree stratum. All units dry g/m²

Elevation belt, sample number, and species	Stem "heartwood"	Stem "sapwood"	Stem bark	Branch live wood and bark	Dead branch wood	Current twigs	Leaves (1966)	Fruits	Aboveground total	Root crown	Roots	Belowground total	Full total
Low elevations (71)													
<i>Acer saccharum</i>	33	3578	496	860	13	4	102	7	5093	356	644	1000	6093
<i>Betula lutea</i>	109	1942	268	770	39	4	68	8	3208	271	425	696	3904
<i>Fagus grandifolia</i>	95	4542	303	2329	169	8	120	5	7571	354	969	1323	8894
<i>Acer spicatum</i>	11	2	7	1			1		22	3	2	5	27
<i>Picea rubens</i>	16	3	4	2			3		28	4	6	10	38
<i>Fraxinus americana</i>	50	7	12				1		70	5	8	13	83
<i>Acer pensylvanicum</i>	35	5	30	4			1		75	5	8	13	88
<i>Prunus pensylvanica</i>	12	2	4						18	2	2	4	22
Total	237	10186	1086	4016	228	16	296	20	16085	1000	2064	3064	19149
Middle elevations (72)													
<i>Acer saccharum</i>	41	4293	496	1465	74	8	169	1	6547	492	841	1333	7880
<i>Betula lutea</i>	266	2008	259	1684	34	2	47	3	4303	374	609	983	5286
<i>Fagus grandifolia</i>	119	2370	153	945	214	3	55	9	3868	262	555	817	4685
<i>Acer spicatum</i>	37	6	20	3			2		68	11	8	19	87
<i>Picea rubens</i>	42	7	10	6			7		72	9	17	26	98
<i>Acer pensylvanicum</i>	47	7	30	5			2		91	9	12	21	112
<i>Prunus pensylvanica</i>	55	7	28	1			2		93	8	13	21	114
Total	426	8852	935	4182	337	13	284	13	15042	1165	2055	3220	18262
High elevations (73)													
<i>Acer saccharum</i>	43	1514	211	756	93	3	69		2689	252	284	536	3225
<i>Betula lutea</i>	140	1255	176	798	79	4	71	6	2529	269	264	533	3062
<i>Fagus grandifolia</i>	69	1720	122	663	73	5	76	6	2734	340	311	651	3385
<i>Acer spicatum</i>	80	13	32	6			5		136	30	20	50	186
<i>Picea rubens</i>	2	276	43	67	37	1	44	1	471	59	105	164	635
<i>Abies balsamea</i>	2	290	45	76	38	1	44	1	497	62	109	171	668
<i>Acer pensylvanicum</i>	83	12	49	8			4		156	19	21	40	196
<i>Prunus pensylvanica</i>	1	59	8	30	2		5		105	12	13	25	130
<i>Acer rubrum</i>	1	56	8	16	2		3		86	9	11	20	106
<i>Betula papyrifera</i>	9	387	50	179	11	2	28	2	668	75	73	148	816
<i>Pyrus americana</i>	21	3	11	2			1		38	6	5	11	49
<i>Prunus virginiana</i>	1	.1	.3						1			.3	1
Total	267	5742	691	2677	351	16	350	16	10110	1133	1216	2349	12459
Area-weighted means	315	7907	872	3526	316	15	315	16	13281	1112	1714	2826	16107

for the elevation belts may be compared with the 1966 leaf masses in Table 5 and the 1961–65 leaf totals in Table 6. To Gosz' leaf weights should be added his data on insect frass (with production equivalents suggested): 28.7 (33.6), 20.7 (24.2), and 8.2 (9.6) g/m²/yr. (The values in Table 6 include corrections for insect consumption.) With these additions Gosz' leaf litter values become 322, 306, and 265 g/m²/yr; and true foliage production should be still higher (because of insensible losses). Gosz' collections were taken in a different year (1969) from that of the dimension analysis (1966). Year-to-year variation in leaf fall (cf. Sykes and Bunce 1970) at Hubbard Brook is reflected in autumn collections of 340 and 270 g/m²/yr in 1968 and 1969 below the watershed of this study (Stuart Fisher, *pers. comm.*, Gosz et al. 1972).

The Brookhaven program computes stem wood volume growth by 5- or 10-yr periods throughout the life of each tree, and regressions of these period

volume increments on current dbh for a set of trees (Whittaker and Woodwell 1968). Fig. 2 plots means of actual volume increments by 5-yr periods for the 10 largest trees analyzed, and estimated sums for the three elevation belts (applying the regressions to the stand counts). A striking decrease in volume growth occurred from 1956–60 to 1961–65, the latter a period of drought. Forest net primary production was computed and summarized for both periods, and estimates for the period of higher production, 1956–60, are given, together with the totals by elevation belts for the 1961–65 estimates (Table 6). The 1956–60 leaf production estimates seem consistent with Gosz' litter data when effects on the latter of herbivore consumption and insensible loss are considered.

Stand dynamics

Stem sizes and ages.—Fig. 3 plots numbers of stems on a logarithmic scale against diameter classes.

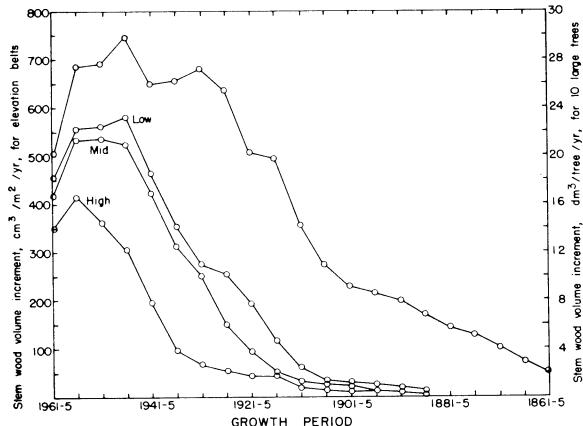


FIG. 2. Patterns of stem wood volume growth for the Hubbard Brook forest, based on analysis of volume increments by 5-yr periods. The upper curve shows mean volume growth for 10 large trees, in $\text{dm}^3/\text{tree}/\text{year}$ as indicated on the right ordinate. The three lower curves show total forest volume growth by trees now living for the three elevation belts, in $\text{cm}^3/\text{m}^2/\text{year}$ as indicated on the left ordinate.

Despite the wide dispersions of ages for a given diameter, these plots give some indications of stand dynamics. A straight line would be expected in a steady-state stand in which the rates of mortality and of diameter growth were constant for different age and size classes. Climax stands with essentially continuous and equal mortality and replacement of trees give evenly convex curves because of the decrease in diameter growth rate with increasing age (Whittaker 1956). Young (but not single-aged) stands with heavy recent reproduction usually give straight or concave curves, and young stands with peak reproductive periods in the past give curves of more complex form with convexities representing periods of reproduction.

All species are combined by elevation belts in the upper part of Fig. 3. The stem diameter distributions at low and middle elevations are similar, and the same smoothed curve has been drawn for these. A convexity in the 16–30 cm classes is followed by a slower increase in stem numbers up to the smallest class (1–5 cm); a past pulse of heavier reproduction corresponding to the 16–30 cm classes is suggested. The data for high elevations suggest a slowing of reproduction during the period corresponding to the 31–40 cm classes, and more rapid reproduction for the 15–30 cm class and continuing to the present. The crossing of the curves reflects the increased density of smaller and younger trees toward high elevations as shown also in the means of Table 4A and the data of Bormann et al. (1970).

Age-diameter relations of the three major species

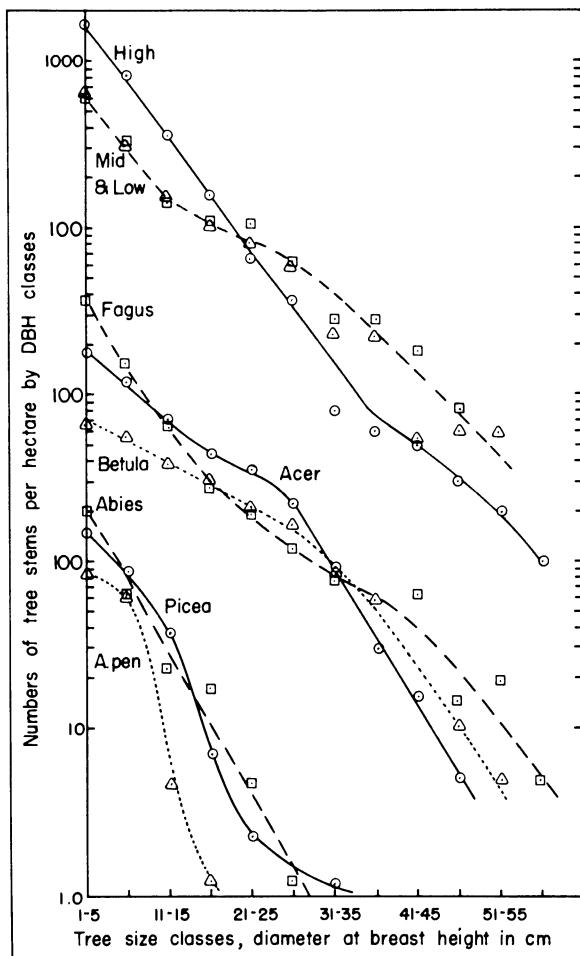


FIG. 3. Stand curves for species and elevation belts in the Hubbard Brook forest. Numbers of stems, on a logarithmic scale, are indicated on the ordinate for 5-cm diameter classes, on the abscissa. To save space the three sets of curves have been displaced along the ordinate. For the three sets the log cycles should be carried up and down from the three points at which 100 is indicated on the ordinate. Upper set: all species together by elevation belts—high (circles), mid (triangles), and low (squares). A single curve has been fitted by eye to the mid- and low-elevation data. Middle set: the three dominant species, all elevations combined—*Acer saccharum* (circles), *Betula lutea* (triangles), and *Fagus grandifolia* (squares). Lower set: three minor species in the high-elevation belt only—*Picea rubens* (circles), *Abies balsamea* (squares), and *Acer pensylvanicum* (triangles).

are largely similar. The stand curves for these species in the middle of Fig. 3 are, however, of different shapes. The curve for *Acer saccharum* at all elevations is similar to the lower elevation curves for all species, whereas *Fagus* shows larger and *Betula* smaller numbers of stems in the smallest and youngest classes. *Picea* reproduction appears to slow at high elevations, while the steep curve for *Abies*

TABLE 6. Production summary for the Hubbard Brook forests, tree stratum. All units are net primary productivity in dry g/m²/yr, calculated for 1956–60 (except for the mean, 1961–65, in the last row)

Elevation belt, sample number, and species	Stem wood	Stem bark	Branch wood and bark	Current twigs	Leaves	Fruits	Aboveground total	Root crown	Roots	Belowground total	Full total
Low elevations (71)											
<i>Acer saccharum</i>	156.0	20.4	108.8	7.1	180.1	8.2	480.6	15.9	86.8	102.7	583.3
<i>Betula lutea</i>	55.1	6.4	73.2	4.4	67.9	7.7	214.7	7.4	38.4	45.8	260.5
<i>Fagus grandifolia</i>	99.5	7.2	141.1	8.5	120.9	5.4	382.6	8.8	62.1	70.9	453.5
<i>Acer spicatum</i>	.5	.1	.9	.1	.7		2.3	.2	.3	.5	2.8
<i>Picea rubens</i>	.5	.1	.1	.1	.4		1.2	.1	.2	.3	1.5
<i>Fraxinus americana</i>	1.8	.2	1.3	.1	1.6	.1	5.1	.2	.8	1.0	6.1
<i>Acer pensylvanicum</i>	1.2	.1	2.8	.1	1.8		6.0	.3	.9	1.2	7.2
<i>Prunus pensylvanica</i>	.4	.1	.5		.5		1.5	.1	.2	.3	1.8
Total, 1956–60	315.0	34.6	328.7	20.4	373.9	21.4	1094.0	33.0	189.7	222.7	1316.7
(Total, 1961–65)	277.8	30.1	260.2	16.8	293.8 ^a	19.6	898.3	25.8	150.5	176.3	1074.6
Mid elevations (72)											
<i>Acer saccharum</i>	164.2	19.6	140.3	9.5	193.8	2.4	529.8	19.0	86.0	105.0	634.8
<i>Betula lutea</i>	60.8	6.7	77.3	4.3	78.4	3.1	230.6	10.0	29.5	39.5	270.1
<i>Fagus grandifolia</i>	60.9	4.8	69.7	4.3	72.8	9.9	222.4	7.3	43.5	50.8	273.2
<i>Acer spicatum</i>	1.9	0.3	2.6	.1	1.9	.1	6.9	.6	1.1	1.7	8.6
<i>Picea rubens</i>	1.4	0.2	0.4	.1	1.0	.1	3.2	.3	.9	1.2	4.4
<i>Acer pensylvanicum</i>	2.3	0.3	3.7	.1	2.2	.1	8.7	.4	1.5	1.9	10.6
<i>Prunus pensylvanica</i>	2.1	0.2	3.2	.1	2.4	.1	8.1	.3	1.5	1.8	9.9
Total, 1956–60	293.6	32.1	297.2	18.5	352.5	15.8	1009.7	37.9	164.0	201.9	1211.6
(Total, 1961–65)	239.1	26.8	225.5	14.9	279.0 ^a	13.2	798.5	32.1	121.4	153.5	952.0
High elevations (73)											
<i>Acer saccharum</i>	47.1	6.2	44.2	2.4	60.7	.1	160.7	7.8	17.5	25.3	186.0
<i>Betula lutea</i>	56.0	6.3	61.9	4.1	78.0	6.7	213.0	12.0	21.8	33.8	246.8
<i>Fagus grandifolia</i>	44.1	3.7	55.9	5.0	75.8	5.6	190.1	10.1	28.5	38.6	228.7
<i>Acer spicatum</i>	5.3	0.9	5.0	.4	5.2	.3	17.1	2.0	3.4	5.4	22.5
<i>Picea rubens</i>	10.2	1.3	2.6	.9	8.6	1.0	24.6	2.1	5.4	7.5	32.1
<i>Abies balsamea</i>	11.0	1.4	2.8	.9	8.7	1.0	25.8	2.3	5.2	7.5	33.3
<i>Acer pensylvanicum</i>	4.2	0.7	6.3	.3	5.9	.2	17.6	.7	2.8	3.5	21.1
<i>Prunus pensylvanica</i>	3.0	0.4	3.5	.3	5.6	.1	12.9	.6	1.6	2.2	15.1
<i>Acer rubrum</i>	2.1	0.3	1.8	.1	2.8	.1	7.2	.4	1.3	1.7	8.9
<i>Betula papyrifera</i>	17.9	2.1	20.7	1.7	32.8	2.3	77.5	3.4	9.1	12.5	90.0
<i>Pyrus americana</i>	1.1	0.2	1.5	.1	1.1	.1	4.1	.3	.7	1.0	5.1
<i>Prunus virginiana</i>	.04	.01	.06		.15		.3				.3
Total, 1956–60	202.0	23.5	206.3	16.2	285.4	17.5	750.9	41.7	97.3	139.0	889.9
(Total, 1961–65)	160.0	18.7	158.9	15.8	273.2 ^a	16.5	643.1	33.7	74.8	108.5	751.6
Area-weighted means, 1956–60	261.4	29.2	267.7	18.0	330.3	17.9	924.5	38.3	143.0	181.3	1105.8
(Area-weighted mean, 1961–65)	216.2	24.3	206.8	15.7	280.2 ^a	16.1	759.4	31.2	109.5	140.7	900.1

^a Differs from leaf column in Table 4 by weight of evergreen leaves of *Picea* and *Abies*.

balsamea suggests reproduction continuing to the recent period. Other minor species (*Acer pensylvanicum*, *A. spicatum*, *Betula papyrifera*, *Prunus pensylvanica*, and *P. virginiana*) have curves implying decreasing current reproduction. The last three of these are successional species likely to disappear from the climax forest; but *Betula lutea* and *Acer pensylvanicum* may both take important parts in successional stands and persist (as a smaller fraction of stand composition) in climax stands. *Betula lutea* is expected to decrease relative to *Acer saccharum* and *Fagus* as the forests mature, but to remain important, particularly at lower elevations. *Picea rubens* and *Abies balsamea* should make up an increasing part of the high-elevation stand as the present young trees mature. Their current rate of

reproduction does not indicate, however, that they will become more than a fraction of stands that continue to be dominated by the broadleaf species.

Ground-level ages are available only for the 93 trees subjected to dimension analysis. The ages of the 10 largest trees analyzed approach or exceed 200 yr; the oldest tree, a *Fagus*, was 260 yr. The smallest and youngest trees (excluding *A. spicatum*) were 19–40 yr; and these trees showed the slow growth of subordinate, suppressed trees. The ages most strongly represented are 55–61 yr. The concavities in the 16–30 cm classes in some of the curves of Fig. 3 represent concentrations of trees 55–61 years old in 1966. The ages of the *Acer spicatum* analyzed were rather evenly distributed from 12 to 39 yr. These ages indicate, more strongly

than the stand curves of Fig. 3, reduced reproduction by most species in recent periods.

The age, diameter, and density relationships express forest history: (1) The largest and oldest trees in the forest are survivors from the period before White settlement. Since the forests are believed to have been undisturbed by the Indians at that time, the meaning of the heavy branches of these trees (Fig. 1) is uncertain. The possible effects of hurricanes cannot be assessed. The heavy branches are not close to the ground; and they are interpreted as branches of trees that while young grew beneath a forest canopy, but were later exposed to light with consequent heavy branch growth. Many of these trees are of poor form, which saved them from cutting when they were of merchantable size. (2) The major part of the forest canopy is made up of trees 80–180 yr old and in the 21–50 cm diameter classes in 1966. These trees (also with fairly heavy branches) represent continuing reproduction and growth, 1785–1885, following settlement, and may have been affected by selective cutting in the last part of that period. (3) A pulse of reproduction, 1909–17, followed the most recent, intensive logging, and the faster growing members of this age class predominate in the 16–30 cm diameter classes. (4) Trees have reproduced in smaller numbers since that time, and trees in the 1918–45 age classes have grown slowly in competition with the 1909–17 trees and under the partial canopy of older trees. (5) The canopy opened in about 1909–17 is now largely closed. There has been only limited tree reproduction in the forest since 1945, though the stand includes fair numbers of the shade-tolerant seedlings of *Acer saccharum*. Canopy closure occurred later in the high-elevation belt and there are larger numbers of younger trees there, including 10–20 yr *Acer spicatum* and successional species (*Betula papyrifera*, *Prunus pensylvanica*).

Period volume increments.—To these observations may be related the volume growth patterns of Fig. 2. Forest history is reflected in the sections of the graph for the 10 largest trees: (1) The increments for the 10 trees show gradually increasing growth, as the trees themselves enlarged, during the first century (1760–1860, not plotted in Fig. 2) and up to about 1905. (2) A steepening of the growth rate followed cutting of the forest 1909–17 and continued until 1930. (3) A somewhat irregular plateau of stem growth was reached by 1931–35 and persisted until 1951–55 or 1956–60. (4) From the latter period stem growth in all species and sizes of trees sampled dropped abruptly to the 1961–65 period.

Fig. 2 also gives period volume increments for elevation belts, summing all trees in the samples for

these. The graphs indicate (1) slow growth prior to 1905 by the trees then present in the stand, and (2) increased rate of growth (with reproduction contributing to this) from the 1906–10 period on to (3) a peak of growth that the stands reached later than the large individual trees, 1946–50 at low and middle elevations, followed by (4) the abrupt decrease in growth, 1961–65. The somewhat slower growing trees of high elevations apparently responded to cutting more slowly, and reached peak growth later, than those at low and middle elevations. (It is not known whether the high-elevation belt was cut later; the ground-level ages do not establish this.)

Woody litter and biomass maturity.—An important question for the study of nutrient balance is the degree to which the forests have approached a climax, steady-state biomass and pool of nutrients in plant tissue. Maturity in the sense of maximum biomass is separate from, and normally later than, maturity in the sense of steady-state productivity (Duvigneaud 1971). The peak period increments, 1946–60, may well represent the steady-state level of productivity for the forest, but biomass should still be increasing. The relation of biomass to production may be expressed as the biomass accumulation ratio—the current biomass divided by net annual productivity (both usually as aboveground dry weights). Biomass accumulation ratios in the Great Smoky Mountains ranged from 13–21 in some forests with smaller trees, to 29–40 in medium-sized oak and spruce forests, to 41–52 in mature cove forests (Whittaker 1966). The ratios for the Hubbard Brook elevation belts (14.4, 14.5, and 13.0 for the three elevation belts) are low for mesophytic deciduous forests, though not much below those of high-elevation forests with small trees in the Smokies (Table 4D, samples 25, 26, 28). There is thus a question whether the Hubbard Brook forests are now approaching climax biomass values in the range of those of some small forests of marginal environments for deciduous trees, or whether their biomass should be expected to increase twofold or more (from present values of 162, 151, and 102 t/ha to as much as 400–500 t/ha as in some of the mature forests of the Smokies). No easy and decisive answer is known.

One approach, based on measurements internal to the stands, seeks to determine the extent to which growth and death of stems and branches are in balance, and stem and branch biomass consequently in steady state. Gosz et al. (1972) litter collections give averages for the whole watershed of 127 g/m²/yr for branch wood with attached bark, 80.5 g for stem wood and bark, and 9.7 g for detached bark. The total of 217 g/m²/yr may be compared with wood

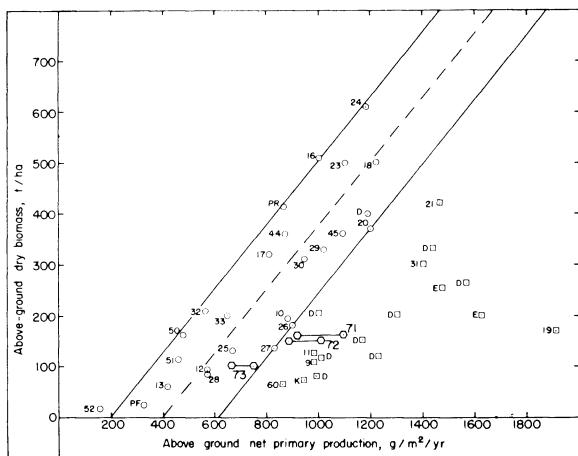


FIG. 4. Forest biomass in relation to net primary productivity. Forest and woodland samples are plotted from the Great Smoky Mountains, Tennessee (13 to 32, Whittaker 1966), Santa Catalina Mountains, Arizona (44–52, unpublished), Brookhaven National Laboratory (60, Whittaker and Woodwell 1969), a *Cupressus pygmaea* pygmy forest (PF) and *Pinus muricata/Rhododendron* forest (PR) in Mendocino County, California (Westman 1971), West European oak forests (D, compiled by Duvigneaud et al. 1971) and a coppice (K, Kestemont 1971), two young spruce forests (E, Arvisto 1970), and the Hubbard Brook elevation belts (71–73, this study, with lower [1961–65] and higher [1956–60] production estimates connected by bars). Young stands are indicated by squares, climax and near-climax stands by circles. The oblique band thus includes climax forests of "normal" temperate-zone stature (with biomass above about 300 t/ha), small climax forests of limiting environments (biomass about 150–300 t/ha), and woodlands (below 100 or 150 t/ha). The dashed line indicates the trend for climax biomass in relation to NPP with an equation of $\text{Mass} = 0.625 \text{ Prod} - 250$. Stands above the dashed line appear to be fully stabilized climates; however, some of those represented by circles below the dashed line are near-climax but affected by disturbance (notably death of *Castanea dentata* in the Great Smoky Mountains).

and bark productions averaging 338 g/m²/yr in stems plus 332 in branches in the two lower elevation belts, and 225 plus 222 in the high-elevation belt (Table 6, including current twigs with branch wood and bark). There are difficulties with this approach to the balance. The litter collections underestimate the rate at which living stems and branches become dead wood and bark, both because of insensible loss from dead branches and, in a young forest, because of the lag between death and fall of wood and bark. The branch production figures in contrast overestimate current growth if wood growth is declining, for they are inferred from growth rates throughout the lives of branches. The data are thus indecisive. They do not, however indicate that the Hubbard Brook forests are now near

steady-state biomass with values similar to those of the subalpine deciduous forests in the Smokies.

Biomass and production correlations.—Two indirect, comparative approaches to the question of biomass steady state are worth considering. First is the normal relation of biomass to production in climax forests. In Fig. 4 the stands judged mature or climax are included between the solid lines, whereas the clearly immature stands given, and many others tabulated by Ovington (1962), Rodin and Bazilevich (1967), and Art and Marks (1971), fall below this band and to the right. (*Sequoia sempervirens* and other large-tree western forests are omitted from the plot.) The interception of the oblique band with the abscissa suggests threshold productivities (variously between 200 and 600 g/m² in different areas) below which accumulation of biomass in trees does not occur. The stands in the lower left part of the plot, with biomasses below 200 t/ha and productions below 600 g/m²/yr, are not forests but woodlands of small trees in open growth. At still lower productions, not woodlands but grasslands or shrublands occur. In this plot the Hubbard Brook forests are located close to the deciduous subalpine stands of the Smokies if the low estimates of production, 1961–65, are used. If the higher production estimates for 1956–60 are used, then the plot suggests as more likely biomass values for the Hubbard Brook forests 400–50 t/ha at low and 300–400 t/ha at high elevations.

Second, a multiple regression may be considered for prediction of net aboveground production and biomass from elevation and a compositional moisture index, developed for the forests of the Great Smoky Mountains (Whittaker 1966). Predictions for the Hubbard Brook forests are given in Table 4F. The moisture index (MI) uses the same weightings for major species as those applied to the Smokies forests, though it cannot be assumed that the tree species are identical in genetics and response to moisture in the two areas; inferred weights have been used for minor species not present in the Smokies. (O = mesic for all species except that 1 = submesic for *Acer pensylvanicum*, *Prunus virginiana*, *P. pensylvanica*, *Betula papyrifera*, and *Acer rubrum*.) Temperature equivalences have been based on open season (8-mo) soil temperature measurements by Shanks (1954, 1956) in the Smokies, and Federer (1973) at Hubbard Brook. These data suggest adding 660 m to the elevations at Hubbard Brook to give equivalents that may be used in the equations for the Smokies. The effect is to assign to the Hubbard Brook samples elevation equivalents of 1,250, 1,330, and 1,410 m, of which the last is in the transition to subalpine forests in the Smokies. Approximate as these moisture and elevation equiv-

alents may be, they provide the necessary leverage for predicting aboveground biomass and production from the Smokies equations:

$$\text{Production (g/m}^2/\text{yr}) = 1,511 - 0.356 \text{ Elev. (m)} \\ - 197 \text{ MI.}$$

$$\text{Biomass (t/ha)} = 643 - 0.230 \text{ Elev. (m)} \\ - 195 \text{ MI} + 60 \text{ DE}$$

(DE = 1 for deciduous, 2 for evenly mixed, and 3 for evergreen forests.)

The predicted productivities for Hubbard Brook are 1,062, 1,027, and 995 g/m²/yr aboveground, hence about 1,290, 1,235, and 1,200 g/m²/yr above and below the ground. These values are above the low estimates for 1961–65, but convergent at low and middle elevations with the higher estimates for 1956–60. The results suggest that the 1961–65 production is below normal, and that the 1956–60 estimates and the 1946–55 plateau of wood growth at low and middle elevations (Fig. 2) represent climax productivity. Aboveground biomass predictions for the three elevation belts are 411, 386, and 365 t/ha; aboveground and belowground equivalents should approximate 490, 460, and 440 t/ha. The predicted productivity for the high elevation belt is too high, and the predicted biomass for this belt seems also too high.

The predictions suggest, however, that (1) The climax production and biomass characteristics of the Hubbard Brook forests are not those of the subalpine deciduous forests in the Smokies, but are similar to those of higher elevation (but not subalpine) mesophytic forests of the Great Smoky Mountains. (2) Net primary productivities were probably at climax levels in 1956–60, on the lower edge of the "normal" range of 1200–1500 g/m²/yr for mature temperate forests of favorable environments (Whittaker 1966). (3) The abrupt decrease in productivity, 1961–65, may well be a reduction from the climax level, rather than a decrease toward climax levels following higher productivity in subclimax condition. (4) Apart from possible effects of this reduction, biomasses at Hubbard Brook might be expected to increase to 2–3 times their present levels as the stands mature to a full climax condition. (5) Though the Hubbard Brook forests are not subalpine, the lower productivity (and divergence from predicted productivity) of the high-elevation belt presumably reflects a marginal climate for deciduous forest, nearing an exposed ridgeline at an elevation transitional to subalpine forest.

Biomass projection.—One means of biomass projection is the Jabowa computer model developed by the Hubbard Brook ecosystem study (Botkin et al. 1972). This model simulates the growth of individual trees in a mixed-species forest, taking

into account competition among trees, environmental variables, and growth and survival characteristics of species. The model gives as output annual values for dbh of individual trees, and density and basal area per unit area for each species. It thus predicts successional changes, with stochastic effects based on observed variability in the northern hardwoods and boreal forests. Applying the biomass regression equations from this paper to the output, the model predicts that total tree biomass will average 173 ± 18 (for the 95% confidence intervals) t/ha 50 yr following clearcut, a prediction that compares with the 161 t/ha for the lower elevation belt in Table 4. The model further predicts that biomass in the simulated stand should increase until approximately 200 yr after cutting, to an average biomass of 390 t/ha, and then decrease by 400 yr to a long-term average of about 300 t/ha. The peak in biomass that occurs about year 200 is due to the contribution from yellow birch, which comes into the stands in large numbers early in succession, but is relatively long-lived. (D. Botkin, pers. comm.)

Biomass increase can also be projected from values for production and woody litter fall. The woody litter collections of Gosz et al. (1972) averaged 217 g/m²/yr for the watershed. Given a mean aboveground wood and bark biomass (W_w) of 133 t/ha, the implied rate "constant" (k_w) for woody litter fall is $217/13,300 = 0.0163/\text{yr}$. This, with the woody production estimate $P_w = 576 \text{ g/m}^2/\text{yr}$ from Table 6 in the relationship $\Delta W_w = P_w - k_w W_w$, implies a woody biomass accumulation (1956–60) of $576 - 217 = 359 \text{ g/m}^2/\text{yr}$ above ground, of which 200 g would be stems and 159 g branch wood and bark. (For the lower production period of 1961–65, the corresponding accumulation would be 246 g/m²/yr, 151 g in stems and 95 g in branches, about 70 g in roots.) The climax biomass when $\Delta W_w = 0$ should be $W_w = P_w/k_w = 353 \text{ t/ha}$. Despite the limitations of litter collections (and the assumption that k_w is constant) for such an estimate, it seems plausible.

The aboveground biomass may also be treated as three major components—foliage, branches, and stems—of different turnover times and different times to reach steady-state mass (in a few years, decades, and centuries respectively). Foliage biomass reaches its climax value within 3–5 years (Marks 1971); our present concern is with projection of woody biomass to climax. Separate calculations, parallel to the preceding, for stems and branches give rate constants of $k_s = 90/8222 = 0.0109/\text{yr}$ for stems, and $k_b = 127/3867 = 0.0328/\text{yr}$ for branches. With production values from Table 5, climax biomasses can be estimated as $M_s = P_s/k_s = 291/0.0109 = 267 \text{ t/ha}$ for stems, and $M_b = P_b/k_b = 291/0.0328 = 8,880 \text{ t/ha}$ for branches.

$k_b = 286/0.0328 = 87 \text{ t/ha}$ for branches. These together make up an aboveground woody biomass of 354 t/ha (plus leaf biomass of 3.5 t/ha and root biomass of about 70 t/ha). Separate climax estimates by elevation belts, using more typical branch/stem ratios, are these: low 437 t/ha (372 stems and 65 branches) mid 390 t/ha (325 and 65), and high 265 t/ha (205 and 60). A mean aboveground woody biomass of 354 t/ha is reasonably consistent with the weighted mean for the regression estimates (379 t/ha) and is within the climax band for Fig. 4; it has been used to prepare a projection of biomass growth for the watershed.

A biomass history is suggested (Fig. 5) in which (A) A climax biomass of about 350 t/ha may have been stabilized (or subject to fluctuation with hurricane effects) before settlement by Whites. (B) Limited, selective cutting between 1800 and 1900 is suggested, on the basis of the recorded lumber mill in the area and the heavy branches of older trees. (C) The watershed was lumbered, 1909–17. There is no record of how complete the cutting was, but the volume increment data suggest that a small fraction of the stand (less than 5% of present biomass) remained. During the period 1910–50 the forest recovered by rapid, exponential growth. The curves are based on actual wood volume growth by trees now standing, with a natural rate of increase of $r = 0.075/\text{yr}$, and ratios of branch to stem mass thought typical for small trees. The cross-hatched area represents a pulse of successional *Prunus pensylvanica* believed to have come up following cutting, and to have been the source of many of the *Prunus* seeds now in the soil in the area (Marks 1971, Marks and Bormann 1972). (D) Stem and branch productivity were apparently at their steady state by 1950. From that date onward the aboveground woody biomass (W_w) curve was first extrapolated to a climax biomass, $M_w = 350 \text{ t/ha}$, using the k_w and P_w given and the approach to steady state as $W_w = M_w(1 - e^{-k_w t})$. Second, separate extrapolations were prepared for stem and branch biomass; but these were modified for the assumption that the fraction of production and biomass in stems will gradually increase, and that in branches decrease, as the forest matures. Stabilization of branch mass at 65 t/ha within 150 yr after cutting was assumed. (E) Woody biomass should reach 90% of climax by about 250 yr after cutting; asymptotic approach to 350 t/ha is indicated for the remaining period.

Production balance

The conclusions to this point permit estimation of a production balance for the forest. No direct measurements of respiration are available. It may

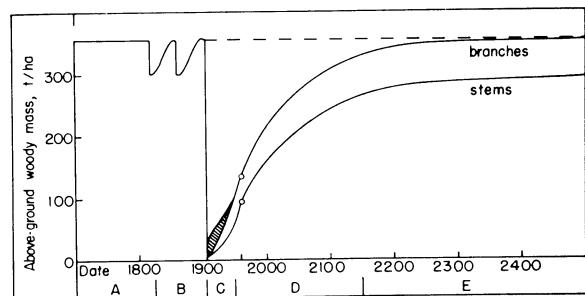


FIG. 5. An interpretation of biomass history for the Hubbard Brook forest. (A) presumed woody (stem + branch) climax biomass before White settlement, (B) opening of canopy by selective cutting in the 19th century, (C) logging of the watershed, 1909–17, followed by exponential regrowth of forest biomass (the cross-hatched area represents successional *Prunus pensylvanica*), (D) slower relative growth in biomass after 1950, when productivity reached climax levels, (E) asymptotic approach to the assumed climax level.

be reasonable, however, to apply the Brookhaven forest autotroph respiration rate ($R_a = 55\%$ of gross primary production) to this forest of somewhat larger trees in a somewhat cooler climate. Gross primary productivity (GPP) may then be partitioned among woody production (P_w) and leaf production (P_l) of trees, fruit, flower, and bud-scale production (P_f), undergrowth production (P_u), and autotroph respiration (R_a) as

$$\begin{aligned} \text{GPP} &= P_w + P_l + P_f + P_u + R_a \\ &= \text{NPP} + R_a \end{aligned}$$

$$\begin{aligned} \text{Above ground} \quad 2127 &= 576 + 330 + 29 + 22 + 1170 \\ &= 957 + 1170 \text{ g/m}^2/\text{yr} \end{aligned}$$

$$\begin{aligned} \text{Total} \quad 2547 &= 758 + 330 + 29 + 30 + 1400 \\ &= 1147 + 1400 \text{ g/m}^2/\text{yr} \end{aligned}$$

The measurements of leaf consumption by insects were 1%–3% of blade area, low values compared with those reported for late-summer leaves (Bray 1961, Bray and Gorham 1964, Whittaker and Woodward 1968, Andersson 1970). Reichle et al. (1973) estimate that over 7% of missing area in mature leaves represents a smaller fraction of leaf production (2.4% of mature dry weight, 9 g/m²/yr) consumed by insects before the leaves expanded. The frass collections by Gosz et al. (1972) average 18 g/m²/yr for the watershed, and this value corrected for insect assimilation is 21 g/m²/yr, or 6% of leaf production. Heterotroph respiration is unknown but may, if the litter is in steady state, equal animal consumption (C_a) plus tree leaf fall (L_1), fruit, flower, and bud-scale fall (L_f), stem and branch fall (L_w), and undergrowth litter fall (L_u). The accumulation of woody biomass (1956–60) has been computed at 359 g/m²/yr above ground. This

accumulation, from the difference between net primary productivity and heterotroph respiration, is net ecosystem production (NEP) (Whittaker and Woodwell 1969, Duvigneaud 1971). With values available for the preceding aboveground, and inferences on belowground values, the forest production balance (1956–60) may be suggested:

$$\text{NEP} = \text{GPP} - R_a - C_a - L_t - L_f - L_w - L_n$$

Above ground	$350 = 2127 - 1170 - 21 - 330 - 29 - 217 - 10 \text{ g/m}^2/\text{yr}$
Total	$435 = 2547 - 1400 - 30 - 330 - 29 - 313 - 10 \text{ g/m}^2/\text{yr}$

Total L_w has been estimated from aboveground litter fall of 217 g/m²/yr plus woody root turnover of $1112 \times 0.0109 + 1714 \times 0.0328 = 67 \text{ g/m}^2/\text{yr}$, plus death of fine roots of $143 \times 0.20 = 29 \text{ g/m}^2/\text{yr}$. The estimate of NEP, 435 g/m²/yr, is smaller than that for the younger Brookhaven forest (540 g/m²/yr, Whittaker and Woodwell 1969), larger than that for a young *Liriodendron tulipifera* forest (320 g/m²/yr, Reichle et al. 1973).

For the period of reduced forest growth, 1961–65, the following balance is suggested:

$$\text{NEP} = \text{GPP} - R_a - C_a - L_t - L_f - L_w - L_n$$

Above ground	$238 = 1760 - 968 - 21 - 280 - 26 - 217 - 10 \text{ g/m}^2/\text{yr}$
Total	$290 = 2090 - 1150 - 21 - 280 - 26 - 313 - 10 \text{ g/m}^2/\text{yr}$

The estimate of NEP for this period as 290 g/m²/yr is close to the *Liriodendron* estimate. It may also be more representative of the period of study of nutrient cycling since 1963 (Likens and Bormann 1972) than the higher value for 1956–60.

CONCLUSION

The biomass and production data discussed offer a choice of interpretations: (1) that the forest is in a limiting, cold-temperate environment, in which the low productivity of 1961–65 may represent its climax level and the current biomass may be not too far from climax; in both respects the Hubbard Brook forests may resemble the small deciduous forests of the subalpine zone in the southern Appalachians; or (2) that the forest is in a cool-temperate but not subalpine climate, the higher productivity of 1956–60 should reasonably represent its climax level, and the biomass may be expected to increase 2–3 times to climax; in both respects the Hubbard Brook forests may resemble higher-elevation but not subalpine deciduous forests of the southern Ap-

palachians. No single evidence toward the latter choice is compelling, but a convergence of considerations—climate, production vs. litter-fall rates, typical production-biomass relations of forests, regression predictions of production and biomass, and the fact 1961–65 was a drought period—suggest preference for interpretation (2).

On this basis the Hubbard Brook forests may be characterized, averaging the three elevation belts, as cool-temperate mesophytic deciduous forests, with a net primary productivity (1150 g/m²/yr) on the lower margin of the normal range for such forests, at present young (following cutting in 1909–17) and of low basal area and biomass (24 m²/ha and 135 t/ha above ground) compared to climax forests of similar environments, but having full canopy with a leaf area ratio of 5.8 m²/m² and a ratio of net primary production to leaf area (165 g/m²/yr aboveground) typical for such forests. The recent rate of net ecosystem production or accumulation of woody biomass, based on litter fall and the 1956–60 production, is 350 g/m²/yr aboveground and about 435 g/m²/yr aboveground and belowground. Peak productivity has already been reached, and the NEP will decrease as the forest matures. At full maturity NEP will be zero, but the climax biomass, reached by accumulation of NEP, should be about 350 t/ha above ground and 425 t/ha above and below ground.

In productivity and NEP the Hubbard Brook forest is comparable to, but lower than, other young temperate deciduous forests studied by Whittaker and Woodwell (1968) Andersson (1970, 1971), Duvigneaud et al. (1971), and Reichle et al. (1973). In composition it seems typical of northern hardwoods of cool mesophytic environments in the northeastern United States (Bormann et al. 1970, Siccama et al. 1970). As such, however, the forest is marginal, for the upper third of the watershed is in the transition to subalpine, *Picea-Abies* forest. Effect of the transition appears both in composition—increasing occurrence of *Picea rubens*, *Abies balsamea*, and other subalpine species toward the upper part of the watershed (Bormann et al. 1970)—and in decreasing forest dimensions, productivity, and biomass. Averages of the two lower belts of the watershed compared to the upper belt show weighted mean tree height decreases from 16.8 to 10.8 m, stem wood volume from 165 to 108 m³/ha, biomass from 187 to 125 t/ha, and net primary production from 1265 to 890 g/m²/yr. Trees of the upper part of the watershed are smaller, younger, and denser, with lower height/diameter ratios and rates of wood growth as reflected in mean radial increments of 1.25 and 0.89 mm/yr.

The volume of stem wood in the forest grew at

an exponential rate ($r = 0.075/\text{yr}$) from the logging in 1909–17 until 1950 at lower elevations, a somewhat lower rate ($r = 0.065$) until 1960 in the high-elevation belt. In the lower elevation belts productivity of stem wood, and presumably of the rest of the forest, was stable from 1950 to 1960, following which productivity dropped in the 1961–65 period. The decrease was not only abrupt but intense (with wood volume growth reduced by 18% 1956–60). 1961–65 was a period of both drought and increasing acidity of rainfall from air pollution by sulfur and nitrogen oxides from industry in the northeastern United States (Likens et al. 1972). Reduction of forest production by acidity of rain has been suggested (Bolin 1971). The history of wood volume growth for the Hubbard Brook forests, which in some trees can be followed for more than two centuries, records no previous decrease in growth such as occurred in 1961–65. The decrease consequently suggests an anomaly of forest function in the present period of increasingly widespread pollution. The decrease is deserving of further study.

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