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DIMENSION AND PRODUCTION RELATIONS OF TREES AND SHRUBS IN THE BROOKHAVEN FOREST, NEW YORK*

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INTRODUCTION

Extensive tracts of oak-pine forest grow on the level, sandy soils of glacial outwash derivation on Long Island, New York (Conard 1935). The forests are small and unimpressive to a forester. In mature stands older and larger pines (*Pinus rigida* Mill.) rise above a canopy of oaks (*Quercus alba* L., *Q. coccinea* Muench, and few *Q. velutina* Lam. and other species). The canopy is open, with light intensity below the trees sufficient to support a shrub stratum of small Vacciniaceae of high coverage (Reiners 1965). These forests are floristically related to the pine forests of New Jersey and the Coastal Plain southward, and to the pine heaths of the Great Smoky Mountains (Whittaker 1956), with which they share a number of major species. All of these forests have been subject to repeated fires, and dense, immature successional stands with *Pinus rigida* and scrub oak (*Quercus ilicifolia* Wang.) occur over extensive areas.

The small size of the trees at Brookhaven has facilitated development of a system of detailed dimension analysis useful for various problems related to forest volume, biomass, production, surface and nutrient circulation. The methods are developments from forest measurements used by Burger (1929, 1953), Boysen Jensen (1932), Möller (1945, 1947), Ovington (1957), Ovington & Madgwick (1959a, b) and others, but are intended to advance beyond those measurements in important respects. They use the wood rings and bud-scale scars which mark annual increments of growth in some climates for assessment of current net production and nutrient movement in forests. They are designed specifically to deal with the complexities of many-aged stands including climaxes, as distinguished from plantations.

The work is part of a long-term study of various aspects of the Brookhaven forest as an ecosystem, a study which includes experimental irradiation of a segment of the forest with gamma radiation from a cesium source (Woodwell 1962, 1965). The plants of the present study have been taken from the forest outside the area of radiation effects. Included in this report are results of dimension analysis of trees and shrubs as a first phase of the research on biomass, production and nutrient circulation.

METHODS

Species

Fifteen plants with roots were taken for each of the seven principal species of the forest during September and October, 1964. Species included *Pinus rigida* (pitch pine), *Quercus*

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coccinea (scarlet oak) and *Q. alba* (white oak), which are the dominant trees. *Q. ilicifolia* (scrub oak) is a many-stemmed shrub, some stems of which are 1–3 cm diameter at breast height and 2–3 m tall. It is of low coverage in the forest. The shrub stratum is dominated by the small vacciniaceous species, *Gaylussacia baccata* (Wang.) K. Koch (black huckleberry), which has shoots mostly 0.4–0.9 m tall, *Vaccinium vacillans* Torr. (low-bush blueberry), usually 0.2–0.5 m tall and *V. angustifolium* Ait., a dwarf low-bush blueberry with shoots 0.1–0.2 m tall. In tree species, individuals representing the range of stem sizes in the forest were selected; in the shrubs an individual was a root or rhizome system with its shoots.

Field sampling procedure

Trees were felled and a tape was laid along the axis of the stem from the tip to the base. For each branch, distance below the tip, basal diameter and age were recorded. Branch ages were determined: (a) for younger branches by counting bud-scale scars on the branches and on the stem down to the points supporting them, (b) for branches of intermediate age by counting bud-scale scars and by counting wood rings in the laboratory on a disc from the base of the branch, (c) in older branches primary reliance was on study of basal discs, checked by apparent bud-scale age and age of the stem at the point of emergence when missing rings in an older branch of slow growth were suspected. All three tree species produced branches low on the stem that were younger than the stem at the point of their emergence. Secondary twigs or Lammas shoots are common in open-growth *Pinus rigida* and occur on some twigs of upper branches in the forest; they were not observed in the oaks (except following spring defoliation by late frost in 1961). While the approach to branch age does not produce certainty in *P. rigida* and older oak branches, branch ages are thought to be of sufficient reliability for the purpose.

Five sample branches were selected for each tree to represent upper, upper-middle, middle, lower-middle and lower positions along the stem, with random choice within each of these classes. For sample branches, numbers of current twigs and branch lengths were recorded in addition to positions, basal diameters and ages; and the branches were divided into current twigs with leaves, living branch wood with bark, dead branch wood with bark, older leaves and fruits, if any. Fresh weights were obtained for each of these fractions in the field; dry weights were taken after drying to constant weight at 105° C. For large branches, subsamples of wood and of twigs with leaves were dried, and the ratios of dry to live weights for the subsamples were applied to the live weights to obtain dry weight of wood and of twigs for the whole branch. Twigs were taken separately from each of the levels in the crown and frozen for later determination of leaf number, area, insect loss, twig diameter and length, and distribution of dry weight among twig, leaf blades and petioles. Samples of twigs, whole leaves and branch wood and bark from branch segments of different sizes were subjected to chemical analysis. Leaves were collected for chlorophyll determinations, and twigs with flowers or fruits were collected when available.

After removal of branches, tree stems were cut into logs 1 m long, and a sample disc 10 cm thick was cut from the base of each log. Length, basal (disc) diameter of wood and of wood with bark, mid-diameter with bark and fresh weight of the log and of the disc were recorded. Sample discs (and stumps, cut at ground level after felling the tree to produce a basal disc or first log 15–25 cm long) were returned to the laboratory for dry weights and other measurements. For the dry discs were recorded (from means of readings on four points on the disc perimeters) bark thickness, apparent sapwood age and thick-

ness, and wood radial increment thicknesses by 5-year periods from the current ring to the centre of the disc; dry wood diameter, disc age, and, in shrubs, pith diameter also were recorded. Bark and wood were separated for some sample discs and weighed fresh and dry. Samples of whole bark, and of sapwood and heartwood from the interior of these discs were used in chemical analyses of nutrient elements.

Root systems were excavated with dynamite and a power winch and were thoroughly washed to remove any soil remaining. In the sandy soil at Brookhaven substantial fractions of the roots came out of the ground attached to the crowns. Diameters of broken ends of roots were measured, roots were cut from root crowns, and roots and crowns were weighed. Samples of these roots, smaller root crowns and pieces of larger root crowns were returned to the laboratory for extended drying to obtain live/dry weight ratios. Sample roots were dug by hand with care to obtain complete roots. For these were recorded basal diameter, length and live and dry weight. Samples of root crown wood, and of roots of different diameters with bark, were subjected to chemical analysis.

Field methods for the many-stemmed shrubs differed in that: (a) the several shoots were measured separately, (b) the stem from each shoot was divided into two to seven sections which were dried whole, and on which the same measurements that were made on discs from trees were taken, (c) bark and wood were separated for whole stems of *Gaylussacia baccata* and *Vaccinium vacillans*, (d) branches were tallied by individual shoots; sample branches were not classified by crown position, (e) root systems of *Quercus ilicifolia* were obtained by power winch, but rhizome systems of *Vacciniaceae* were traced and dug by hand, (f) the diminutive shoots of *Vaccinium angustifolium* were each treated as a sample branch.

All data were entered on specially prepared forms from which computer cards could be punched directly. Copies of the Brookhaven plant analysis forms, designed to accommodate data for woody plants of all sizes, are available on request. A computer programme was prepared to carry out various calculations, including the following.

Computations

Volume and mass

Cross-sectional areas of wood and of bark were calculated from measurements at the ends of the logs before drying. The means of the areas at the ends of the log, times the length of the log (or log plus disc), gave volumes of wood and bark (Smalian formula). From the measurements on the dry discs, volumes of dry bark, wood, sapwood and heartwood also were obtained. In trees, dry weight of the log was obtained from fresh weight divided by the live/dry weight ratio determined from the basal disc. Dry weight of the log times the ratio of bark volume to log volume, and wood volume to log volume, gave first estimates of wood and bark dry weights. Bark density differs from wood density, however, especially if the bark is furrowed, since the bark volume includes the volume of furrows. The discs provided: first, ratios of true bark weight to the estimate of bark weight based on bark and log volume; second, regressions of these ratios on disc diameter, and third, wood and bark densities. The ratios were used to correct the preliminary estimate of weight of bark. Dry weights of logs minus the corrected dry weights of bark were used for a corrected weight of wood.

Corrected weights of wood times ratios of sapwood to heartwood gave dry weights of sapwood and heartwood. Fresh volumes of sapwood and heartwood were computed from dry volumes times the ratio of fresh to dry volume of wood. The outside surface of

the log (for an imaginary smooth bark surface) was computed from the length and mid-diameter of the log. Wood or cambial surface was also computed using mid-diameter minus the mean of bark thicknesses at the ends of the log. All weight, volume and surface values for logs were summed to calculate the values for the whole stem.

Branches

The sets of sample branches (seventy-five branches per species) were used to compute various regressions. Among these the logarithm of branch basal diameter, as the independent variable, was related to the logarithms of dry weights of (a) living branch wood with bark, (b) current twigs with leaves, and (c) older leaves if any, as dependent variables. Because many branches lacked dead wood and fruit, and these data could not be treated logarithmically, the cube of branch basal diameter was used as an independent variable for linear regressions of (d) dead wood and (e) fruit. These regressions enabled estimation of the dry weight of each living branch in the branch tally from its basal diameter. The resulting estimates were summed to give weights of living branch wood and bark, current twigs with leaves, older leaves if any, for the whole tree or shrub and an indication of the weight of fruits and dead branch wood.

From the twig samples were computed dry weights of current twigs with leaves, weights of petioles and weights of blades with correction for insect consumption, weight per unit area of leaf blades and chlorophyll content per unit area. From means of these values for the various crown levels, values for leaf dry weight, twig dry weight and leaf surface area and leaf blade chlorophyll content were obtained for the whole shoot.

Bark surfaces of branches were estimated from the relation

$$S_b = \pi d_b L_s \sum_{x=1}^{x=g} (2t)^{x-1}$$

in which d_b was branch basal diameter, L_s was the mean length of unbranched segments of the branch ($L_s = L/g$, L was branch length), g was the number of orders or generations of branch segments ($g = 1 + (\log n / \log 2)$, n was the number of current twigs) and t was a mean taper factor from one generation of branch segments to the next ($\log t = 0.5 (\log d_t^2 - \log d_b^2) / (g - 1)$, d_b was the mean diameter of current twigs). This computation gave an overestimate of branch surface since L was a maximum, not mean, distance from branch base to current twig tip; branch surface areas may be multiplied by a correction of 0.8 obtained from a study of *Rhododendron* branches. This study and other problems of surface estimation have been discussed in a separate paper (Whittaker & Woodwell 1967). Branch surface of the whole shoot was estimated by applying to the branch tally a logarithmic regression of branch surface on branch basal diameter.

Root weights

Small root crowns and rhizomes were dried whole after removal of roots. Live weight/dry weight ratios for small root crowns and fractions of larger ones were used to obtain dry weights of larger root crowns from their fresh weights. Regressions of the logarithm of sample root dry weight on the logarithm of root basal diameter were computed for each species; separate regressions were computed for the shallow crown roots and the nearly vertical tap roots of *Pinus rigida* because of the very different taper patterns of these. The regressions were applied to the broken ends of roots to estimate weights of roots lost in excavation. Root system dry weights reported are the sums of crown or rhizome weight, plus excavated non-tap roots corrected for loss, plus (in *P. rigida* and the *Vaccinium* species) excavated tap roots corrected for loss.

Production

The annual growth of wood in a log was computed by applying to the total weight of wood the ratio of cross-section area increment to wood cross-section area at the middle of the log. The formula used was

$$\Delta W = W[r^2 - (r-i)^2]/r^2$$

where ΔW was annual wood dry weight growth, W was corrected wood dry weight, r was wood radius at the middle of the log and i was the mean annual radial increment of wood at the ends of the log. For the Brookhaven trees, i was one-fifth of wood thickness increment for the last 5 years; for the shrubs the thickness of the current year's wood increment was measured. Bark growth of logs has been estimated in three ways: (a) using mean growth rates for different ages, inferred from curves of bark thickness with age (Whittaker 1962), (b) division of the dry weight of the bark by mean age of the log, and (c) multiplication of dry weight of bark by the wood growth rate, $\Delta W/W$, for that log. Of these (b) was believed to underestimate bark growth, and (c) has been preferred for the Brookhaven studies.

Branch growth was estimated by the relation $\Delta W_b = BW_b/a$, in which ΔW_b was annual growth of branch wood and bark, W_b was dry weight of branch wood and bark, estimated from the logarithmic regression of branch wood and bark weight on branch basal diameter, and B was a growth-rate slope computed from the regression of dry weight of the branch on age, $\log W_b = A + B \log a$, in which a was age and A and B were constants (Whittaker, Cohen & Olsen 1963). Basis and limitations of the estimate have been discussed by Whittaker (1965a). Current twig and leaf dry weight, summed for all branches of the shoot, was corrected for insect loss to obtain current twig and leaf annual production. Needles of *Pinus rigida* are relatively short-lived, persisting only through their second summer. The needles did not increase in dry weight between the end of the first summer and the second summer, in contrast with the continued growth from middle of the first to middle of the second summer observed in other evergreen species (Whittaker & Garfine 1962; Whittaker 1962; Whittaker *et al.* 1963). Fruits were mature at the time the trees were being studied, and dry weights of fruits collected from all branches of these trees have been used in preference to estimates of fruit weight based on the branch regressions. Separate collections and field observations provide means of estimating production of male flowers of the trees and of fruits and flowers in the shrubs.

Application to communities

Calculations to this point provide values for volume, biomass, production and surface of different plant fractions in the plants sampled; these values, and their relations to other plant dimensions, are to be used for calculations on the structure and function of plant communities. Community samples (Whittaker 1961, 1963, 1966) include clippings of undergrowth plants (current twigs with leaves from shrubs and tree seedlings less than 2 cm dbh, above-ground parts of herbs and biomass of thallophytes, from twenty random 0.5 × 2.0 m quadrats) and stand data on trees (diameters at breast height of all trees and shrubs of 2 cm dbh or more, together with heights, bark thickness, current wood increment and age from increment borings of all large trees and a sample of smaller trees, in a 0.1 ha or larger quadrat).

The data from sample plants may be applied to the community either by the simpler

and more direct use of ratios, or by calculations through regressions. For shrub communities estimates of biomass, production and leaf surface have been based primarily on ratios of other variables to clipping dry weight (Whittaker 1962, 1963); but the analysis also makes possible an approach of forestry in miniature for shrub communities based on regressions on shoot basal diameters or heights (Whittaker 1962, 1963). Approaches to forest tree strata can also be based on ratios for samples of dominant trees (Whittaker *et al.* 1963) or selected mean trees (Ovington & Pearsall 1956; Ovington 1957; Ovington & Madgwick 1959a; Peterken & Newbould 1966); but even for single-aged plantations these approaches are vulnerable to error (Ovington & Madgwick 1959b; Baskerville 1965). For many-aged forests with trees of a wide size range the approach through regressions is almost inescapable. Calculations for the sets of sample plants consequently include logarithmic regressions of all volume, mass, production and surface values for whole shoots on basal diameter (at breast height, 1.37 m, for trees, just above ground surface for shrub shoots), together with alternative regressions of these values on other appropriate independent variables. The results which follow are presented both as means for sets of sample plants, from which dimensional relations of woody plants are more easily understood, and as regressions which, though they may express these relationships in a more useful way, are largely opaque to the reader.

RESULTS

Shoot biomass distribution

The distribution of the biomass of shoots, expressed as a per cent of dry weight, in the major plant fractions shows consistent patterns in the three tree species (Table 1D). Somewhat more than half (52–54%) of the biomass is stem wood and another 12–17% is stem bark; 20–26% is branch wood and bark and 5–9% current twigs with leaves (with an additional 6% in older leaves in *Pinus rigida*). Variability of the fraction in branch wood and bark is high—from 10 to 30% among five *Quercus alba* between 8 and 12 cm dbh, for example—and without evident trend in relation to tree size. Among other plant fractions, the fractions in stem wood weight increase, whereas those in stem bark weight and current twig and leaf weight decrease, from smaller trees to large (cf. Ovington 1962, 1965). In *Q. coccinea* of different sizes from the three smallest (1–3 cm dbh) to the three largest (17–23 cm dbh) stem bark weight decreased from 15 to 9% and current twig and leaf weight from 12 to 5%, while stem wood increased from 44 to 55%. The fraction of the stem wood which is heartwood necessarily increases with size and age of the tree (from 34 to 53% in *Q. alba*, 38 to 66% in *Q. coccinea* and 1 to 14% in *Pinus rigida*).

All these trees are small (diameters of largest individuals were 18 cm in *Quercus alba*, 23 cm in *Q. coccinea* and 31 cm in *Pinus rigida*). Fractions of stem wood were higher in the larger trees studied at Oak Ridge National Laboratory (Whittaker *et al.* 1963)—76% in *Liriodendron tulipifera*, 80% in *Pinus echinata* and 59% in older *Quercus alba* of open growth form. Fractions of weight in other major parts of the plant were correspondingly lower, except for the 27% in branch wood and bark in the Oak Ridge *Q. alba*. Extension of the size trends in the opposite direction is reflected in the mean biomass distributions of shrub shoots in which stem wood is 17–41% of shoot weight and current twigs with leaves 18–45%. Similar biomass distributions occurred in the smaller shrub species studied in the Great Smoky Mountains (Whittaker 1962).

Table 1. *Mean dimensional relations of trees and shrubs at Brookhaven National Laboratory*

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>	<i>Vaccinium angustifolium</i>
A. MEAN SHOOT DIMENSIONS							
Number of shoots	15	15	15	30	30	30	30
Diameter at breast height (cm)	15.2	10.7	9.33	—	—	—	—
Diameter at ground-level (cm)	20.0	16.6	14.2	0.98	0.58	0.32	0.18
Height (m)	8.88	8.71	7.29	0.94	0.59	0.32	0.15
Age (years)	40.6	33.5	32.8	9.0	9.2	5.6	3.6
Biomass (dry g)	85 500	70 500	36 600	140.7	12.3	3.53	0.84
Net production (dry g/yr)	9840	9830	4875	32.00	3.96	2.12	0.54
Bark thickness (mm)	12.05	4.79	5.67	0.50	0.20	0.26	—
Wood radial increment (mm/yr)	1.08	1.16	0.64	0.14	0.12	0.08	—
B. VOLUME (cm³)							
Parabolic volume estimate ^a	114 100	72 400	40 700	114.5	10.20	1.63	—
True stem volume	125 100	75 200	42 100	94.3	9.16	1.37	—
Wood volume	94 400	62 700	32 600	76.5	7.91	0.93	—
Heartwood volume	8860	39 800	15 200	—	—	—	—
Estimated volume increment ^a	2100	2690	995	3.00	0.58	0.13	—
True volume increment	3410	3620	1410	3.71	0.548	0.094	—
C. SURFACE (cm²)							
Conic surface estimate ^a	23 300	18 300	12 600	226.6	58.60	17.68	—
Parabolic surface estimate ^a	33 600	26 110	18 300	302.1	78.13	23.57	—
Stem bark surface	31 700	23 200	16 000	250.5	67.21	15.65	—
Stem wood surface	27 600	21 000	13 900	—	—	—	—
Branch bark surface	168 000	136 000	83 400	607.1	152.3	74.0	—
Leaf blade surface ^b	682 500	324 000	226 000	1258	314	158	—
D. SHOOT DRY WEIGHT DISTRIBUTION, % in:							
Stem wood	53.8	51.9	54.3	41.0	38.8	17.0	—
Stem bark	12.2	12.9	17.1	11.1	11.5	10.3	—
Branch wood and bark	22.1	26.3	20.2	29.7	28.4	28.0	57.5
Current twigs and leaves ^c	5.2	8.7	7.9	18.2	21.3	44.7	42.5
Older leaves	5.9	—	—	—	—	—	—
Fruits	0.8	0.2	0.5	—	—	—	—
E. ROOT/SHOOT RELATIONS							
Mean root system dry weight ^d (g)	21 000	30 460	34 100	2697	139.1 ^e	62.2 ^e	28.25 ^e
Mean root/woody shoot ratio ^d	0.28	0.467	0.908	6.28	2.28	4.85	3.81
Ratio in large plants	0.27	0.44	0.65	4.88	—	—	—
Ratio in small plants	0.33	2.05	2.74	85.8	—	—	—
Mean biomass % in:							
Stem	58.5	46.5	39.8	8.4	20.1	8.5	—
Branches	19.6	21.7	12.7	5.4	11.3	8.8	21.1
Root crown or rhizome	10.8	14.0	26.5	40.4	60.9	71.7	68.3
Roots	6.9	17.8	21.0	45.8	7.7	3.7	5.4
Taproots	4.2	—	—	—	—	7.3	5.2
F. ABOVE-GROUND NET PRODUCTION DISTRIBUTION, % dry weight in:							
Stem wood	18.6	19.6	15.4	8.0	9.8	5.3	—
Stem bark	4.6	4.9	4.8	3.7	2.9	3.3	—
Branch wood and bark	23.0	22.8	24.4	19.5	24.6	17.1	32.5
Current twigs and leaves ^c	49.5	50.6	51.6	68.5	60.5	65.9	66.9
Fruits and peduncles	4.1	1.9	3.4	0.01	1.7	6.7	0.4
Flowers	0.16	0.18	0.4	0.27	0.5	1.7	0.2

Table 1 (continued)

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>	<i>Vaccinium angustifolium</i>
G. INTERRELATIONS							
Biomass accumulation ratio	8.7	7.2	6.9	3.5	2.9	1.6	1.55
Basal area increment/basal area (%)	3.63	6.10	3.93	6.28	8.45	12.0	—
Wood density (dry g/fresh cm ³)	0.49	0.61	0.63	—	—	—	—
Bark density	0.41	0.59	0.58	—	—	—	—
Production/EVI ^a (g/cm ³)							
Stem wood production/EVI	0.84	1.07	1.06	0.95	0.81	0.60	—
Stem bark production/EVI	0.24	0.21	0.38	0.67	0.24	0.58	—
Branch production/EVI	1.12	1.42	1.85	1.79	2.77	5.08	—
Twig and leaf production/EVI	2.59	4.14	4.13	15.68	6.76	25.9	—
Shoot net production/leaf dry weight	1.10	2.23	2.24	1.61	2.09	1.98	2.00
Shoot net production/leaf surface ^b (g/cm ²)	155	304	216	254	126	134	163
Shoot net production/leaf chlorophyll (g/g)	550	570	414	494	512	522	455
Shoot net production/stem and branch surface (g/m ²)	457	455	389	374	180	236	—
Stem production/stem surface (g/m ²)	720	1042	615	154	75	30.4	—

^a Parabolic volume, estimated volume increment (EVI), conic and parabolic surface, and basal area use diameter at breast height in the three trees, ground-level diameter in the four shrubs. See 'Estimative ratios'.

^b Leaf surfaces are for the needle perimeter in *Pinus rigida*, one side of the blade only in other species.

^c Leaf values are corrected for loss by insect consumption.

^d Root systems may (except in *P. rigida*) bear more than one shoot; the root/shoot ratio relates the root system to all its shoots, not to the mean shoot values in part A.

^e Largest seven individuals.

Shoot production distribution

Patterns of production distribution above ground are also consistent among the three tree species—about half in the current twigs and leaves, a quarter in branch growth, a fifth in stem wood and bark growth together and a small fraction (2–4%) in fruit (Table 1F). These are not patterns typical of forest trees; the smallness and open-growth form of the Brookhaven trees is expressed in branch growth which exceeds stem wood growth, and in current twig production percentages as high as those of many shrubs in the Great Smoky Mountains (Whittaker 1962). In the larger Oak Ridge trees twig and leaf production was about one-third of above-ground production, and stem wood and bark growth together 38–51%. In temperate-zone plantations stem production exceeds leaf production by amounts averaging about two times in deciduous stands, three times in evergreen stands (Bray & Gorham 1964).

Trends of shifting emphasis among stem, branch and foliage production may also be extended downward to small shrubs. In the Brookhaven shrubs current twig and leaf production was 60–70% of above-ground production; stem wood and bark production together, 9–13%. Shrub production analyses of *Vacciniaceae* in the Great Smoky Mountains (Whittaker 1962) included *Gaylussacia baccata* in pine heath, *G. ursina* (M. A. Curtis) Torr. & Gr. in oak forest and *Vaccinium pallidum* Ait., a close relative of *V. vacillans* with taller shoots, in pine heath. The fraction of growth in twigs and leaves

was in general higher, and that in stems lower, in the Brookhaven shrubs. The Brookhaven shrubs, which grow in a more shaded environment, have mean stem radial wood increments, and percentages of above-ground production in stem wood and bark growth, about half those of their equivalents in the pine heaths. Stems were not separated from

Table 2. *Twig and leaf, and flower and fruit data for trees and shrubs at Brookhaven National Laboratory*

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>	<i>Vaccinium angustifolium</i>
A. CURRENT TWIGS WITH LEAVES							
Mean twig diameter (mm)	4.34	2.92	2.44	1.98	1.18	1.18	0.57
Mean twig length (cm)	5.52	7.98	5.72	5.15	3.52	2.43	1.43
Dry weight, twig with leaves (g)	4.195	3.458	1.821	1.366	0.117	0.215	0.024
% in twig	13.6	13.4	13.0	9.1	22.4	23.0	25.0
% in petioles or sheaths	4.5	5.3	3.2	2.4	3.4	2.1	1.8
% in blades or needles ^a	81.9	81.3	83.8	88.4	74.2	74.9	73.2
Insect damage (% of blades)	—	15.6	8.7	7.0	0.05	1.6	0.02
Number of leaves per twig	96	7.14	5.43	4.59	4.62	3.16	3.90
Leaf blade area ^b per leaf (cm ²)	3.42	38.16	31.36	19.68	2.93	1.82	0.78
Blade weight/area ^b (mg/cm ²)							
mean	11.33	9.80	8.31	13.4	6.14	7.42	5.75
Upper leaves	12.16	11.88	10.00	—	—	—	—
Lower leaves	10.21	8.51	6.25	—	—	—	—
Dry weight of upper twigs (g)	1.59	0.843	0.368	—	—	—	—
Dry weight of lower twigs (g)	0.135	0.312	0.162	—	—	—	—
Leaf chlorophyll (mg/dry g ^c)	2.0	4.7	5.8	3.5	4.2	3.8	4.4
Bud scales, dry weight/bud (mg)	15.8	3.1	2.0	1.9	1.0	1.1	0.5
B. FLOWERING TWIGS							
Dry weight per peduncle (mg) of:							
Peduncle, pedicels ^d	—	4.5	4.5	2.0	7.1	9.3	8.5
Flowers ^e	58.0	9.0	17.8	5.0	10.6	11.4	5.2
Bud scales ^f	25.2	9.8	4.9	4.2	1.6	2.2	1.4
Number of flowers/peduncle	1.0	28.4	24.0	21.2	7.0	5.7	4.1
C. FRUITING TWIGS							
Dry weight per peduncle (mg):							
Peduncle, pedicels, cone	1540	44.3	50.4	26.8	1.53	2.73	1.00
Fruits, seeds of pine	2770	2840	3140	716	40.5	45.2	12.9
Number of fruits per peduncle	286	1.24	2.1	1.65	0.9	2.9	1.4
Dry weight of cup (mg)	—	680	335	212	—	—	—
Dry weight of acorn (mg)	—	1607	1161	222	—	—	—

^a Corrected for insect consumption.

^b For one side of deciduous leaves, perimeter of pine needles.

^c Dry weight of blade plus petiole.

^d Includes ovaries in Vacciniaceae.

^e One male strobile in pine, all flowers with ovaries and receptacles from one strobile in oaks, all corollas with stamens from a peduncle in Vacciniaceae.

^f Scales of larger buds from which both flowers and twig develop.

branches in the dwarf blueberry (*V. angustifolium*) but in this about two-thirds of production was in twigs with leaves, one-third in wood and bark.

Insect consumption of oak leaves (Table 2A) was near average values of 6–8% for deciduous forests (Rothacher, Blow & Potts 1954; Bray 1964; Bray & Dudkiewicz 1963) in *Quercus alba* and *Q. ilicifolia*, but particularly high (15.6%) in *Q. coccinea*. As in the Smokies (Whittaker 1962) consumption of vacciniaceous leaves was low. With the exception of *Vaccinium vacillans*, the fraction of production spent on flowers and bud

scales together was less than 1% of the above-ground total (Tables 1F and 2A). In the other species corollas of the shrubs and male strobili of the trees were 0.2–0.5% of above-ground production. Higher flower production has been reported in other communities (Whittaker 1962; Ovington 1962, 1963), and the shrub species studied at Brookhaven produce copious flowers and fruits in open environments. Within the study forest, however, the fraction of plants and twigs bearing flowers was small and the fruit production of one species, *Quercus ilicifolia*, was near zero. On the basis of bud-scale weights in relation to twig-and-leaf weights (Table 2), the fraction of above-ground production in bud scales was 0.1–0.2% in the trees and *Q. ilicifolia*, 0.3–0.5% in the *Vacciniaceae*.

Root–shoot relations

In *Pinus rigida*, in which the root crown and shoot are of the same age, the mean root/shoot ratio is 0.283 (comparing total dry weight of the root system with dry weight of wood and bark of stems and branches). The ratio is in the 0.20–0.30 range of values observed in many forest trees (Ovington 1962) and is the only root/shoot ratio among the Brookhaven species in this range (Table 1E). In *P. rigida*, as in the oaks, roughly one-half of root system weight is in the root crown and one-half in roots. *P. rigida* in this forest has both large and rapidly-tapering tap roots extending down toward the water table to depths exceeding 2 m in larger individuals, and predominantly horizontal and very attenuate crown roots mostly within 3 dm of the soil surface.

Since the oaks of the Brookhaven forest are adapted to resprouting after fire, age of the root systems may exceed that of the shoots. Accumulation of root mass through more than one generation of shoot growth results in root/shoot ratios which are atypical for forest trees—averaging around 0.9 in *Quercus alba* and 0.5 in *Q. coccinea*. Many, probably the majority, of root crowns bear more than one living shoot. In some cases shoots separated by nearly a metre at ground level may rise from opposite points on the periphery of a large root crown which also supports smaller suckers. If the Brookhaven trees are ranked by the size of the largest shoot, marked trends in root/shoot ratios with shoot size appear (Table 1E; cf. Ovington 1957; Whittaker 1962). Smaller, relatively suppressed shoots which do not share a root system with a larger shoot may be outweighed more than twice by their roots, and oak trees were collected in which root weight exceeded shoot weight by four to five times.

Q. ilicifolia dominates stages in fire succession before the trees and persists with declining coverage and vitality under the later forest canopy. In the forest, numerous small and short-lived shoots are produced from the root crowns, the mass of which was produced earlier by vigorous shoots during the open growth of the shrub stage. It appears that vitality of the root crowns, as expressed in shoot growth, gradually declines in the forest, smaller and smaller shoots being produced until the root system dies unless released by a new fire. Notably asymmetric root/shoot relations result. In two individuals the ratios of the root system, including dead heartwood of the root crown, to stem and branches of all living shoots were 89 and 117. More vigorous shrubs in the forest have ratios averaging 4.9, probably within the range of values for other shrubs of repeated shoot growth from massive, fire-resistant root crowns.

In the three *vacciniaceous* shrubs extensive rhizome systems branch and cross over one another in the surface layers of the soil. Numerous ‘shoots’ rise from the underground stem, the full length of which may be several metres. *Vaccinium vacillans* plants possess at least one large, nearly vertical tap root of attenuate form, which may exceed

2 m in length. *V. angustifolium* plants have smaller and usually oblique tap roots, while no tap roots were found on *Gaylussacia baccata* (Reiners 1965). Root/shoot ratios, including the rhizome with the root system, vary widely among the three species; all three are higher than the ratios for forest *G. ursina* (1.34) and other forest shrubs in the Great Smoky Mountains (Whittaker 1962). Root/shoot ratios were high also in *G. baccata* and *Vaccinium pallidum* in pine heath in the Smokies, but rhizome systems could not be collected whole from these communities. Root/shoot ratios increase with increased exposure to light among individual plants of a species (Shirley 1929; Harley 1939; Goodall 1955; Maggs 1960). Root/shoot ratios tend also to be higher in species of drier soils (Bray 1963). It seems likely that these ratios increase on the whole from the woody plants of forests to those of shrub communities and other 'open' environments, whether trees are compared with shrubs, or forest shrubs with those of open environments. The shrub of a well-lighted open environment may have high production per unit of leaf weight and surface (Whittaker 1962) and smaller expenditure of this production on supporting stem and branch tissue than is the case in forest trees. A larger fraction of production is utilized in root growth, and the resulting massive root has survival value both for water-obtaining ability and for its capacity to survive fire, browsing and drought which may damage or destroy the shoots.

Only in *Pinus rigida* may it be assumed that stem and root system are contemporaneous. Dead stem bases on the vacciniaceous shrubs imply that in these, as in the oaks, root system age exceeds age of the present shoots. If in *P. rigida* one assumes that the ratio of production to biomass in the root system is somewhat less than in the shoot system with its leaves, then root production may be about one-fifth of shoot production (cf. Bray 1963). Root/shoot ratios for the Brookhaven oaks do not indicate current root production; but the ratio of root to shoot production is probably higher in these small oaks than in *P. rigida* because of the large root mass and surface. From root/shoot ratios of smaller trees in other areas (Ovington 1962), root/shoot production ratios of 0.3–0.4 were taken as reasonable for the Brookhaven oaks. Contemporaneous root and shoot systems of *Kalmia latifolia* L., *Gaylussacia ursina*, *Hydrangea arborescens* L. and smaller *Rhododendron maximum* L. in the Great Smoky Mountains, gave root/woody shoot biomass ratios of 1.3–1.8 (Whittaker 1962). It seems likely that root/shoot production ratios are in the same range for both these and the Brookhaven shrubs, but ratios for the non-contemporaneous roots and shoots of the latter do not provide effective evidence.

Surface and production relations

As indicated in Table 1C, branch bark surface much exceeds stem bark surface—by 2–4 times in many of the shrubs and 4–6 times in many of the trees. In general, the ratio of branch to stem surface increases with increasing size of plants; but among plants of a given size it is much higher in heavy-branched, open-growth forms than in light-branched, shade-growth forms. The ratios range around 20 in older, open-growth *Quercus alba* at Oak Ridge. Stem wood or cambial surface is around 0.9 of stem bark surface, with differences resulting from plant size and bark thickness of different species. Leaf surface is two to three times branch bark surface in many plants, but the ratio is somewhat lower in large open-growth trees.

Shoot net production per unit leaf surface ranges between 130 g/m² and 300 g/m² in the Brookhaven plants (Table 1G). The lower of these values occurs in the shade-affected shrubs (still lower values (50–80) occur in forest shrubs in the Smokies—Whittaker 1962),

B J.E.

and in *Pinus rigida*, in which photosynthesis of 2 years' needles supports current growth. A ratio of 300, combined with a root/shoot production ratio of possibly 0.3 implies around 400 g/m² total net annual production in relation to leaf blade surface, for the Brookhaven deciduous trees. A ratio of 130, combined with root/shoot ratio of 1.4 (for comparable Smokies shrubs—Whittaker 1962) implies a corresponding ratio of about 300 for total production/leaf surface in Brookhaven shrubs growing in partial shade. Ratios of above-ground production to leaf weight are rather consistently 2.0–2.25 in these plants, as in many deciduous shrubs in the Smokies (Whittaker 1962), but lower in *P. rigida* and *Quercus ilicifolia*, which has rather heavy leaves and a low rate of wood growth. A ratio of 2.25 for above-ground production/leaf weight, combined with a root

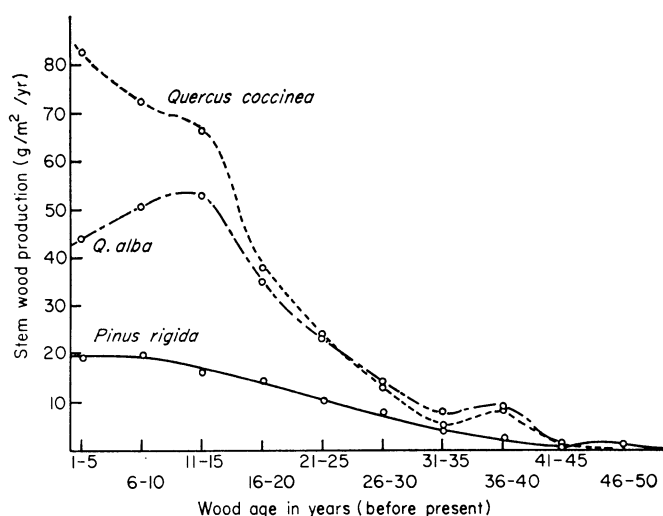


FIG. 1. Annual production of wood in stems (dry weight) of the three dominant trees of the Brookhaven forest for the last 50 years, based on measurements of increments of wood for 5-year periods. The curves show growth by trees now living in the forest, and hence reflect development of the forest following a fire 45–47 years before the study.

production estimated at 0.3 of shoot production, implies a ratio of total net production to leaf weight of 2.9. The latter value is in the range of, but lower than, the average of 3.7 for such ratios in temperate deciduous plantations (Bray & Gorham 1964).

Other production ratios are in the range of those for Appalachian plants (Whittaker 1962; Whittaker *et al.* 1963). Biomass accumulation ratios (of above-ground biomass to above-ground net annual production, dry weights) of 1.6–8.7 reflect the small stature and youth of the Brookhaven plants, compared with other shrubs (Whittaker 1962) and forest trees (ratios of 14–17 for the Oak Ridge trees, up to 50 for large forests—Whittaker *et al.* 1963; Whittaker 1966). Ratios of stem production to stem surface area (cf. mean basal wood radial increments, Table 1A) indicate the broad trend of increasing thickness of wood production with increasing size of plants, and the fact that of the two oaks which share dominance, *Q. coccinea* is currently growing faster than *Q. alba*.

Stem wood growth history

Radial wood increments were measured for all past 5-year periods on the discs, and from these measurements past rates of stem wood growth were computed on the

same basis as current rates. The resulting pentad volume increments, averaged for sample trees of a species and converted to $\text{g/m}^2/\text{yr}$ for a Brookhaven forest sample, are plotted in Fig. 1. Of the three species, the growth of *Q. alba* is currently slowing and that of *Q. coccinea* still increasing but at a slower rate than before, while growth of *Pinus rigida* appears to be stabilized.

The oblique, convex earlier parts of these curves indicate how widely stem weight divided by age would underestimate current wood production. The varied slopes of the recent parts of the curves indicate that errors of different magnitudes would result from such a production estimate for the different species in the forest. During the last three pentads stem wood growth has been consistently $150\text{--}160 \text{ g/m}^2/\text{yr}$, despite the shifting production balance between *Quercus alba* and *Q. coccinea*. The data thus suggest that the forest is 'mature' in a limited sense of relative stabilization of production. In this forest there are few dead trees, and most of these are small. It is likely that most trees which came up following the fire are still alive, and that the curves in Fig. 1 represent in large part the history of stem wood production by trees in the forest since the fire. In the period before the recent pentads, most production of the community was probably by dense *Q. ilicifolia*, of which some plants are still present. The technique of analysing past wood growth can thus in some circumstances (which may include some plantations) provide information of interest on production history of a forest.

Estimative ratios

Preliminary estimations of net production and other community variables are possible on the basis of ratios of these variables to field measurements. The field measurements, or expressions derived from them, on which estimations from ratios have been based are:

1. Clipping dry weight of undergrowth species—current twigs with leaves for shrubs and tree seedlings, and above-ground parts of herbs, per square metre (mean of twenty quadrats).

2. Parabolic volume of trees— $V_p = 0.5 \pi r^2 h$, in which r is radius at breast height and h is tree height. Both stem parabolic volume, with r including bark thickness, and wood parabolic volume have been used. (Expressions 2, 3 and 4, are summed usually for all trees in a 0.1 ha/quadrat . When applied to non-arborescent shrub shoots, r is ground-level radius.)

3. Conic stem surface— $S_c = \pi r h$, or parabolic surface— $S_p = [\pi/6k^2] [(4kh + 1)^{3/2} - 1]$, $k = (h - 137 \text{ cm})/r^2$ for trees, $k = h/r^2$ for small shrubs.

4. Estimated volume increment (one-half basal area increment times height), $\text{EVI} = 0.5 \pi h(r^2 - c^2)$, $c = r - i$, i is the annual wood radial thickness increment at breast height.

The dimension analysis of shrubs provides ratios between weight of current twigs with leaves and total above-ground production (Table 1F, cf. Whittaker 1962). The reciprocals of the current twig production in percentages give ratios of $1.50\text{--}1.65$ (which may be subject to correction for insect loss) by which weights of current twig clippings in quadrats may be multiplied to estimate above-ground net production of the shrub community. Clipping weights in quadrats are subject to high dispersions (Whittaker 1966), and results of dimension analysis of shrubs to moderate dispersions (standard errors of means for the ratios of total above-ground to clipping production are $3\text{--}6\%$ of the mean for sets of

ten dominant shrubs—Whittaker 1962). Although all ratios of estimation shift with size of plants, error should not result from this shift if the shrub sample has been chosen to represent the shrub population fairly. The individuals of the shrubs studied at Brookhaven included many shoots of different sizes in essentially unbiased representation of these sizes in the forest.

Parabolic volume is often an overestimate of the true volume of a stem, as indicated in Table 1B for shrubs, in which the radius is that at the base of the stem. In small trees, when radius at breast height is used to compute parabolic volume, parabolic volume is an underestimate because radius at breast height is small in relation to the true basal radius at ground level. For the largest of the Brookhaven oaks, ratios of parabolic and true stem volume are close to unity, for both stem volumes (with bark) and wood volumes; and wood volume is 0.80–0.85 times parabolic stem volume. Parabolic volume overestimates by varying amounts the merchantable volume used by the forester. For ecological purposes, however, it provides an effective approach to estimation of volume and a reasonable basis for comparing forests (Whittaker 1966). It offers also another variable which has advantage over diameter alone for estimation of other tree characteristics related to volume (Table 4).

True stem surface (for a hypothetical smooth bark) lies between the conic and parabolic estimates of surface (Table 1C). Only *Vaccinium vacillans* is exceptional in this respect; conic and parabolic surface values in this species are both overestimates because stems are short in relation to plant height. Stem surface (and branch and leaf surface) may be estimated either from ratios or linear regressions of true surface on conic surface (Table 4), or from logarithmic regressions on diameter (Table 3). There seems to be no reason to prefer the more complex parabolic surface computation over conic surface as an approach to estimation.

Estimated volume increment (EVI) was chosen as an approach to estimation of forest production (Whittaker 1961) because it combines in one expression tree size and growth rate and is strongly correlated with various aspects of tree production. Coefficients of correlation are generally 0.98 or 0.99 for linear correlations of wood growth with EVI in the Brookhaven trees, 0.85–0.95 for branch wood and bark growth with EVI; lower coefficients are obtained for other plant fractions and for shrubs, somewhat higher coefficients for logarithmic regressions (Table 4D). Ratios of total above-ground net production to EVI shift with plant size, but give standard errors of 7–15% of the mean for ten individuals of canopy trees or dominant shrubs (Whittaker 1962; Whittaker *et al.* 1963). These ratios, for the dominant individuals in which production is strongly concentrated in many communities, may consequently be used to estimate production (Whittaker 1963, Whittaker *et al.* 1963). They may have advantage for this purpose over mean-tree approaches since a value of EVI can be obtained summarizing dimensions and indicated growth-rates of all trees in a sample quadrat. EVI provides a most useful first index of relative growth-rate of forests and communities of larger shrubs (Whittaker 1963, 1966); but ratios of total production to EVI shift with climate, stand maturity, and other factors which affect the relation of rate of wood growth at breast height to other aspects of production. EVI is smaller than true volume growth in many forest trees, in which wood increment thickness at breast height is less than that above and below breast height (Farrar 1961; Senda & Satoo 1956; Whittaker *et al.* 1963). True volume growth was 1.2–1.5 times EVI in a number of tree and shrub samples (Whittaker 1962, and Table 1); but 1.09 in Oak Ridge *Quercus alba* of open growth form, and less than 1.0 in smaller shrubs.

Regressions

Tables 3 and 4 compile various regressions which are of interest for community analysis. Regression constants, mostly using diameter at breast height as the independent variable, are available for other communities (Kittredge 1944, 1945; Ovington 1957; Ovington & Madgwick 1959a, b; Satoo, Negisi & Senda 1959; Shanks, De Selm & Clebsch 1961; Ogawa, Yoda & Kira 1961; Tezuka 1961; Kimura 1963; Nomoto 1964; Young, Strand & Altenberger 1964) and their application to tropical forests has been discussed by Ogawa *et al.* (1965). Duplications of the dependent variables in the tables result from the attempt to offer options on independent variables which may be preferred by different investigators for different estimations. Expressions of closeness of fit of the regressions are given in two forms, the conventional r or coefficient of correlation, and 'relative errors of estimate' (e and E).

The coefficients of correlation are unduly impressive; a large share of the values range above 0.90 and some above 0.99. Coefficients of correlation are relatively ineffective for expressing the closeness of fit and reliability of estimation for data such as these. High coefficients result from elongate scatter figures produced by a wide range of sizes of individual plants in a sample. The effect is illustrated by the coefficients of correlation in the last column of Table 3. The regressions in this column have been computed for ten species combined; to the plants studied at Brookhaven have been added the larger Oak Ridge trees (ten individuals each of *Liriodendron tulipifera* L., *Pinus echinata* Mill. and *Quercus alba* (Whittaker *et al.* 1963)) and, for the transition between shrubs and trees, the first author's data on *Rhododendron maximum* in the Great Smoky Mountains. In several cases these mixed-species regressions combining data on shrubs and trees have higher coefficients of correlation than samples of individual species.

We have sought means of expressing more effectively the relative accuracy of estimations. The 'standard error of estimate' for a regression is, $S.E. = \sqrt{[\sum d^2/(n-1)]}$, 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. To express the relative spread of the points from the linear regressions, the standard error of estimate has been divided by the mean value of y to produce the 'estimate of relative error', e , for a linear regression. As the standard error of estimate is analogous to a standard deviation for departures of points from a regression line rather than from a mean, so the estimate of relative error is analogous to the coefficient of variation. A value of 0.10 for e thus suggests an expected error of $\pm 10\%$ for a given estimate of y . In the logarithmic regressions the standard error of estimate is a logarithm added to or subtracted from an estimate of $\log y$; its antilog is consequently a factor by which a given value of y is multiplied or divided. A value for E , the estimate of relative error for a logarithmic regression, of 1.10 thus suggests an expected error range from $1.10y$ to $y/1.10$.

In Tables 3 and 4 estimates of relative error range from 1.10 for a few relationships, through many values of 1.15–1.30, to extreme values above 2.0. The errors of estimation are not small, and as may be expected, they are larger for estimates of branch dimensions from stem diameter than for estimates of other stem dimensions from stem diameter. Most of the errors are larger for shrubs, with their widely variable relations of branches and stems, than for trees. Errors above 2.0 appear where wide scatter of points might be expected—for the small and highly variable amounts of heartwood in *Pinus rigida*, for production by *Vaccinium vacillans* stems, which are variable in both length and rate of

Table 3. Regressions of shoot dimensions on diameter for trees and shrubs at Brookhaven National Laboratory

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>	All species
A. WHOLE-SHOOT REGRESSIONS ON LOG ₁₀ BASAL DIAMETER (cm) (x)							
Log, shoot height (cm) (y)							
A	2.2819	2.2574	2.3312	1.9518	1.9441	2.1269	2.2481
B	0.5699	0.6783	0.5629	0.9523	0.8101	1.3060	0.7042
r	0.970	0.975	0.971	0.875	0.667	0.875	0.995
E	1.102	1.138	1.101	1.474	1.166	1.252	1.169
Log, stem volume (cm ³)							
A	2.2362	2.3640	2.3351	1.4847	1.5271	1.4436	2.3269
B	2.3153	2.2493	2.2063	2.7700	3.1174	3.0043	2.3329
r	0.996	0.996	0.995	0.970	0.947	0.841	0.999
E	1.155	1.188	1.162	1.659	1.189	1.823	1.317
Log, wood volume (cm ³)							
A	2.0218	2.2025	2.1493	1.3730	1.4751	1.3031	2.2263
B	2.3906	2.3148	2.2683	2.8175	3.1979	3.0669	2.3428
r	0.996	0.996	0.994	0.970	0.950	0.852	0.999
E	1.156	1.202	1.188	1.685	1.209	1.794	1.316
Log, stem surface (cm ²)							
A	2.7533	2.7814	2.8208	2.2035	2.2777	2.1903	2.8108
B	1.4538	1.4805	1.3869	1.8959	2.2231	2.2530	1.4855
r	0.933	0.995	0.991	0.958	0.948	0.772	0.997
E	1.129	1.134	1.138	1.517	1.155	1.781	1.225
Log, branch surface (cm ²)							
A	2.6985	2.9356	2.8073	2.3792	2.7890	3.1331	3.3165
B	2.1814	2.1553	2.2071	2.4094	2.5754	2.5973	1.6957
r	0.986	0.974	0.957	0.918	0.881	0.833	0.990
E	1.287	1.521	1.610	2.156	1.457	1.711	1.737
Log, leaf surface (cm ²)							
A	3.5494	3.8493	3.4597	2.9943	2.9376	3.2006	3.6471
B	1.8745	1.6436	1.7369	1.5291	2.2096	2.2023	1.6395
r	0.983	0.983	0.957	0.905	0.873	0.796	0.995
E	1.274	1.291	1.453	1.694	1.329	1.685	1.494
Log, stem dry weight (g)							
A	1.8758	2.1564	2.1436	1.3561	1.3681	1.2758	2.1543
B	2.3261	2.2391	2.1844	2.7146	3.1008	2.9605	2.2830
r	0.996	0.996	0.996	0.974	0.960	0.846	0.998
E	1.153	1.186	1.150	1.590	1.219	1.685	1.309
Log, stem wood dry weight (g)							
A	1.7226	2.0001	1.9610	1.2442	1.2449	1.1773	2.0736
B	2.3779	2.3025	2.2537	2.7663	3.1767	3.1513	2.2336
r	0.996	0.995	0.995	0.973	0.947	0.830	0.997
E	1.165	1.205	1.176	1.616	1.227	1.931	1.506
Log, stem bark dry weight (g)							
A	1.3832	1.6767	1.7075	0.6958	0.6536	0.7705	1.5487
B	2.1249	1.9909	1.9747	2.5831	2.6971	2.8065	2.0978
r	0.987	0.996	0.998	0.968	0.890	0.813	0.986
E	1.262	1.153	1.101	1.636	1.252	1.870	1.201
Log, stem heartwood dry weight (g)							
A	1.7553	1.8955	1.3220	—	—	—	—
B	2.3291	2.0316	2.4628	—	—	—	—
r	0.996	0.991	0.964	—	—	—	—
E	2.433	1.190	1.614	—	—	—	—

Table 3 (continued)

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>	All species
Log, branch wood and bark dry weight (g)							
<i>A</i>	1.1100	1.7045	1.4383	0.8596	1.1167	1.1999	1.8518
<i>B</i>	2.5516	2.2889	2.3371	3.2040	3.0648	2.6115	2.0748
<i>r</i>	0.988	0.972	0.957	0.917	0.904	0.859	0.990
<i>E</i>	1.318	1.591	1.624	2.794	1.506	1.622	1.611
Log, above-ground dry weight (g)							
<i>A</i>	2.0171	2.3948	2.3058	1.7076	2.4200	1.6937	2.2968
<i>B</i>	2.3373	2.1900	2.1666	2.3551	1.8627	2.4995	2.1357
<i>r</i>	0.998	0.994	0.993	0.953	0.961	0.866	0.991
<i>E</i>	1.109	1.121	1.196	1.725	1.253	1.563	1.724
Log, stem wood production (g/yr)							
<i>A</i>	0.9369	0.8163	0.6318	0.1286	-0.0062	0.2332	0.8809
<i>B</i>	1.8667	2.2888	2.2029	2.1640	2.1069	3.2677	2.0828
<i>r</i>	0.933	0.988	0.979	0.957	0.840	0.759	0.996
<i>E</i>	1.637	1.346	1.379	1.623	1.208	2.399	1.530
Log, stem bark production (g/yr)							
<i>A</i>	0.4784	0.6953	0.5848	-0.1405	-0.6796	0.0648	0.3934
<i>B</i>	1.7180	1.7784	1.6842	1.6609	1.6053	2.8588	1.8073
<i>r</i>	0.979	0.994	0.989	0.916	0.806	0.661	0.992
<i>E</i>	1.279	1.165	1.192	1.703	1.225	2.745	1.682
Log, branch wood and bark production (g/yr)							
<i>A</i>	0.8928	0.9795	1.0142	0.3102	0.4376	0.6609	1.1714
<i>B</i>	2.0078	2.2145	2.0201	2.8004	2.4561	2.4755	1.8069
<i>r</i>	0.960	0.989	0.955	0.905	0.667	0.776	0.990
<i>E</i>	1.499	1.322	1.555	2.638	1.317	1.870	1.726
Log, current twig and leaf production (g/yr)							
<i>A</i>	1.3625	1.8565	1.5849	1.1797	0.7915	1.1556	1.6842
<i>B</i>	1.8772	1.6436	1.7380	1.6100	2.0600	2.1026	1.6526
<i>r</i>	0.983	0.983	0.957	0.896	0.787	0.802	0.989
<i>E</i>	1.273	1.290	1.453	1.743	1.329	1.627	1.794

All regressions are in the form $\log_{10} y = A + B \log_{10} x$, in which x is breast-height diameter (cm) in the first three species (trees), and shoot ground-level diameter (cm) in the last three species (shrubs) and y is the dependent variable indicated. Coefficients of correlation are given as r , estimates of relative error (E) as antilogs of the standard errors of estimate.

wood growth, and for dimensions of branches of *Quercus ilicifolia*, which are widely variable among shoots of a given size.

While the relative errors of estimate suggest certain preferences in use of the regressions, they do not show clear and consistent advantage of any other independent variable over basal diameter. Basal diameter consequently seems the most widely useful, as well as the most convenient, measurement to use as an independent variable, when regressions derived from plants of a given community are applied to estimating dimensions of that community. The estimates of relative error do not, however, provide expression for what seems in practice a principal source of error in the application of these regressions. The regressions, though much influenced by the largest individuals of a sample set, tend to estimate the production by large trees of slowing growth on the basis of the slope of production on diameter among smaller trees whose wood growth is not yet slowing (cf. Ogawa *et al.* 1965). Substantial overestimation of community production can result from this overestimation of growth by the few largest individuals in the sample quadrat.

Table 4. Regressions for trees and shrubs at Brookhaven National Laboratory

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>
B. REGRESSIONS ON PARABOLIC VOLUME (cm ³) (x)						
Linear, stem volume (cm ³) (y)						
a	4661.4	3259.3	2782.3	3.1241	1.3384	−0.0713
b	1.0515	0.9940	0.9651	0.7960	0.7675	0.8856
r	0.991	0.995	0.993	0.985	0.800	0.720
e	0.112	0.105	0.082	0.400	0.702	0.568
Linear, wood volume (cm ³)						
a	5022.4	1645.9	978.1	1.0469	1.0945	−0.0791
b	0.7781	0.8428	0.7760	0.6589	0.6688	0.6200
r	0.996	0.999	0.999	0.984	0.792	0.771
e	0.109	0.031	0.051	0.395	0.680	0.656
Linear, stem dry weight (g)						
a	3509.6	2706.1	1866.5	0.0354	1.0640	−0.0057
b	0.4596	0.5884	0.5896	0.6206	0.5073	0.5710
r	0.995	0.999	0.997	0.995	0.811	0.874
e	0.125	0.057	0.093	0.227	0.610	0.408
Linear, branch dry weight (g)						
a	2335.8	−4064.1	−733.8	−5.3728	0.8281	0.2104
b	0.1422	0.3503	0.2269	0.4882	0.2552	0.5101
r	0.936	0.944	0.977	0.976	0.823	0.783
e	0.432	0.550	0.281	0.551	0.536	0.465
Log, stem dry weight (g)						
A	0.1760	0.6140	0.4989	−0.0577	−0.2600	−0.2664
B	0.9055	0.8348	0.8532	0.9132	1.0163	0.9196
r	0.998	0.996	0.998	0.983	0.929	0.890
E	1.107	1.183	1.092	1.462	1.553	1.644
Log, branch dry weight (g)						
A	−0.7120	0.1667	−0.3216	−0.7845	−0.4911	−0.1586
B	0.9841	0.8444	0.9129	1.0572	1.0029	0.7688
r	0.980	0.962	0.962	0.907	0.873	0.856
E	1.415	1.716	1.600	2.954	1.837	1.631
Log, current twig and leaf dry weight (g)						
A	0.0238	0.6961	0.2543	0.3559	−0.2998	0.0450
B	0.7228	0.6073	0.6790	0.5086	0.7173	0.6509
r	0.975	0.975	0.960	0.903	0.837	0.796
E	1.334	1.369	1.434	1.704	1.667	1.684
Log, above-ground dry weight (g)						
A	0.3222	0.8985	0.6750	0.4865	0.1515	0.3929
B	0.9070	0.8136	0.8462	0.7876	0.9193	0.7474
r	0.997	0.991	0.996	0.957	0.911	0.876
E	1.137	1.284	1.157	1.698	1.571	1.541
C. REGRESSIONS ON CONIC SURFACE (cm ²)						
Linear, stem bark surface (cm ²)						
a	1061.4	1298.5	1076.2	15.152	9.3265	−2.2655
b	1.3112	1.1967	1.1891	1.0389	0.9879	1.0134
r	0.999	0.999	0.999	0.989	0.784	0.832
e	0.042	0.031	0.038	0.231	0.490	0.442
Linear, branch bark surface (cm ²)						
a	−29557.0	−104170.0	−62614.0	−139.66	3.1674	3.1032
b	10.926	18.875	16.171	3.574	2.7161	4.9925
r	0.952	0.880	0.950	0.971	0.738	0.762
e	0.367	0.705	0.394	0.486	0.548	0.477

Table 4 (*continued*)

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>
D. REGRESSIONS ON ESTIMATED VOLUME INCREMENT (cm³/yr)						
Linear, stem wood production (g/yr)						
<i>a</i>	-3.8064	220.74	71.715	0.2871	0.1545	-0.0090
<i>b</i>	0.8109	0.7708	0.8451	0.8281	0.3862	0.6677
<i>r</i>	0.983	0.994	0.988	0.923	0.682	0.896
<i>e</i>	0.154	0.113	0.195	0.735	0.552	0.536
Linear, stem bark production (g/yr)						
<i>a</i>	79.082	57.158	78.403	0.2543	0.0573	130.73
<i>b</i>	0.1284	0.1238	0.1197	0.3168	0.0711	0.4833
<i>r</i>	0.774	0.928	0.907	0.872	0.558	0.767
<i>e</i>	0.492	0.361	0.380	0.868	0.542	0.667
Linear, branch production (g/yr)						
<i>a</i>	238.17	112.94	251.19	-4828.0	0.4276	0.1507
<i>b</i>	0.9456	1.0180	1.1189	2.347	0.9410	1.798
<i>r</i>	0.848	0.852	0.954	0.866	0.666	0.616
<i>e</i>	0.445	0.680	0.349	1.138	0.545	0.745
Linear, current twig and leaf production (g/yr)						
<i>a</i>	830.54	917.07	681.98	8.273	1.506	0.8956
<i>b</i>	1.7577	1.295	1.7261	4.215	1.734	5.446
<i>r</i>	0.687	0.865	0.946	0.900	0.428	0.606
<i>e</i>	0.678	0.526	0.335	0.578	0.737	0.553
Log, stem wood production (g/yr)						
<i>A</i>	0.1030	0.3382	0.2728	-0.0774	-0.2583	-0.2853
<i>B</i>	0.9394	0.8880	0.9010	0.9600	0.7775	1.0040
<i>r</i>	0.994	0.997	0.996	0.949	0.815	0.904
<i>E</i>	1.160	1.152	1.147	1.657	1.707	1.775
Log, stem bark production (g/yr)						
<i>A</i>	0.0046	0.3429	0.3596	-0.2986	-0.8853	-0.4301
<i>B</i>	0.7669	0.6835	0.6698	0.7367	0.5578	0.8419
<i>r</i>	0.924	0.994	0.978	0.909	0.736	0.755
<i>E</i>	1.578	1.173	1.282	1.740	1.643	2.418
Log, branch production (g/yr)						
<i>A</i>	0.1492	0.5549	0.6553	0.0398	0.299	0.3020
<i>B</i>	0.9594	0.8462	0.8378	1.1664	0.6162	0.5524
<i>r</i>	0.971	0.982	0.985	0.843	0.440	0.671
<i>E</i>	1.405	1.416	1.291	3.402	3.382	2.086
Log, current twig and leaf production (g/yr)						
<i>A</i>	0.8186	1.5492	1.2772	1.0241	0.4417	0.5656
<i>B</i>	0.8466	0.6254	0.7203	0.6664	0.4971	0.4200
<i>r</i>	0.938	0.973	0.986	0.830	0.450	0.621
<i>E</i>	1.571	1.382	1.237	2.089	2.305	1.895
E. BRANCH REGRESSIONS ON BRANCH BASAL DIAMETER (mm)						
Log, branch wood and bark dry weight (g)						
<i>A</i>	-1.6262	-1.4895	-1.4907	-2.3086	-1.4970	-1.3123
<i>B</i>	2.8344	2.9524	2.8803	3.8823	2.9531	2.4554
<i>r</i>	0.984	0.967	0.987	0.926	0.863	0.703
Log, current twig and leaf dry weight (g)						
<i>A</i>	-1.0398	-0.5548	-0.8621	-0.4048	-1.0535	-0.8399
<i>B</i>	2.0711	1.9664	2.1074	1.5598	1.8930	1.5486
<i>r</i>	0.918	0.915	0.938	0.907	0.745	0.790
Log, current twig number						
<i>A</i>	-0.6964	-0.9416	-0.6801	-0.4495	-0.2530	0.5186
<i>B</i>	1.7145	2.0339	1.9714	1.8666	1.5856	1.3505
<i>r</i>	0.916	0.947	0.947	0.913	0.735	0.680

Table 4 (continued)

	<i>Pinus rigida</i>	<i>Quercus coccinea</i>	<i>Quercus alba</i>	<i>Quercus ilicifolia</i>	<i>Gaylussacia baccata</i>	<i>Vaccinium vacillans</i>
Log, branch bark surface (cm ²)						
<i>A</i>	0.1739	−0.1304	−0.0188	−0.0380	0.6186	0.6664
<i>B</i>	2.4393	2.7973	2.7309	2.8809	2.2915	2.3639
<i>r</i>	0.953	0.979	0.975	0.918	0.824	0.789
F. LOG BRANCH WOOD AND BARK DRY WEIGHT (g) (<i>y</i>) ON LOG BRANCH AGE (yr) (<i>x</i>)						
<i>A</i>	−0.7547	−0.7093	−1.3217	−1.1672	−1.5115	−1.3080
<i>B</i>	2.3902	2.8243	2.8736	1.9749	1.8210	1.2070
<i>r</i>	0.784	0.841	0.905	0.753	0.677	0.348
G. LOG ROOT DRY WEIGHT (g) ON LOG ROOT (<i>y</i>) BASAL DIAMETER (mm) (<i>x</i>)						
<i>A</i>	−1.9119	−1.6128	−1.7674	−0.9664	−1.2382	−1.1579
<i>B</i>	2.1325	2.1208	2.1829	2.2308	2.2618	2.1330
<i>r</i>	0.964	0.988	0.985	0.991	0.877	0.986

Regressions are in the forms: (linear) $y = a + bx$, and (logarithmic) $\log_{10} y = A + B \log_{10} x$. The independent variable, x , is stated in the heading for the section of the table; the dependent variable, y , is given for the individual regression. Computations using a stem basal diameter employ breast-height diameter in the first three species, ground-level diameter in the last three. Coefficients of correlation are given as r ; estimates of relative error in the forms e (standard error of estimate divided by mean y) for linear regressions, E (antilog of standard error of estimate) for logarithmic regressions.

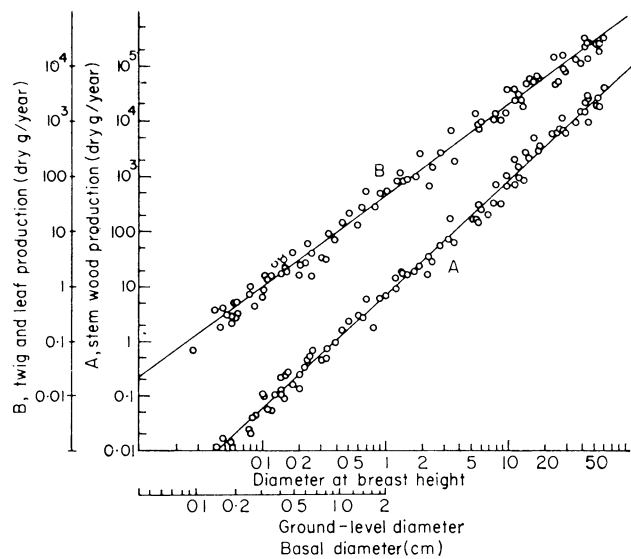


FIG. 2. Interspecies regressions for production of leaves and wood in individual stems of shrubs and trees, plotted against basal diameters. Both scales are logarithmic; see text for the basis of relating diameters at breast height and at ground-level to one another. Points represent individuals of ten species ranging from low shrubs (Vacciniaceae at Brookhaven National Laboratory) to medium-sized trees (Oak Ridge data of Whittaker *et al.* 1963).

Experience in applying these regressions suggests:

1. There is advantage in using EVI as an independent variable to estimate production, because EVI includes an expression of growth rate of the individual tree.
2. When regressions on diameter from one community are applied to a community of different height-diameter relations and growth rate, error results. Regressions on parabolic volume then provide better estimations of biomass; regressions on conic surface, better estimations of surface dimensions; and regressions on EVI, better estimations of stem growth.
3. Rates of wood growth and ratios of foliage growth to wood growth vary widely between species, and between different environments within a species (Burger 1945; Bray & Gorham 1964). We believe production estimation, especially when regressions are applied to communities other than the communities whence they were derived, may best combine an estimate of foliage or twig-and-leaf production by logarithmic regression on parabolic volume, with estimates of stem and branch growth by logarithmic or linear regression on EVI.

Interspecies regressions

The regressions for ten species combined (last column of Table 3) are plotted in Figs. 2 and 3. To relate trees and shrubs on the same scale, a regression of breast-height diameter on ground-level diameter in *Rhododendron maximum* in the Great Smoky Mountains (data of Whittaker 1962) has been extrapolated to compute 'equivalent' breast-height diameters for ground-level diameters of smaller shrubs. The two scales are coordinated as indicated on the abscissa of Figs. 2 and 3.

Data for individual trees and shrub shoots have been plotted in Fig. 2 to indicate both the linearity and the degree of scatter of the relationship. The straight-line form is not a consequence of the manner in which breast-height and ground-level diameters were combined; the same straight-line form was obtained for the data plotted in relation to either ground-level or breast height diameter alone. The data were also tested to determine whether the logarithms of the two variables could be better related to one another by any quadratic equation than by the straight-line equations. In general the quadratic equations did not produce a significantly better fit. Certain ways in which the data depart from the straight-line relations may, however, be observed. Dimensions of the largest and oldest individuals of a species often fall below the lines (Ogawa *et al.* 1965). Stem surfaces of *Vaccinium vacillans* fall below the regression line because of the short-stemmed form of this species; branch surface and current leaf surface of *Rhododendron maximum* fall below the regression lines because of the heavy twigs and leaves of this species; branch surfaces of the largest Oak Ridge *Quercus alba* lie above the regression line because of the open-growth history and large branches of these trees. Twig and leaf weights and leaf and branch surface values for evergreen species have been excluded from the regressions.

The regression lines for height, surface, production and biomass values in relation to basal diameters are plotted together in Fig. 3. The root biomass line is based on 14 points for mean root weights in relation to mean basal diameters in the first author's shrub data (Whittaker 1962), *Gaylussacia baccata* and *Vaccinium angustifolium* at Brookhaven, and the small, medium, and large *Pinus rigida* at Brookhaven. In order to include the small, many-stemmed shrubs in the regression, the 'mean root system weights' have been computed by multiplying a mean shoot (stem and branch wood and bark) weight by a mean root/shoot ratio based on comparing dry weights of root systems with dry weights of all shoots supported by them. The low slope of the root weight line, in relation to the slopes

of the lines for stem and branch wood and bark, reflects the decrease in root/shoot ratios with increasing size of plants already referred to. The latter relation may also be treated as a logarithmic relation: $\log (\text{root/shoot ratio}) = -0.0473 - 0.414 \log (\text{mean shoot basal diameter in centimetres})$.

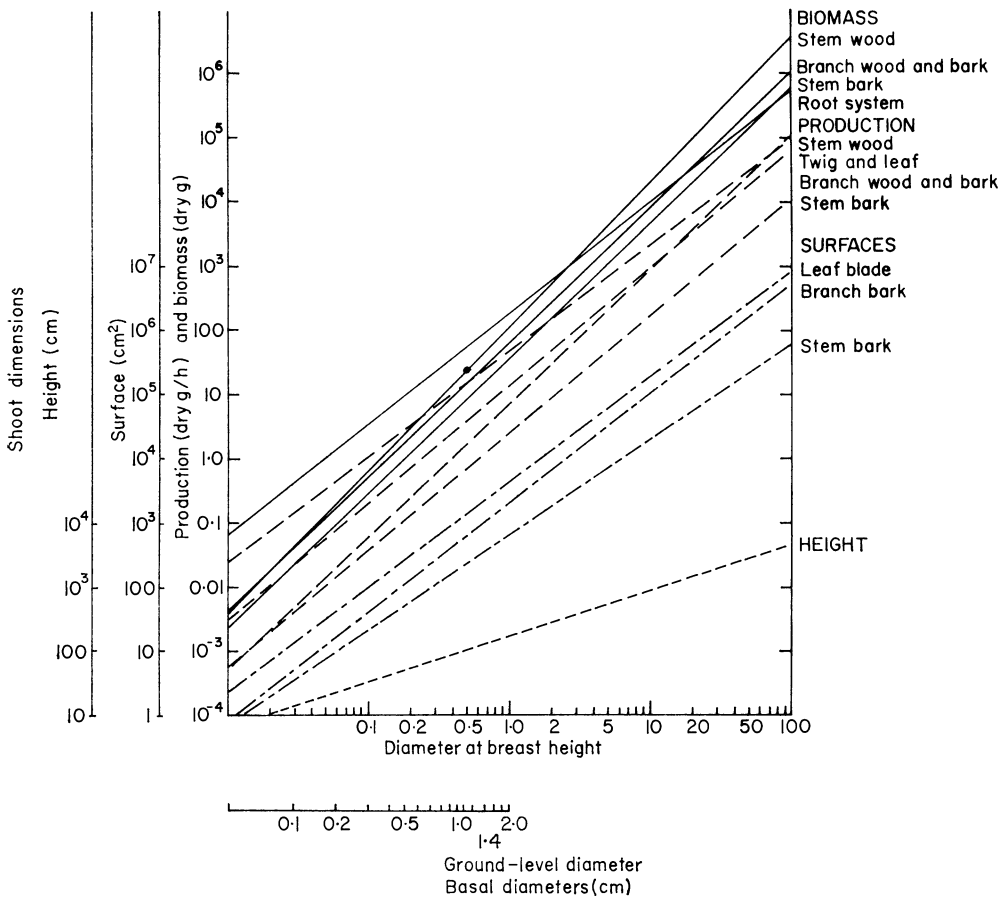


FIG. 3. Interspecies regression lines for various dimensions plotted against basal diameter of stems, illustrating shifts in dimensional relations of woody plants from small shrubs to medium-sized trees. Both scales are logarithmic; see text for the basis of relating diameters at breast height and ground-level to one another. Regressions have been computed for data combining individuals of ten species (see Table 3, Fig. 2), with the exception of the regression for root system biomass (see text). Stem bark biomass and stem wood production are the steeper lines in the pairs of convergent lines.

Slopes of the curves and corresponding regression constants (Table 3) reflect the trends of shifting emphasis among plant fractions which were discussed in terms of mean shoots. In relation to production it may also be observed:

1. Height has necessarily a lower slope and stem and branch weights higher slopes than the various surface relations. Slopes of the production relations, involving the plant's surfaces for gaseous exchange and cambial growth, are in the same range as those for the surface relations themselves.
2. Slopes for stem surface and leaf surface are nearly parallel, though the latter slope is slightly steeper. Mean wood radial increment thickness shows marked increase with increasing plant size, when many species and individuals are treated together (Table 1A,

Whittaker 1962). Stem wood and bark growth consequently increase more steeply with plant size than does the leaf surface supporting by photosynthesis that wood and bark growth.

3. Although stem wood weight increases more steeply than branch weight, the dissected forms of branches imply that their surfaces increase much more steeply than does stem surface. Branch wood and bark production increase less steeply than stem wood production, but more steeply than leaf production and surface. This fact, along with (2), implies that the larger the woody plant, the larger the surface and mass for growth and respiration in fractions other than leaves, which the photosynthesis of a unit leaf surface must support.

4. The point at which the ratio of foliage surface and nonphotosynthetic tissue supported by that surface becomes unfavorable (in relation to a given level of light and other resources) is quite variable within and between species, but has probably much to do with the limits on size of woody plants.

CONCLUSION

It is gratifying, even if not surprising, to find design of blueberry shoots and oak trees linked by allometric trends in common. The method of woody plant analysis described here is intended to provide common procedures and comparable results for shrub, woodland and forest communities. The Brookhaven programme should be fully applicable to large trees, with increased use of branch subsamples and substitution of volumetric computation of log weights for hand weighing. When sample trees can be analysed, in a climate of marked fluctuation, the system provides one solution to the difficulties which affect estimation of current forest growth (Spurr 1952; Husch 1963). It can provide estimates both of merchantable volume growth (which was inappropriate to the small Brookhaven trees) and, when forestry emphasis shifts from wood volume to fibre weight (Young 1965; Young *et al.* 1964; Young & Chase 1965), of total wood production. It offers at the same time various possibilities for study of the living context in which this directly useful production occurs.

As indicated in the present study and applications which are to follow, these possibilities include: (a) biomass and net production values for communities, growth-forms, and plant fractions, and indication of the relation of these to community physiognomy; (b) surface estimates for their own interest and as a basis of applying measured respiration of unit surfaces to plant surfaces of the community; (c) functional characterization of the community by such ratios as leaf area to ground surface, production per unit leaf area and chlorophyll, foliage area to cambial area, and biomass accumulation; (d) means of extrapolating gaseous exchange measurement of gross production by leaves in chambers to the foliage of the community as a whole, and of relating the estimated gross production to net production; (e) indication, in some cases, of production history of the community; (f) ranking of plant species by production, biomass and surfaces for study of dominance-diversity relations and competition (Whittaker 1965b); and (g) a basis for study of nutrient circulation, by applying chemical analyses of plant samples to the biomass and net production values to obtain nutrient standing crops and net movements.

SUMMARY

A system of intensive analysis of weight, production and surface relationships was applied to seven species of trees and shrubs in the Brookhaven oak-pine forest. Distributions of biomass and net production among major plant parts are discussed in terms of

regressions and of averages for the sets. Study of allometric relationships for individuals of all species combined show trends in the dimensional relations of plant parts which shift gradually and continuously with plant size from small shrubs to forest trees. Regressions within species may be effectively used to estimate weight, production and surface relations of shrub communities and forests. For this purpose, and in relation to studies of gaseous exchange, nutrient circulation and dominance–diversity structure, the system of analysis has substantial usefulness for the study of shrubland and forest ecosystems.

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