FOREST RESEARCH BRANCH

DRY MATTER PRODUCTION IN IMMATURE BALSAM FIR STANDS

by

G. L. Baskerville

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Conversion Factors

1 stem per acre	= 2.47 stems per hectare
1 cubic foot per acre	= 0.070 cubic meters per hectare
1 ton per acre	= 2242 kilograms per hectare
1 square foot per acre	= 0.230 square meters per hectare

Dry-Matter Production In Immature Balsam Fir Stands

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Abstract. A study of forest stand production was carried out in natural 40-year-old balsam fir—white spruce—white birch stands of 700, 1000, 1500, 2000, 3000, and 5000 stems per acre in northwestern New Brunswick. A total of 101 fir, 14 spruce, 24 birch and a pin cherry were felled and analyzed to determine the distribution of dry matter among foliage, cones, stem wood, stem bark, branch wood and branch bark. The standing crop and annual increment per acre were found to increase with increasing stand density throughout the density range examined.

Introduction

There are two principal theories dealing with the correlation of forest production to stand density. The one put forward by E. Assmann (1950, 1953 and 1961) states that growth per unit area increases with increased stocking until optimum production is reached at some definable density. Beyond this point, production decreases. Assmann used basal area expressed as a percent of the basal area of a fully stocked stand as his measure of density. His hypothesis was developed largely from an analysis of classical European yield tables and from observation of European thinning experiments. Assmann held that optimum production occurred within a very narrow range of densities and only on exceptionally good sites would the curve have a broad top indicating roughly equivalent production across a wide range of densities.

The second general hypothesis is that put forward by C. M. Möller (1946, 1947, and 1954; and Möller *et al.* 1954a and 1954b). He postulated that production increases with increased stocking up to the point where full occupancy of the site is achieved. Beyond this point increased density does not affect the amount of growth but only its distribution—on a small number of relatively large trees at low densities and a large number of smaller trees at high densities. Only at extremely high density where crowding becomes a limiting factor would production fall off. Möller derived this hypothesis from a theoretical consideration of the relationship between photosynthesis and respiration in forest stands. He observed that the amount of foliage appeared to be constant across a range of

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densities hence production should be equivalent provided the balance of nonphotosynthetic area to photosynthetic area did not exceed critical limits. Respiration would become limiting only in very high density stands where the surface area of boles and branches (the nonphotosynthetic respiring area) increases greatly. Möller tested his hypothesis using Danish thinning practice in Norway spruce and beech and found it was upheld.

The two hypotheses are seen to vary only in respect to the range of densities across which production is optimum. Of critical importance therefore is the parameter of density. There is a need for a measure of stocking which is related to full occupancy (carrying capacity in the sense of population dynamics) in absolute terms. One would expect that for a given soil there must be a maximum rate at which nutrients and water can be made available to plants and that rate determines the amount and nature of roots occupying that soil. Similarly the maximum amount of foliage a given species, or combination of species, can effectively display to the sun determines the upper limit of intercepted and hence effective radiation. The interaction of these maxima would produce the greatest dry-matter product; all other combinations would produce lesser amounts. It would be convenient to express this measure of stocking in terms of a common stand parameter such as basal area per acre.

Before such an ideal density parameter can be established, however, a greater knowledge of the physio-ecological aspects of forest growth is needed. Significant steps to this end have been made by Ovington (1956, 1957, 1959) and his co-workers in England. Working with plantations of *Pinus sylvestris* of several ages and with several other species these men have estimated total production for each species and age and have examined some of the physiologically important relationships involved in forest production. Madgwick (1962) has made a similar examination of red pine stands in New York State. The work of Satoo *et al.* (1955, 1956), Senda *et al.* (1952), Kira (1953), Hirai (1955), Iwaki (1958), Kuroiwa (1960), and Monsi (1960) in Japan is particularly important in that their sampling of *Chamaecyparis obtusa*, *Populus davidiana* and *Pinus strobus* was much more extensive than that of the English workers. The literature relating to forest production, particularly that by the Japanese and English workers, and its application in support of the Möller hypothesis has been dealt with more fully by Baskerville (1962).

The present paper presents the results of a production study in natural immature fir–spruce–birch stands of varying density. Ideally such a study should be conducted in pure stands developed from seed of known provenance planted on the same site at various densities. Unfortunately such a series of plantations was not available to the author.

The Study Area

The study area is located at the northern end of the Green River Watershed in northwestern New Brunswick (Lat. 47° 51′ N, Long. 68° 20′ W). The dominating climatic influences are abundant precipitation, long cold winters, and short cool summers. The average annual frost-free period is 110 days and the mean annual temperature is 36° F. Annual precipitation amounts to 42 inches of which 18 inches falls between June and September.

The Green River forest consists of balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) BSP.), white spruce (*P. glauca* (Moench.) Voss), white (paper) birch (*Betula papyrifera* Marsh), and yellow birch (*B. alleghaniensis* Britt.) with balsam fir predominating. The area lies in the Green River site district of the Gaspé–Cape Breton Ecoregion according to Loucks (1962) and is classified as section B.2 of the boreal forest by Rowe (1959).

The study area is typical of the almost pure 40- to 50-year-old balsam fir stands which occupy about 25 percent of the Green River Watershed. These stands originated from advance growth released when the spruce budworm outbreak of 1913-1919 destroyed the overmature balsam fir in the overstory (Swain and Craighead, 1924). The advance growth was about one foot in height in the period 1920-1923 when release occurred (Vincent 1962). Observation during and following the recent budworm outbreak in the same area (1951-1958) suggests that the amount of advance growth was determined by variation in structure and amount of the destroyed overstory. This in turn gave rise to stands of variable density, despite their uniform outward appearance.

The study area is 1640 feet above sea level and the relative elevation is 30 feet above the valley bottom. The area lies on a gentle and even lower slope (5 percent) with a southwest aspect.

The bedrock is a steeply dipping, highly fractured soft shale covered by a loose rubbly till. Drainage is unimpeded throughout. Preliminary examination indicated the soil to be uniformly of the Monquart series (Langmaid 1963) which is a strongly podzolized slightly stony silt-loam. More detailed examination[1] revealed some soils of the Glassville series which differs from the Monquart in that it is more stony. There was no pattern in the distribution of stand structure and density and they were unrelated to the Glassville soil. Both soils are rated Site II for balsam fir and white spruce (Langmaid 1963).

Procedures and Results

The data required for a meaningful estimate of dry-matter production were progressively built up through a combination of field sampling, laboratory techniques and office compilation. The interrelationship of these procedures was as follows: (1) Small sample plots were established in natural stands of various densities. (2) From these plots, sample trees were selected for analysis of the distribution of standing crop and increment by tree component. (3) The information from the analyzed trees was applied to the remaining trees on each plot to obtain estimates of standing crop and increment on an area basis.

Stand Sampling

On the basis of soil profile, topographic position, estimated local climate, slope, aspect and drainage, an area imputed to be of constant site was delineated for purposes of this study. All sampling was carried out within this area.

Plot establishment. The initial problem was to establish plots over as wide a range of densities as possible within the delineated area. Of the various measures of stocking (number of trees, basal area, volume, Reineke stand density index, and spacing), number of trees per acre proved the easiest to establish at set values. Therefore number of trees per acre was the criterion used to set out five plots in each of six densities. A plot was arbitrarily defined to contain a constant number of trees (about 24) regardless of the stand, hence plot area varied inversely with density. The centers of these plots were selected by trial and error and finally established where an appropriate integral number of trees fell within the fixed radii. By this method 700 and 5000 stems per acre were the extremes of density obtained. The radii and number of stems corresponding to the six densities are shown in the following tabulation.

Stems per acre	*Equivalent square spacing (ft)*	*Stems per plot*	*Plot radius (ft)*
700	7.9 × 7.9	24	22
1000	6.6 × 6.6	24	18
1500	5.4 × 5.4	24	15
2000	4.7 × 4.7	24	13
3000	3.8 × 3.8	26	11
5000	2.9 × 2.9	23	8

[1] By K. Langmaid, Soil Research Officer, Canada Department of Agriculture.

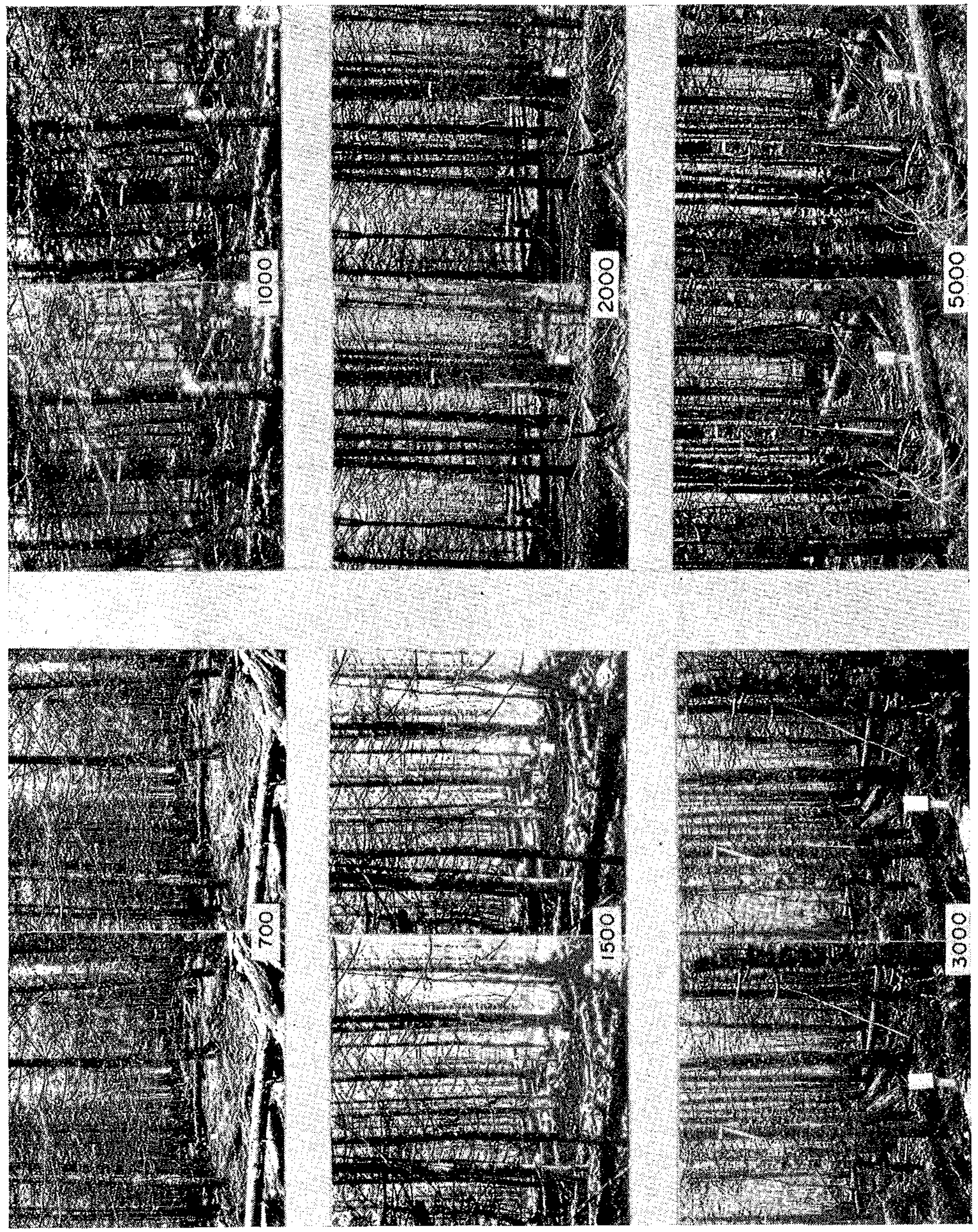

FIGURE 1. *Stereograms of each stand density.*

All plots were free from overstory and from evidence of cutting. There was no systematic spatial distribution of densities. Each tree on a plot was labelled and the following data recorded: tree identification number (metal tag at breast height), species, diameter at breast height to the nearest .01-inch with vernier diameter tape, crown position (dominant, codominant, intermediate, suppressed), total height, crown length, height on the crown where closure with surrounding crowns occurred, the age at release (by examination of increment borings at ground level) and the height at release (by examination of the whorls and increment core). A stem position and crown projection map was prepared for each plot. The projection area of each crown was determined and from this the average crown width was calculated. The maps also provided estimates of percentage crown closure for each plot.

Preliminary information indicated that a few plots showed marked deviations from the average for a density. Two plots in particular, each with 700 stems per acre, were found to have a much greater average height at release and greater total age than other plots. Accordingly, limiting criteria of total and release age as well as height at release had to be set up and the number of plots in each density reduced from five to three by objective application of the criteria. All data presented in this paper refer to the three plots retained in each density.

Description of the stand. Crown closure averaged 84 percent in the most open stands and 96 percent in the densest group. All stands had the outward appearance of being well stocked (Fig. 1). With the exception of a single bush in one of the plots containing 700 stems per acre shrubs were absent. Ground cover

TABLE 1. Descriptive data, based on all species, for the 18 plots.

Plot No.	No. trees per acre	Ave. spacing	BA (sq ft)	Volume per acre (cu ft)	Stand density index	Crown closure (percent)	Percent of No. per acre			Percent of basal area per acre			Total age	Release age
							Fir	Spruce	Birch	Fir	Spruce	Birch		
700 stems/acre														
13	744	7.65	124	2520	285	88	73.1	11.6	15.3	74.2	21.8	4.0	49	42
26	831	7.24	168	3660	376	80	96.5	3.5	—	95.2	4.8	—	50	43
27	659	8.13	154	3250	333	81	95.6	4.4	—	97.4	2.6	—	53	42
1000 stems/acre														
5	1155	6.14	125	2340	316	92	66.7	3.7	29.6	89.4	0.3	10.3	60	40
21	1027	6.41	189	3750	428	92	95.8	—	4.2	98.9	—	1.1	50	43
28	1026	6.41	144	2885	345	76	91.8	—	8.2	97.2	—	2.8	44	41
1500 stems/acre														
2	1652	5.04	190	3630	477	77	96.2	—	3.8	98.4	—	1.6	52	42
9	1624	5.18	164	3315	421	88	73.4	3.8	22.8	92.1	1.8	6.1	46	43
18	1784	4.84	222	4300	539	93	96.5	3.5	—	99.5	0.5	—	52	40
2000 stems/acre														
4	1969	4.60	200	3330	510	84	91.7	—	8.3	98.5	—	1.5	44	42
6	1804	4.81	239	4570	575	90	86.4	4.5	9.1	95.4	2.1	2.5	45	44
15	2051	4.51	232	3985	584	86	92.0	4.0	4.0	98.7	0.4	0.9	45	42
3000 stems/acre														
3	3209	3.68	261	4740	684	96	92.8	3.6	3.6	90.0	8.6	1.4	46	42
8	3094	3.75	252	4410	665	92	81.5	3.7	14.8	93.6	0.8	5.6	43	43
19	2980	3.82	236	4540	629	92	88.4	—	11.6	96.2	—	3.8	46	40
5000 stems/acre														
7	4983	2.96	248	4315	722	92	82.6	4.4	13.0	90.3	0.8	8.9	52	41
12	5199	2.89	307	5585	879	95	100.0	—	—	100.0	—	—	44	41
22	4983	2.96	315	5530	882	99	82.6	8.7	8.7	91.4	6.7	1.9	45	43

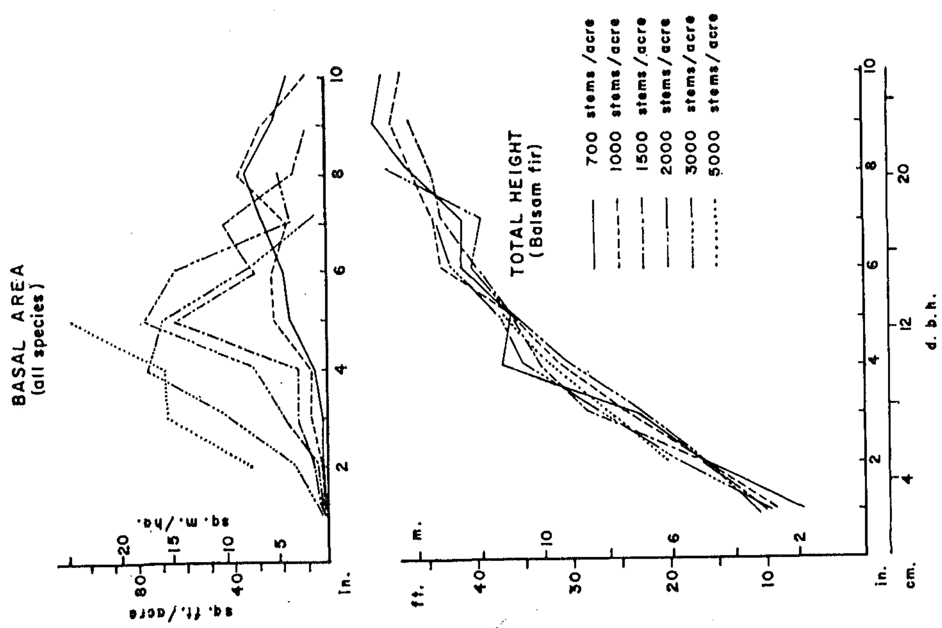

FIGURE 2a. *The distribution of basal area by diameter and the relationship of total height to diameter for the six stands.*

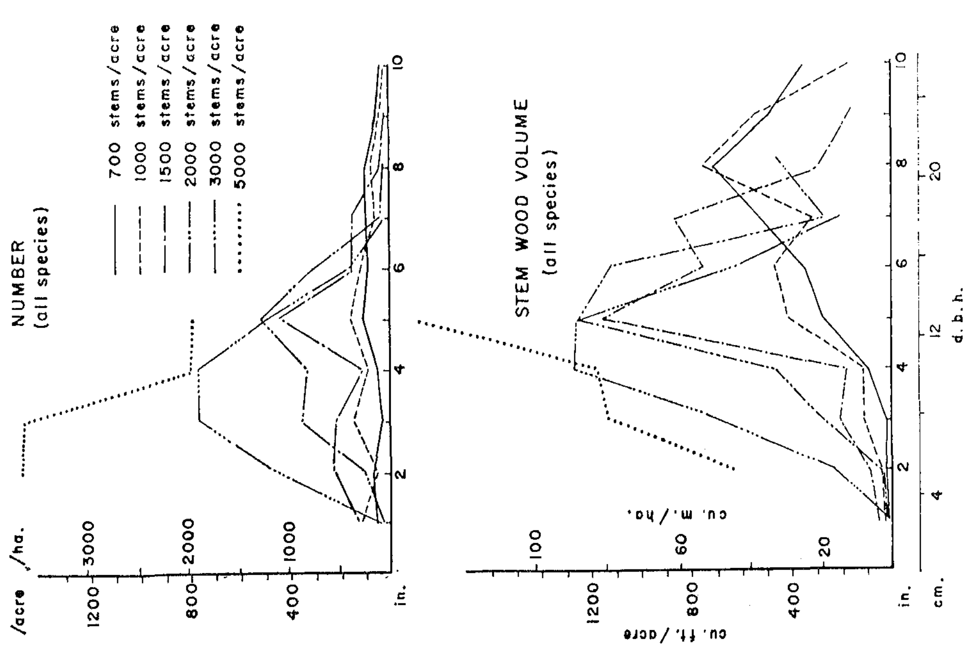

FIGURE 2b. *The distribution of number and volume by diameter for the six stands.*

consisted of a sparse moss-herb association throughout. The principal species were *Oxalis montana* and *Calliergonella schreberi* with some *Dryopteris spinulosa* in small openings.

Based on number of stems per acre the specific content of the stands in percent was as follows: balsam fir 88, white spruce 3 and white birch 9. The distribution did not vary with density (Table 1). The distribution of number of stems by diameter class showed a regular variation with density (Fig. 2b). The distribution of basal area per acre and total volume per acre (Fig. 2a, b) also showed increasing proportions in larger diameters with decreasing density. The interaction of average size with number of stems is more clearly shown by a histogram where, for a given species, the dimensions of the bar are representative of the plot data as follows: width = average basal area; length = number of stems per acre; and area = basal per acre (Fig. 3). The smaller size and intermediate crown position of the birch relative to the conifers assume considerable importance in this study.

None of the felled birch showed symptoms of birch dieback. The balsam fir and spruce crowns were well differentiated in all densities.

The relationship of total height to diameter at breast height was independent of stand density, hence trees of given diameter had the same height in all densities irrespective of the crown positions they occupied (Fig. 2a). As a result average height of the balsam fir stand decreased with increasing density as follows:

No. stems per acre	*Average height (ft)*	*Average diam. (inches)*
700	36	5.6
1000	32	4.8
1500	31	4.4
2000	32	4.4
3000	32	3.8
5000	27	3.2

The total age of fir and spruce was somewhat variable (43-60 years) but release age averaged 42 years with a range of 38 to 45 years. For balsam fir in this climate the age at release is the more critical expression (Morris 1948). White birch tended to be somewhat younger (36 years) than the softwoods indicating it came into the stand during and shortly after the death of the overstory. In all cases the average height of conifers at release was less than one foot. There was no correlation of tree age to size.

The stand density parameters showed the following ranges of variation among plots:

Total number of stems per acre	659 to 5199
Average square spacing (ft)	8.13 to 2.89
Total basal area per acre (sq ft)	124 to 315
Total volume per acre (cu ft)	2340 to 5585
Stand density index (Reineke SDI)	285 to 882
Crown closure (percent)	76 to 99

There is a considerable degree of intercorrelation among these measures (Table 1).

Individual Tree Sampling

Selection and felling. In an attempt to have the sample proportionate to tree weight, trees to be felled for detailed sampling were chosen on the basis of stem volume[2]. To obtain the sample for each density all trees for each species were arrayed in order of increasing volume, the cumulative volume distribution calculated, and quartile points of this distribution determined. Four balsam fir were randomly selected from each quartile of the volume distribution giving a total of 16 trees for each density. In no case were there more than six trees in the top volume quartile, hence the percentage sampled (number basis) was high in the largest trees and decreased

[2] The volume used here was obtained by double-interpolation in the Dominion Form Class Volume Tables (2nd ed.) for form class 65.

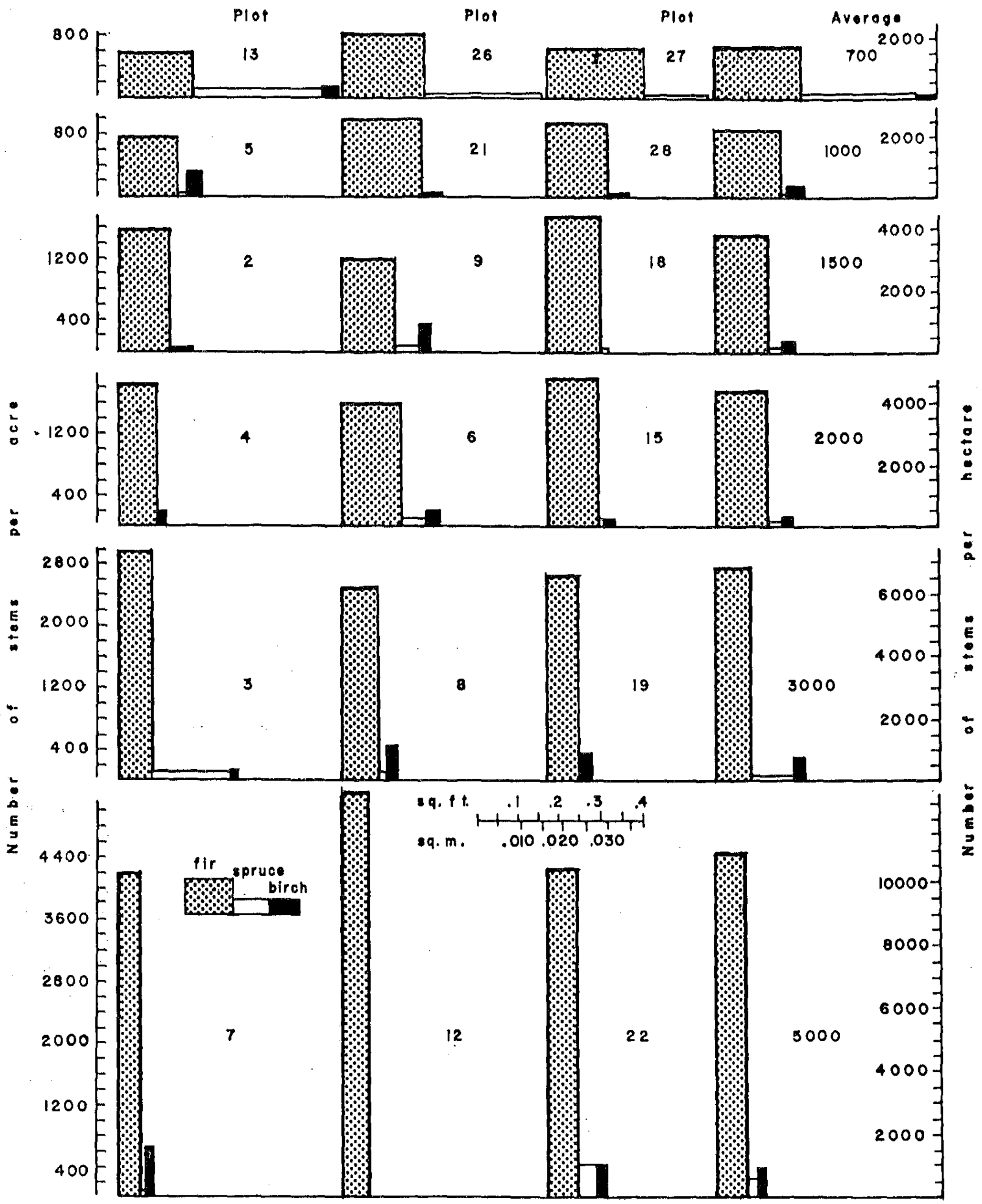

FIGURE 3. *Stand structure histogram by species for each plot and stand average. Bar height shows number of stems per acre, bar width indicates the basal area of the average tree, bar area represents basal area per acre for the spec es.*

rapidly with decreasing size. In the actual sampling an additional five fir were felled so that the total sample consisted of 101 trees. One white birch was randomly chosen from each quartile for felling, giving four per density and a total of 24 for the species. The single pin cherry (*Prunus pensylvanica* L.f.) present was felled and treated like the birch. There were more than four white spruce present in only one density hence all had to be felled and sampled save one, giving a total of 14 for this species. The numbers of trees felled within each density were as follows:

Stems per acre	*Fir*	*Spruce*	*Birch*	*Pin cherry*
700	18	4	4	—
1000	16	1	4	1
1500	18	2	4	—
2000	16	2	4	—
3000	17	2	4	—
5000	16	3	4	—
	101	14	24	1

Felling of fir was not started until the last week in June when about 50 percent of the shoot elongation was complete. The order of felling was staggered across the range of stands to further reduce the possibility of bias from current season growth. Birch samples were all collected in August after leaf expansion had been completed.

Before a tree was felled a diagram was made of its crown to indicate any asymmetry and to show its position relative to neighboring crowns. After clearing debris from a suitable area into which the tree could be dropped, the felling cut was made at ground level. Dead branches were removed and weighed. A 3 x 6-inch beam was rigged between two standing trees to support a block and tackle for lifting the felled tree. The entire tree was then weighed using a dynamometer calibrated to the nearest five pounds. The total height, crown length, and bole length were recorded as well as the length of every internode as far down the tree as they were distinguishable. The diameter at breast height and at one-half the height above breast height were recorded. The branches were removed from fir and spruce by whorls. For each branch total length, green length, green width, and diameter one inch from the base were recorded. All the branches from a whorl were then placed in a large wet-strength paper bag for transport to the drying building. Whorls of the larger trees took several bags. The branches of white birch were combined in one or several bags. Following the removal of the branches the boles were reweighed and those of fir and spruce were sectioned as follows: one disc from each of the 11 uppermost internodes, one disc from 1.5 feet below the 11th internode, and a disc every three feet below that to the butt. The butt was sectioned at its mid point. A final block was cut from the stump or tree butt and taken to the office for a ring count under the miscroscope. White birch boles were sectioned at three-foot intervals throughout their length. The blocks were transported in polyethylene-lined canvas bags.

Dry weight. The bags of *foliage and branches* were brought to a 24 x 24 foot Quonset hut for drying. Initially the aim was to dry the foliage until it fell off the twigs. This was effective for spruce but not for fir and birch. Birch leaves were stripped by hand. To facilitate the drying of balsam fir foliage, three tiers of racks were built in the hut and the bags placed on these. An oil space heater maintained the temperature in the hut as high as possible, usually in excess of 100° F in daytime and about 80° F at night. To hasten desiccation of foliage, surplus atmospheric humidity was withdrawn by bags of calcium chloride hung from the rafters and a double squirrel-cage fan was used to circulate the air and exhaust it from the building periodically. The first foliage collected was dipped in an Ammate[3] solution before going onto the racks in an effort to speed the drying and

[3] "Ammate x" is a commercial preparation of ammonium sulphamate.

to prevent weight losses from prolonged respiration. When no discernible difference was found in either speed of drying or leaf weight between dipped and undipped foliage this practice was discontinued.

After several weeks of drying the needles and twigs for each whorl were separated. The material for each individual whorl was placed in a large canvas bag and vigorously shaken or beaten until the needles, which were brittle by this time, had broken off. The twigs and foliage were then separated using one of two winnowing machines—an A. T. Ferrill Company "Clipper" and a Forano "No. 2". Similar slotted trays were used in both machines; the dimensions of the slots were $\frac{7}{64} \times \frac{3}{4}$ inch in the top tray and $\frac{1}{12} \times \frac{1}{2}$-inch in the bottom tray. By the combination of air fans and vibrating screens, both machines gave excellent separation of foliage from twigs. The process resulted in a bag of foliage and a bag of twigs for each whorl.

To obtain the oven-dry weight of foliage and branches, sample whorls were oven-dried in metal containers for 24 hours at 105° C. The relationship of oven-dry weight to air-dry weight was soon found to be a straight line and from then on only air-dry weight was recorded. A few whorls were oven-dried each day to verify that the drying procedure was still producing a constant dryness. No difficulties were encountered in this respect and the relationships in grams of oven-dry weight (o.d.wt.) to air-dry weight (a.d.wt.) are shown in the accompanying tabulation.

These relationships were used to convert the air-dry weights to oven-dry equivalents.

The total oven-dry weights of foliage and branches on a tree were obtained by summing the values for all whorls. Total branch weight included wood and bark as separation of these two components was logistically unrealistic.

It is apparent from the equations that oven drying reduced the foliage weight

Foliage

Fir o.d.wt. = 1.11 + .903 a.d.wt. ($n = 89, r^2 = .9928$)

Spruce o.d.wt. = −1.21 + .932 a.d.wt. ($n = 20, r^2 = .9997$)

Birch o.d.wt. = 5.35 + .842 a.d.wt. ($n = 14, r^2 = .9980$)

Twigs

Fir o.d.wt. = 11.52 + .880 a.d.wt. ($n = 25, r^2 = .9169$)

Spruce o.d.wt. = .12 + .893 a.d.wt. ($n = 25, r^2 = .9997$)

Birch o.d.wt. = 10.47 + .842 a.d.wt. ($n = 8, r^2 = .9979$)

by about 10 percent. Clark[4] made a study of oven drying as compared to water removal by distillation techniques for obtaining dry weight of spruce and fir foliage. He found that oven drying gave roughly 30 percent greater weight loss than did distillation. The difference is presumably due to the fact that certain of the essential oils and other relatively volatile components are driven out of the foliage by oven drying but are retained by the distillation method. It may be inferred from this that the values given in the present study are underestimates of the water-free weight of foliage. However, since the literature primarily reports oven-dry weight values no attempt has been made to adjust the data.

Total dry-weight of foliage and branches was found to be closely correlated to stem diameter at breast height (Fig. 4; Tables 2, 3 and 4). This relationship has the characteristic exponential form for fir, spruce and birch and was found to be independent of stand density and crown position. Similar conclusions were reached by Kittredge (1944). A single equation was fitted to the data from all densities. For small diameters the weight of spruce crowns slightly exceeds that of fir but beyond 7.5 inches (dbh) fir crowns weigh more than spruce. In the size range of

[4] Clark, J. Unpublished data.

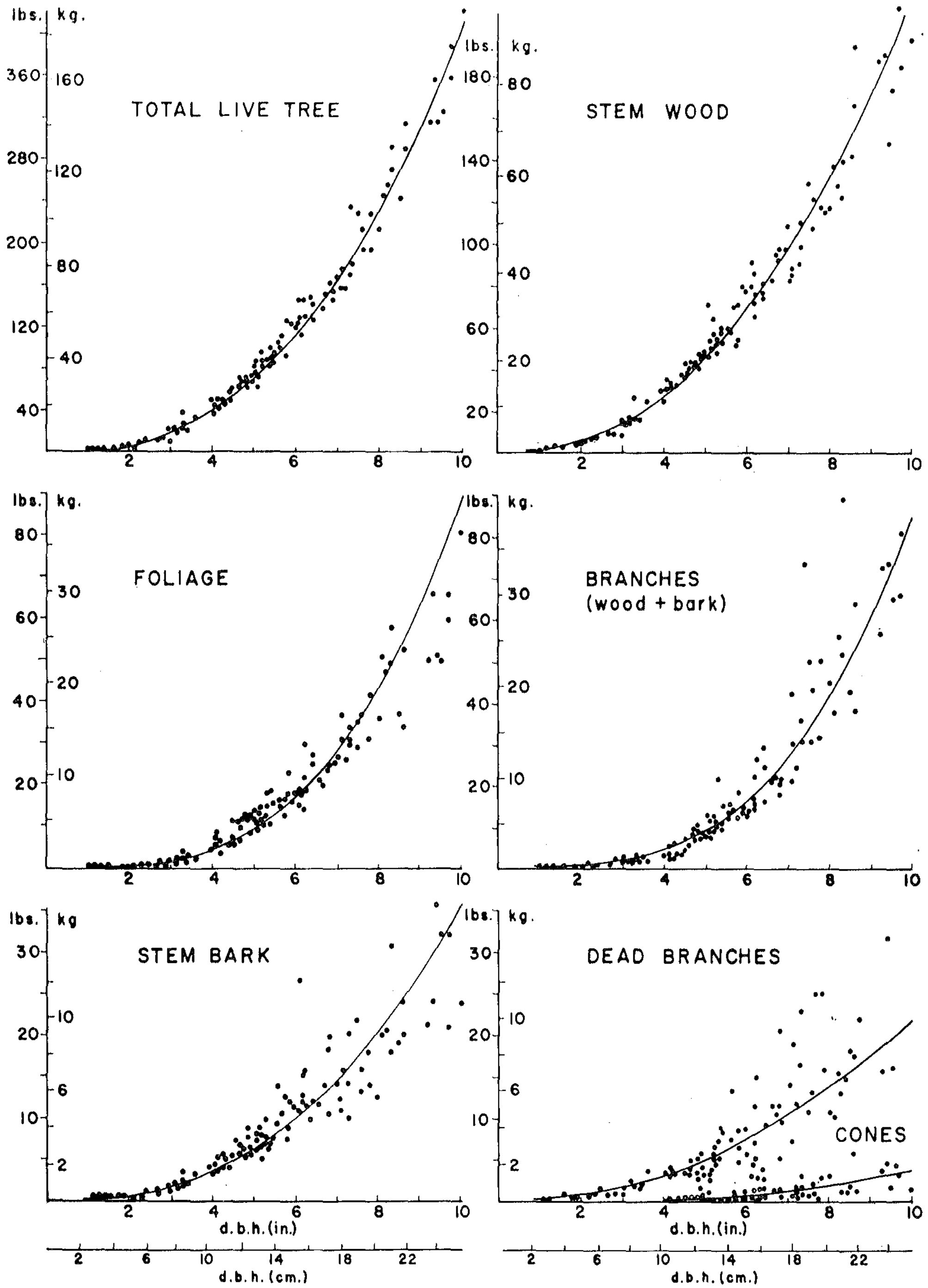

FIGURE 4. *Oven-dry weight of some components of balsam fir, for all stands combined. The corresponding equations are given in Table 2.*

TABLE 2. Equations for the weight, volume and surface area of components of balsam fir trees.

Component		Equation	n	r	range x	range y
Total fresh weight		log W = 0.343 + 2.68 log D	98	.99	1 - 10	4. - 900
Total oven-dry weight		log W = 0.086 + 2.53 log D	101	.96	1 - 10	2. - 400
Oven-dry weight						
Standing crop						
stem wood		log W = 0.062 + 2.28 log D	101	.96	1 - 10	1. - 250
stem bark		log W = -0.916 + 2.47 log D	101	.95	1 - 10	1.0 - 40.
branches (wood & bark)		log W = -1.294 + 3.22 log D	101	.95	1 - 10	.1 - 115.
foliage		log W = -1.258 + 3.21 log D	101	.98	1 - 10	.1 - 90.
cones (Dom. & Codom. only)		log 100 W = -0.625 + 3.20 log D	35	.70	4 - 10	.1 - 6.
dead branches		log 10 W = 0.226 + 2.11 log D	90	.80	1 - 10	.4 - 40.
Increment						
stem wood	1957 - '61	Iw = -0.78 + 5.21 V	101	.94	.05 - 11.	.4 - 68.
stem wood	1952 - '56	Iw = -0.50 + 4.48 V	101	.97	.05 - 11.	.1 - 57.
stem bark	1957 - '61	log 100 Iw = -0.400 + 3.38 log D	101	.96	1 - 10	.01 - 8.
stem bark	1952 - '56	log 100 Iw = -0.023 + 2.95 log D	101	.97	1 - 10	.01 - 8.
branches	1957 - '61	log 10 Iw = -0.184 + 2.59 log D	101	.95	1 - 10	.02 - 30.
branches	1952 - '56	log 10 Iw = -0.195 + 2.46 log D	101	.97	1 - 10	.01 - 20.
foliage	1957 - '61	log 100 Iw = 0.816 + 3.28 log D	101	.95	1 - 10	.1 - 70.
foliage	1952 - '56	log 100 Iw = 0.777 + 3.14 log D	101	.95	1 - 10	.1 - 60.
Volume						
Standing crop						
stem wood	D^2H: 0-400	$V = 0.038 + .0024\ D^2H$	18	.99	11 - 310	.05 - .70
stem wood	D^2H: 401-	$V = 0.254 + .0022\ D^2H$	83	.99	440 - 5000	1.14 - 11.
stem bark		log 1000 V = 0.653 + 2.52 log D	101	.98	1 - 10	.01 - 1.5
branch wood		log 1000 V = 0.230 + 2.61 log D	101	.94	1 - 10	.01 - 1.5
branch bark		log 1000 V = 0.250 + 2.42 log D	101	.95	1 - 10	.01 - .8
Increment						
stem wood	1957 - '61	Iv = -0.061 + .272 V	101	.96	.05 - 11.	.01 - 2.5
stem wood	1952 - '56	Iv = -0.044 + .235 V	101	.98	.05 - 11.	.01 - 3.0
branch wood	1957 - '61	log 1000 Iv = 0.127 + 2.18 log D	101	.93	1 - 10	.002 - .4
branch wood	1952 - '56	log 1000 Iv = 0.119 + 2.08 log D	101	.93	1 - 10	.001 - .3
Surface area						
bole	DH: 0 - 200	SA = 0.61 + .17 DH	45	.99	10 - 200	1. - 32.
	DH: 201 -	SA = 5.07 + 14 DH	56	.96	203 - 530	32. - 81.
branches		log SA = -0.005 + 2.67 log D	101	.94	1 - 10	1.5 - 700.

D: d.b.h., inches
W: weight, lbs
V: total volume, cu.ft.
H: total height, ft.
SA: surface area, sq.ft.

TABLE 3. Equations for the weight, volume and surface area of components of white spruce trees.

Component		Equation	n	r	range x	range y
Total fresh weight		log W = 0.415 + 2.64 log D	12	.99	1 - 10	2. - 700.
Total oven-dry weight		log W = 0.150 + 2.48 log D	13	.99	1 - 10	3. - 400.
Oven-dry weight						
Standing crop						
stem wood		log W = 0.028 + 2.36 log D	13	.99	1 - 10	1. - 175.
stem bark		log 100 W = 0.885 + 2.61 log D	14	.99	1 - 10	.07 - 20.
branches (wood & bark)		log W = -0.855 + 2.78 log D	14	.97	1 - 10	.5 - 50.
foliage		log 10 W = 0.066 + 2.85 log D	14	.97	1 - 10	.2 - 35.
dead branches		log 10 W = -0.175 + 2.49 log D	13	.94	1 - 10	.2 - 15.
Increment						
stem wood	1957 - '61	Iw = 0.57 + 96.64 BA	13	.93	.010 - .490	.03 - 38.
stem wood	1952 - '56	Iw = 0.16 + 81.50 BA	13	.96	.010 - .490	.50 - 36.
stem bark	1957 - '61	log 100 Iw = -0.193 + 3.18 log D	13	.96	1 - 10	.02 - 3.
stem bark	1952 - '56	log 100 Iw = 0.327 + 2.44 log D	13	.98	1 - 10	.02 - 3.
branches	1957 - '61	log 10 Iw = -0.033 + 2.59 log D	14	.91	1 - 10	.1 - 20.
branches	1952 - '56	log 100 Iw = 0.710 + 2.60 log D	14	.95	1 - 10	.1 - 8.
foliage	1957 - '61	log 10 Iw = 0.295 + 2.86 log D	14	.97	1 - 10	.4 - 50.
foliage	1952 - '56	log 10 Iw = 0.258 + 2.69 log D	14	.96	1 - 10	.2 - 40.
Volume						
Standing crop						
stem wood		$V = -0.038 + .0027\ D^2H$	13	.99	21 - 4000	.07 - 8.7
stem bark		log 1000 V = 0.659 + 2.57 log D	14	.98	1 - 10	.02 - 1.
branch wood		log 1000 V = 0.618 + 2.16 log D	14	.97	1 - 10	.01 - .4
branch bark		log 1000 V = 0.614 + 1.97 log D	14	.98	1 - 10	.01 - .3
Increment						
stem wood	1957 - '61	Iv = 0.027 + 0.277 V	14	.97	.05 - 8.7	.004 - 2.0
stem wood	1952 - '56	Iv = 0.010 + 0.230 V	14	.99	.05 - 8.7	.02 - 2.0
branch wood	1957 - '61	log 1000 Iv = 0.515 + 1.82 log D	14	.94	1 - 10	.004 - .15
branch wood	1952 - '56	log 1000 Iv = 0.249 + 2.06 log D	14	.98	1 - 10	.002 - .15
Surface area						
bole		SA = 0.91 + .16 DH	14	.99	15 - 410	3. - 65.
branches		log SA = -0.005 + 2.67 log D	101	.94	1 - 10	1.5 - 700.

D : d.b.h., inches
W : weight, lbs.
V : total volume, cu.ft.
H : total height, ft.
SA : surface area, sq.ft.
BA : basal area at b.h., sq.ft.

TABLE 4. Equations for the weight, volume and surface area of components of white birch trees.

Component	Equation	n	r	range x	range y
Total fresh weight	log W = 0.736 + 2.17 log D	24	.96	1 - 3	10. - 80.
Total oven-dry weight	log W = 0.236 + 2.48 log D	24	.98	1 - 3	2. - 25.
Oven-dry weight					
Standing crop					
stem wood	log W = 0.132 + 2.36 log D	24	.97	1 - 3	2. - 25.
stem bark	log 100 W = 1.32 + 2.35 log D	24	.90	1 - 3	.2 - 8.
branches (wood & bark)	log W = -1.006 + 3.30 log D	24	.86	1 - 3	.2 - 7.
foliage	log 100 W = 0.730 + 2.94 log D	25	.90	1 - 3	.1 - 2.5
dead branches	log 100 W = 0.679 + 3.30 log D	20	.68	1 - 3	.15 - 9.
Increment					
stem wood 1957 - '61	Iw = 0.12 + 4.91 V	24	.87	.05 - .80	.3 - 5.
stem wood 1952 - '56	Iw = -0.02 + 5.95 V	24	.92	.05 - .80	.5 - 5.
stem bark 1957 - '61	log 100 Iw = 0.361 + 2.21 log D	24	.77	1 - 3	.03 - 6.
stem bark 1952 - '56	log 100 Iw = 0.536 + 2.29 log D	24	.76	1 - 3	.04 - 8.
branches 1957 - '61	log 10 Iw = -0.038 + 2.86 log D	24	.87	1 - 3	.1 - 4.
foliage 1957 - '61	log 100 Iw = 1 378 + 3.12 log D	24	.92	1 - 3	.2 - 8.
foliage 1952 - '56	log 10 Iw = 0.302 + 3.11 log D	24	.91	1 - 3	.2 - 10.
Volume					
Standing crop					
stem wood	V = 0.036 + .0021 D^2H	24	.97	25 - 350	.07 - .85
stem bark	log 1000V = 0.938 + 1.96 log D	24	.93	1 - 3	.01 - .15
branch wood	log 1000 V = -0.179 + 3.67 log D	24	.94	1 - 3	.001 - .06
branch bark	log 1000 V = -0.208 + 2.40 log D	24	.93	1 - 3	.001 - .015
Increment					
stem wood 1957 - '61	log 1000 Iv = -0.880 + 1.05 log 1000 V	24	.96	.05 - .80	.02 - 1.5
stem wood 1952 - '56	log 1000 Iv = -0.662 + 0.988 log 1000 V	24	.94	.05 - .80	.02 - 2.0
branch wood 1957 - '61	log 1000 Iv = -0.220 + 3.22 log D	24	.89	1 - 3	.001 - .03
Surface area					
bole	SA = 0.23 + .15 DH	24	.92	21 - 115	4. - 17.
branches	SA = -0.060 + 145.7 BA	24	.92	.010 - .070	1. - 10.

D: d.b.h., inches
W: weight, lbs.
V: total volume, cu. ft..
H: total height, ft.
SA: surface area, sq. ft..
BA: basal area at b.h., sq. ft..

birch trees examined their crowns weighed about one-half those of fir or spruce.

The annual dry-weight increment of fir foliage was estimated by using the percentage that current needles form of total crown weight. This percentage was based on the dissection of a single 8-inch codominant tree. Every branch was clipped so that all ages of foliage were separated for each whorl. The percentages of the total oven-dry weight of crown from the present study (Baskerville) are compared with similar data from Clark (1961) in the following tabulation.

Needle age (years)	*Baskerville*	*Clark*
0 or current	26.2	27.1
1	24.7	19.9
2	20.7	17.5
3	12.5	13.4
4	7.2	8.9
5	3.8	6.9
6	2.3	3.9
7	1.3	1.9
8	.9	.4
9	.2	—
10	.2	—
	100.0	99.9

Clark's data are based on length of foliated shoot of each age class for three average 40-year-old balsam fir trees. Current annual increment of foliage was estimated as 26 percent of crown weight assuming the above proportions to hold for all crown sizes. While the proportions may break down for small crowns they will apply for the greatest proportion of the total foliage per acre since this is on dominant and codominant trees.

The annual increment of foliage for the period 1952-1956 was estimated by taking 26 percent of the 1956 crown weight. The 1956 crown weight was estimated from a logarithmic chart of crown weight over diameter at breast height by reading from the plotted point for an individual tree in 1962 back to the diameter of the tree parallel to the regression line. Foliage increment for white spruce was similarly estimated using the 35 percent value for current foliage cited by Clark (1961) since time did not permit further analysis of crowns on a weight basis. Foliage increment of birch is equal to the standing crop since the species is deciduous. The equations relating foliage increment to diameter at breast height are given in Tables 2, 3 and 4.

An estimate of branch increment for fir and spruce was obtained by calculating the mean annual increment by whorls (total weight of whorl divided by age of whorl) and summing for the tree. This should have had the effect of producing a slight but systematic underestimation. The relationship of branch increment computed on this basis to dbh is given in Tables 2 and 3. White birch branch increment was estimated as the mean annual increment for the whole crown, i.e., by dividing total branch weight by the age at mid-crown.

Since 1962 was a good seed year for balsam fir all *cones* were removed from each tree after felling and samples were oven-dried to obtain a fresh weight—dry weight correlation. Fresh weights were then converted to oven-dry weights. Considerable difficulty was experienced in establishing an equation for estimating cone crop on the standing trees. Cones were found only on dominants and codominants over 4.5 inches in diameter but not on all of these. This partially explains the weak relationship given in Table 2.

Standard procedures were followed in the determination of specific gravity of the *stem*. For each of the first 11 sections, the entire disc taken from the felled tree was used (wood and bark separately.) Below the 11th section each disc was sub-sampled: two wedges were split from opposite sides and in addition two small blocks, consisting of the outer 11 rings, were cut from opposite sides of each disc and a sample of bark was taken.

Volume was determined by the water immersion technique. Each sample block was soaked for at least 20 minutes then excess water was removed by blotting before immersion in the water container on the balance pan. Water at room temperature was used. Blocks were oven-dried for 24 hours at 105° C. After 25 trees had been examined it was apparent that the number of specific gravity determinations per tree could be reduced. Accordingly, subsequent sampling was limited to every third section, except that the two bottom sections were invariably sampled.

The conversion from volume to oven-dry weight was made by sections using the average specific gravity of the two wedges for total weight, and the average of the two 11-year blocks for the increment 1952-1956 and 1957-1961. Stem-bark weight was similarly computed. For the trees where only every third section was sampled for specific gravity the values were applied to the sections on either side as well. Total weight of wood, wood increment, and bark weight were obtained by summation for the tree. The relationships of weight of stem wood and stem bark to diameter are shown in Figure 4 and in Tables 2, 3 and 4.

Increment of stem-bark weight was estimated by reading stem-bark weight for the diameter of each tree in 1956 and 1951 parallel to the regression line. The increment was estimated as the difference 1961-1956 and 1956-1951. This assumes the relationship of bark weight to diameter remained constant with age for at least five years. It also ignores sloughing of outer bark and should therefore be a slight underestimate.

Average specific gravity for each stem was estimated by using the total dry weight as determined above and the total green volume. There was a tendency for specific gravity to increase with decreasing stem diameter for fir and spruce but it remained constant across the range of stand density for any given diameter (Fig. 5). The equations are:

Fir: $\log 10\ SG = .628 - .166 \log D$ $(n = 101, r^2 = .5219)$

Spruce: $\log 10\ SG = .681 - .205 \log D$ $(n = 14, r^2 = .6510)$

There was no apparent correlation of specific gravity and stem size in white birch.

The *dead branches* for each tree were weighed in the field and a sample was taken to the office for oven drying. On the basis of this sample total fresh weight was converted to oven-dry equivalent. The relationship of oven-dry weight of dead branches to stem diameter is shown in Tables 2, 3 and 4.

Volume. Before sampling for specific gravity all disc sections from the *stem* were brought to the laboratory where the mean diameter of each was determined with a vernier diameter tape. Radial lines corresponding to the mean diameter were smoothed with a scalpel and microscopic measurements were made of total bark thickness and ring width for each of the outer 11 years (or as far back as age permitted in the upper sections). From these data, calculations were made of the diameter inside bark at the end of the 1962, 1961, 1956 and 1951 growing seasons. Using these diameters and the section lengths, wood volume was computed for each section for these four dates. Stem-wood volume increment was determined by taking the difference of the computed volumes for 1961-1956, 1956-1951. Stem-wood increment was related to stem volume (Tables 2, 3 and 4).

An equation for total stem wood volume was developed for each species in the form:

$$V = a + b\,(D^2 H).$$

For balsam fir this equation was solved in two portions to avoid an overestimate in small trees. The equations are given in Tables 2, 3 and 4. Since the stem volume relationship proved to be independent of stand density a single equation sufficed.

Form quotient for balsam fir determined as the ratio of diameter inside bark at one-half the height above breast height to diameter inside bark at breast

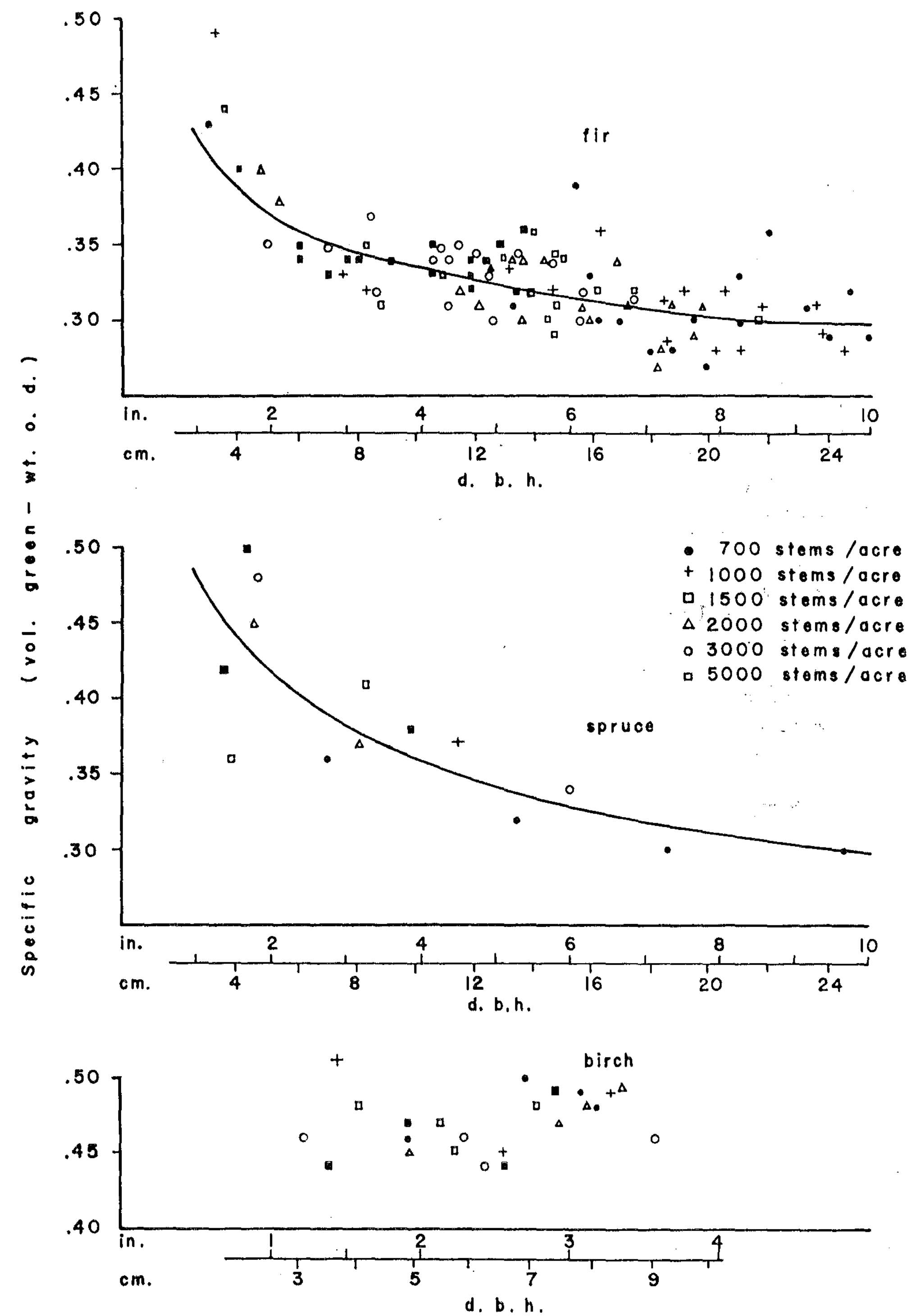

FIGURE 5. *Specific gravity (volume green and weight oven-dry) over diameter for fir, spruce and birch.*

height was independent of stand density within a single diameter class but there was a significant tendency for form quotient (*FQ*) to increase with decreasing diameter (*D*) in the form:

$$FQ = .666 - .0093D \quad (n = 101, r^2 = .0918)$$

On a basis of stand structure one would therefore expect the denser stands to have on the average a higher form class and this was found to be the case.

To establish a basis for estimating the volume of *branch wood* per tree 71 fir branches were selected systematically from various crown levels in trees of various sizes from all densities. These were dissected at each dichotomy and the length and mean diameter of each section determined with a vernier caliper. From these data the total volume for the branch was computed and, by reduction of the diameters by double-bark thickness, the volume of wood was calculated. The relationship of cubic-inch volume (*V*) to total branch length in feet (*L*) for total volume is as follows:

$$\log 100V = -0.720 + 2.14 \log L \quad (n = 71, r^2 = .9408)$$

For wood volume the equation is:

$$\log 100\,V = -1.157 + 2.26 \log L \quad (n = 71, r^2 = .9315)$$

These equations were solved for tenths of feet and tables developed for total volume, wood volume, and bark volume (by difference). The volume of wood and bark was calculated for each whorl of each felled tree by entering the tables with the total length of each branch. Branch volume increment for wood and bark was estimated by calculating the mean annual increment for each whorl (total volume divided by age of whorl) and summing all whorls for the increment of the tree.

Branch volume for spruce was determined using the tables for balsam fir. For white birch, branch volume was calculated from the data recorded in the field assuming the central branch to be a cone. Branch wood and bark volume increment were estimated by dividing total volume by the age at mid-crown.

Surface area. Time did not permit an estimate of foliage surface area during the study. Bole surface area was computed from the data on the sectioned stems. These values were related to diameter and height in the form:

$$SA = a + b\,(DH)$$

Two equations were used for fir, one for small and one for large trees, but for spruce and birch a single equation was sufficient.

Branch surface area was estimated in a manner similar to that for branch volume. Data from the 71 dissected fir branches from various crown levels were recompiled to give their surface area in square inches (*SA*). This was related to length of green branch in feet (*GL*) to give:

$$\text{Log } SA = -1.190 + 2.22 \log GL \quad (n = 71, r^2 = .9918)$$

A table was prepared from this equation for even tenths of feet. For the felled trees surface areas per whorl were calculated by entering the table with green branch length and summing. Total branch surface area per tree was then regressed on diameter (Tables 2, 3 and 4). Branch surface area for spruce was determined using the tables for balsam fir. For white birch, branch surface area was calculated from the field data.

Combining Plot and Single Tree Data

A notable and consistent feature of the data for individual trees is that the various relationships for a given size class are independent of stand density. This feature was checked both by analysis of variance and graphical methods. In all cases where tests indicated significant or near significant differences in slope or the *y* intercept; further examination showed the variation to result from a single density class. Most commonly the aberrant group was the 1000-stem per acre class which contained a large tree that did not conform to the general trends.

In all cases a single equation was fitted to all densities. Thus five-inch dominants in a 5000-stem per acre stand appear to be identical to five-inch intermediate or suppressed trees in a 700-stem per acre stand. They have similar total height, stem form, stem volume, crown weight, specific gravity, stem weight, surface area and current growth. This is logical since the present size of a tree represents the integrated effects of all competition to this point in its life. Thus the five-inch trees in the two extremes of stand density are expressions of equivalent total past competition. However, those in the 5000-stem per acre stand are becoming progressively better established as dominants and are increasing their growth against competition mainly from the side. In contrast the suppressed or intermediate five-inch trees in the 700-stem per acre stand are meeting competition from above as well as from the side and are consequently falling further behind their neighbors in growth rate.

Data on height, diameter and volume growth of individuals for the two periods 1952-1956 and 1957-1961 support this concept. Thus while current growth is the same because current competition is the same—in amount although not in nature—future growth cannot be regarded as equivalent since one tree is moving toward a poorer and the other toward a better competitive position in the stand.

It is likely that at any given age all trees of a given diameter would be similar despite variation in stand density but, since there is a difference in the nature of the competition they will encounter with increasing age, they cannot be projected as a group. For the present study, therefore, it is simplest to estimate only the current annual increment, or rather current periodic annual increment for the period 1957-1961. No attempt is made to project stand development.

With the equations from Tables 2, 3 and 4, and the data recorded on the ground for all trees, dry weight and volume of the various tree components were estimated for the 310 trees which were not felled. The total per acre estimate for a given tree component was then obtained by summing that component for all trees on the plot and multiplying the total by the conversion factor appropriate to the plot size.

In the following discussion of production on a stand per acre basis, number of stems is the parameter used to summarize density effects because the design is orthogonal with respect to number of stems. The relationships are similar regardless of the parameter chosen (see figures) and indeed, are stronger for such measures as basal area than they are for number of stems.

Standing crop. The volume of all species combined in cubic feet per acre of stem wood, branch wood and total volume tends to increase with increasing density as is shown in the following tabulation.

No. stems per acre	*Stem wood*	*Branch wood*	*Total*
700	3140	281	3421
1000	2990	267	3257
1500	3745	307	4052
2000	3962	279	4241
3000	4565	324	4889
5000	5140	340	5480

Data for individual plots are given in Table 5. The percentage that branch wood represents of the total volume decreased from 8.2 percent in the open stand to 6.2 percent at 5000 stems per acre.

The oven dry weight in tons per acre

TABLE 5. Stem wood, branch wood and total volume in 1962 by species and plots.

Plot	Stem wood				Branch wood				Total			
	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
	(cubic feet per acre)											
	700 stems/acre											
13	1960	500	55	2515	190	25	5	220	2150	525	60	2735
26	3475	1[illegible]5	—	3660	270	10	—	280	3745	195	—	3940
27	3185	65	—	3250	330	5	—	335	3515	70	—	3585
	1000 stems/acre											
5	2160	65	115	2340	195	5	10	210	2355	70	125	2550
21	3730	—	20	3750	360	—	2	362	4090	—	22	4112
28	2830	—	55[1]	2885	230	—	3	233	3060	—	58	3118
	1500 stems/acre											
2	3580	—	45	3625	285	—	2	287	3865	—	47	3912
9	3150	45	120	3315	240	5	5	250	3390	50	125	3565
18	429[illegible]	10	—	4305	395	—	—	395	4690	10	—	4700
	2000 stems/acre											
4	3295	—	35	3330	230	—	1	231	3525	—	36	3561
	4420	65	85	4570	325	5	5	335	4745	70	90	4905
15	3945	10	30	3985	300	—	2	302	4245	10	32	4287
	3000 stems/acre											
3	4245	455	40	4740	315	20	1	336	4560	475	41	5076
8	4235	20	155	4410	315	—	5	320	4550	20	160	4730
19	4440	—	100	4540	315	—	5	320	4755	—	105	4860
	5000 stems/acre											
7	4050	15	250	4315	65	—	10	275	4315	15	260	4590
12	5585	—	—	5585	395	—	—	395	5980	—	—	5980
22	5160	300	70	5530	325	20	5	350	5485	320	75	5880

[1] Includes pin cherry.

of the total standing crop of living trees above ground also increases with increasing stand density as is indicated below.

No. stems per acre	*Fir*	*Spruce*	*Birch*	*Total*
700	43.1	4.2	.4	47.7
1000	43.9	.4	1.6	45.9
1500	48.9	.3	1.1	50.3
2000	56.0	.4	.9	57.3
3000	58.5	2.7	1.9	63.1
5000	64.3	2.1	2.2	68.6

The oven dry weight expressed as percent of total weight is shown below.

No. stems per acre	*Fir*	*Spruce*	*Birch*	*Total*
700	90.4	8.8	.8	100
1000	95.6	.9	3.5	100
1500	97.2	.6	2.2	100
2000	97.9	.7	1.4	100
3000	92.7	4.3	3.0	100
5000	93.7	3.1	3.2	100

The drop in weight from 700 to 1000 stems per acre is related to the percentage that birch makes up of the total stems in these two groups of plots. This effect will be discussed in the section on increment.

The weights of the various components, expressed as percentages of the total weight of balsam fir standing crop per acre, show the following trends from the lowest density (700 stems per acre) to the highest density (5000 stems per acre): foliage decreases from 16.4 to 12.8 percent; branches decrease from 17.4 to 10.4; bole wood increases from 57.1 to 67.1 percent; dead branches increase; and cone crop is constant from 700 to 3000 stems per acre, then falls off (Table 6).

Any trends in the distribution of spruce standing crop are masked because of the small sample and the erratic distribution of stem sizes across the range of densities. The discernible trends are, however, parallel to those just described for balsam fir. The foliage of white birch remained a relatively constant proportion of the standing crop for the species across the range of densities. Stem wood showed only a slight increase

TABLE 6. The distribution of standing crop by tree component for each stand.

Component	Number of stems per acre						Number of stems per acre					
	700	1000	1500	2000	3000	5000	700	1000	1500	2000	3000	5000
	tons/acre						*percent of total*					
	BALSAM FIR											
Foliage	7.07	7.07	7.49	8.03	7.77	8.23	16.4	16.1	15.4	14.4	13.3	12.8
Cones	.25	.33	.26	.30	.28	.20	.6	.8	.5	.5	.5	.3
Stem wood	24.63	24.92	29.36	35.25	37.91	43.02	57.1	56.8	60.2	63.0	64.8	67.1
Stem bark	3.65	4.22	4.31	5.05	5.76	6.04	8.5	9.6	8.8	9.0	9.8	9.4
Branch wood	4.38	4.27	4.26	4.14	3.77	3.76	10.2	9.7	8.7	7.4	6.4	5.8
Branch bark	3.12	3.06	3.19	3.18	2.98	3.03	7.2	7.0	6.4	5.7	5.2	4.6
Total	43.10	43.87	48.87	55.95	58.47	64.28	100.0	100.0	100.0	100.0	100.0	100.0
Dead branches	2.61	2.68	3.45	3.61	4.08	5.13						
	WHITE SPRUCE											
Foliage	.66	.08	.04	.04	.44	.42	15.6	19.0	12.5	9.1	16.4	19.6
Cones	—	—	—	—	—	—	—	—	—	—	—	—
Stem wood	2.48	.25	.22	.31	1.67	1.28	58.8	59.6	68.6	70.4	62.8	59.8
Stem bark	.28	.02	.02	.04	.17	.16	6.6	4.8	6.3	9.2	6.3	7.5
Branch wood	.48	.04	.02	.03	.23	.16	11.4	9.5	6.3	6.8	8.5	7.5
Branch bark	.32	.03	.02	.02	.16	.12	7.6	7.1	6.3	4.5	6.0	5.6
Total	4.22	.42	.32	.44	2.67	2.14	100.0	100.0	100.0	100.0	100.0	100.0
Dead branches	.34	.03	.01	.03	.05	.06						
	WHITE BIRCH											
Foliage	.02	.08[1]	.05	.08	.09	.11	4.8	4.9	4.5	9.2	4.8	5.0
Cones	—	—	—	—	—	—	—	—	—	—	—	—
Stem wood	.28	1.14	.81	.58	1.43	1.56	66.7	69.5	72.3	66.7	75.7	71.2
Stem bark	.04	.17	.11	.10	.19	.25	9.5	10.4	9.8	11.5	10.0	11.4
Branch wood	.06	.20	.12	.08	.14	.21	14.3	12.2	10.7	9.2	7.4	9.6
Branch bark	.02	.05	.03	.03	.04	.06	4.7	3.0	2.7	3.4	2.1	2.8
Total	.42	1.64[1]	1.12	.87	1.89	2.19	100.0	100.0	100.0	100.0	100.0	100.0
Dead branches	.03	.13	.13	.02	.10	.06						
	ALL SPECIES											
Foliage	7.75	7.23	7.58	8.15	8.30	8.76	16.2	15.7	15.1	14.2	13.2	12.8
Cones	.25	.33	.26	.30	.28	.20	.5	.7	.5	.5	.4	.3
Stem wood	27.39	26.31	30.39	36.14	41.01	45.86	57.4	57.3	60.4	63.1	65.0	66.9
Stem bark	3.97	4.41	4.44	5.19	6.12	6.45	8.3	9.6	8.8	9.2	9.7	9.4
Branch wood	4.92	4.51	4.40	4.25	4.14	4.13	10.3	9.8	8.7	7.4	6.6	6.0
Branch bark	3.46	3.14	3.24	3.23	3.18	3.21	7.2	6.8	6.5	5.6	5.1	4.6
Total	47.74	45.93	50.31	57.26	63.03	68.61	100.0	100.0	100.0	100.0	100.0	100.0
Dead branches	2.98	2.84	3.59	3.66	4.23	5.25						

[1] Includes pin cherry.

with increased density. The weight of branches increased both in absolute terms and as a percentage of the total birch crop with increased density (Table 6).

From the point of view of stand production the critical factor is the amount of foliage per acre. Weight of foliage in tons per acre increases with density as follows:

Stems per acre	*Fir*	*Spruce*	*Birch*	*All*
700	7.07	.66	.02	7.75
1000	7.07	.08	.08	7.23
1500	7.49	.04	.05	7.58
2000	8.03	.04	.08	8.15
3000	7.77	.44	.09	8.30
5000	8.23	.42	.11	8.76

The relationships of total dry-weight of foliage in pounds to number of stems (N), basal area (BA), and stem volume (V) are shown in Figure 6. The corresponding equations are:

$$\text{o.d.wt. foliage} = 14631 + .578\,N \quad (n = 18, r^2 = .0878)$$
$$= 9049 + 32.97\,BA \quad (n = 18, r^2 = .4143)$$
$$= 6545 + 2.39\,V \quad (n = 18, r^2 = .5634)$$

In all cases the slope is significantly different from 0 indicating a positive increase in the amount of foliage with increasing density.

Increment. As with any stem analysis or stand projection technique the data of this study yield a direct estimate of gross periodic annual growth (1957-1961). Gross periodic annual increment is comprised of the growth on the surviving trees, ingrowth (natality in the sense of population dynamics), and mortality and is therefore representative of total production on an area. Unless otherwise specified the term increment in this paper means gross periodic annual increment for the period 1957-1961. Since all the tree species beyond the seedling stage were included in the sample the only forms of ingrowth would be new seedlings. The annual seedling crop, which survives only one or a few years, is negligible with respect to the tree stand and has not been estimated. Mortality has been estimated for the period 1955 to 1961 from a series of 12 ¼-acre plots in the same stand type and ranging from 1000 to 5000 stems per acre[5].

The gross annual volume increment of stem wood increases with increasing density (Fig. 7 and Tables 7, 8 and 9). The equations relating gross periodic annual volume increment in cubic feet per acre per year to number of stems (N), basal area (BA), total volume (V) and total dry-weight of foliage in pounds (F), in Figure 7 are as follows:

$$\text{Branch wood} = 9.82 + .0018\,N \quad (n = 18, r^2 = .6061)$$
$$= 2.53 + .0544\,BA \quad (n = 18, r^2 = .8379)$$
$$= .162 + .0035\,V \quad (n = 18, r^2 = .8764)$$
$$= -.447 + .0009\,F \quad (n = 18, r^2 = .6028)$$
$$\text{Stem wood} = 130.5 + .0156\,N \quad (n = 18, r^2 = .4074)$$
$$= 49.4 + .557\,BA \quad (n = 18, r^2 = .7569)$$
$$= 19.4 + .0373\,V \quad (n = 18, r^2 = .7433)$$
$$= -14.3 + .0113\,F \quad (n = 18, r^2 = .6977)$$

In all cases the trend was significant. Gross annual increment of branch-wood volume also increased significantly with these measures of density.

For individual plots the gross annual dry-weight increment of all above ground

[5] Baskerville, G. L. Unpublished data.

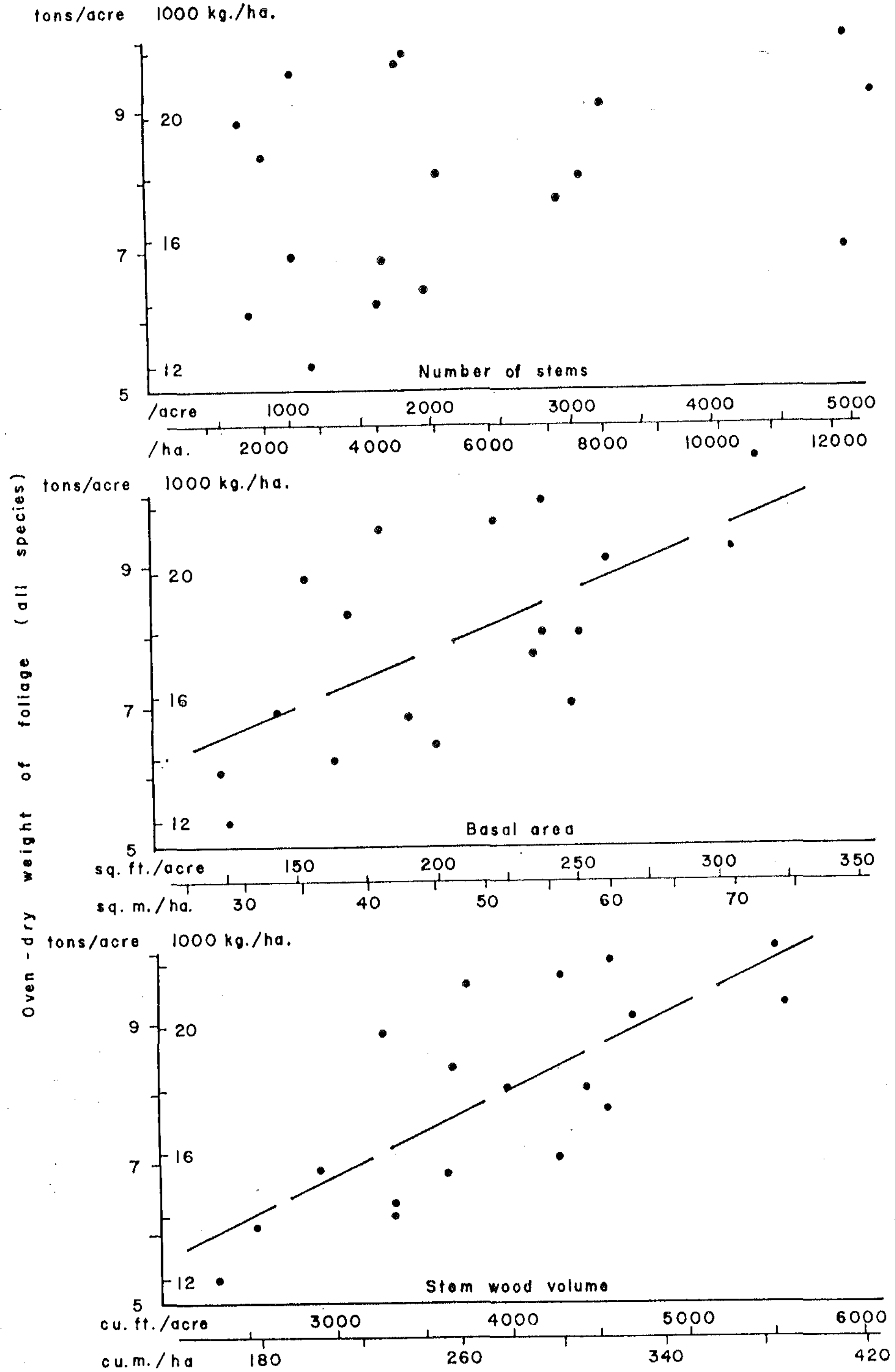

FIGURE 6. *Oven-dry weight of foliage, all species, over number of stems, basal area and stem wood volume for all species.*

TABLE 7. Gross periodic annual volume increment, 1957-61.

Plot	Stem wood				Branch wood				Total			
	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
	cubic feet per acre per year											
	700 stems/acre											
13	88.7	25.7	2.0	116.4	7.5	2.0	.4	9.9	96.2	27.7	2.4	126.3
26	147.0	11.8	—	158.8	10.5	.8	—	11.3	157.5	12.6	—	170.1
27	156.3	4.9	—	161.2	13.3	.4	—	13.7	169.6	5.3	—	174.9
	1000 stems/acre											
5	88.9	4.9	4.0	97.8	7.5	.5	1.2	9.2	96.4	5.4	5.2	107.0
21	184.0	—	.8	184.8	14.5	—	.2	14.7	198.5	—	1.0	199.5
23	133.2	—	1.3	134.5	9.5	—	.2	9.7	142.7	—	1.5	144.2
	1500 stems/acre											
2	139.4	—	1.6	141.0	11.1	—	.3	11.4	150.5	—	1.9	152.4
9	112.8	1.8	4.1	118.7	9.2	.3	.8	10.3	122.0	2.1	4.9	129.0
18	188.2	.2	—	188.4	16.1	.1	—	16.2	204.3	.3	—	204.6
	2000 stems/acre											
4	128.6	—	1.1	129.7	11.1	—	.2	11.3	139.7	—	1.3	141.0
6	199.1	1.4	3.2	203.7	13.9	.4	.4	14.7	213.0	1.8	3.6	218.4
15	165.2	.1	1.5	166.8	13.4	—	.3	13.7	178.6	.1	1.8	180.5
	3000 stems/acre											
3	173.2	33.3	1.2	207.7	14.8	2.2	.2	17.2	188.0	35.5	1.4	224.9
8	172.4	.3	4.7	177.4	14.7	—	.6	15.3	187.1	.3	5.3	192.7
19	182.9	—	3.9	186.8	15.3	—	.6	15.9	198.2	—	4.5	202.7
	5000 stems/acre											
7	158.8	1.0	11.8	171.6	14.0	.2	1.5	15.7	172.8	1.2	13.3	187.3
12	220.1	—	—	220.1	19.6	—	—	19.6	239.7	—	—	239.7
22	196.8	19.3	2.6	218.7	16.5	2.3	.4	19.2	213.3	21.6	3.0	237.9

components ranged from 3.17 tons per acre per year to 6.22 tons per acre per year (Table 11). The average for each density in tons per acre per year is summarized in the following tabulation.

Stems per acre	*Fir*	*Spruce*	*Birch*	*All*
700	3.84	.33	.04	4.21
1000	3.97	.05	.15	4.17
1500	4.18	.02	.09	4.29
2000	4.58	.02	.12	4.72
3000	4.71	.31	.17	5.19
5000	5.11	.27	.23	5.61

These may be compared with the mean annual increment values to age 40 to 47 presented by Ovington and Pearsall (1956) for several species: *Pinus sylvestris*, 3.6 tons per acre per year; *Pinus nigra*, 4.2; *Pseudotsuga menziesii*, 4.4; and *Picea abies*, 3.4 to 4.2 tons per acre per year.

Annual dry-weight increment was significantly correlated to number of stems, basal area, stem wood volume and oven-dry weight of foliage per acre (Fig. 8). The gross annual production of stem wood alone ranged from 1 ton per acre per year to 2.34 tons per acre per year and was also

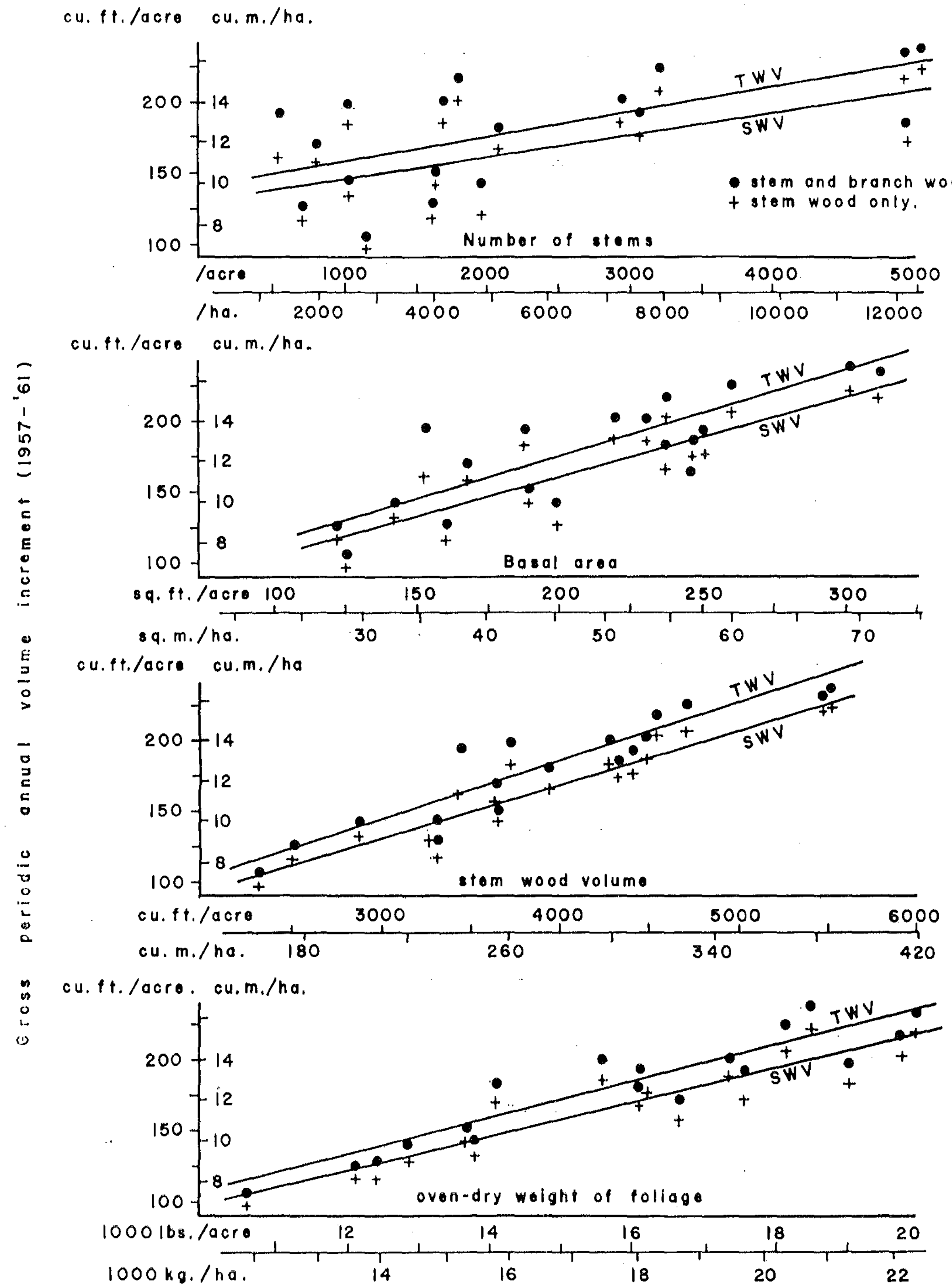

FIGURE 7. *Annual wood volume increment (1957–1961) of stem wood (SWV) and stem plus branch wood (TWV) plotted over: number of stems, basal area, stem wood volume, and oven-dry weight of foliage, for all species combined.*

TABLE 8. Gross periodic annual volume increment, 1952-56.

Plot	Stem wood				Branch wood				Total			
	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
	cubic feet per acre per year											
	700 stems/acre											
13	78.6	22.4	2.6	103.6	6.2	1.7	.4	8.3	84.8	24.1	3.0	111.9
26	134.7	9.4	—	144.1	8.9	.6	—	9.5	143.6	10.0	—	153.6
27	134.8	3.5	—	138.3	10.2	.3	—	10.5	145.0	3.8	—	148.8
	1000 stems/acre											
5	79.0	3.2	4.2	86.4	6.2	.4	1.2	7.8	85.2	3.6	5.4	94.2
21	155.1	—	.8	155.9	11.4	—	.2	11.6	166.5	—	1.0	167.5
28	114.4	—	1.6	116.0	7.8	—	.2	8.0	122.2	—	1.8	124.0
	1500 stems/acre											
2	124.4	—	2.3	126.7	9.2	—	.3	9.5	133.6	—	2.6	136.2
9	99.4	2.4	4.1	105.9	7.6	.3	.8	8.7	107.0	2.7	4.9	114.6
18	157.3	.5	—	157.8	12.9	—	—	12.9	170.2	.5	—	170.7
	2000 stems/acre											
4	116.1	—	1.3	117.4	9.2	—	.2	9.4	125.3	—	1.5	126.8
6	169.5	2.7	4.0	176.2	10.9	.4	.4	11.7	180.4	3.1	4.4	187.9
15	148.8	.6	1.7	151.1	16.1	—	.3	16.4	164.9	.6	2.0	167.5
	3000 stems/acre											
3	153.9	21.4	.9	176.2	12.4	.2	.1	12.7	166.3	21.6	1.0	188.9
8	158.6	.8	6.2	165.6	12.4	.1	.6	13.1	171.0	.9	6.8	178.7
9	163.8	—	4.1	167.9	12.7	—	.6	13.3	176.5	—	4.7	181.2
	5000 stems/acre											
7	137.7	1.0	10.4	149.1	11.3	.1	1.5	12.9	149.0	1.1	11.9	162.0
12	204.6	—	—	204.6	16.4	—	—	16.4	221.0	—	—	221.0
22	178.6	13.0	2.6	194.2	13.8	1.9	.4	16.1	192.4	14.9	3.0	210.3

correlated to density (Fig. 8). The equations for gross periodic annual weight increment in tons per acre per year corresponding to the lines in Figure 8 are as follows:

Total living tree

$$= 3.88 + .000348\ N \quad (n = 18, r^2 = .3191)$$

$$= 1.97 + .0129\ BA \quad (n = 18, r^2 = .6768)$$

$$= 1.14 + .000896\ V \quad (n = 18, r^2 = .7922)$$

$$= .03 + .000291\ F \text{ (lbs)} \quad (n = 18, r^2 = .8962)$$

Stem wood only

$$= 1.24 + .000197\ N \quad (n = 18, r^2 = .2508)$$

$$= .43 + .00601\ BA \quad (n = 18, r^2 = .7906)$$

$$= .04 + .000417\ V \quad (n = 18, r^2 = .9198)$$

$$= -.18 + .000117\ F \text{ (lbs)} \quad (n = 18, r^2 = .7442)$$

TABLE 9. The distribution of the standing crop by tree component and species for each plot.

Component	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
	tons per acre											
700 stems/acre	*Plot 13*				*Plot 26*				*Plot 27*			
Foliage	4.76	1.28	.06	6.10	7.85	.50	—	8.35	8.62	.22	-	8.84
Cones	.19	—	—	.19	.29	—	—	.29	.26	—	—	.26
Stem wood	16.62	5.06	.86	22.54	30.34	1.75	—	32.09	27.02	.67	—	27.69
Stem bark	2.39	.61	.13	3.13	4.44	.16	—	4.60	4.12	.06	—	4.18
Branch wood	2.83	.95	.19	3.97	4.62	.33	—	4.95	5.72	.17	—	5.89
Branch bark	2.04	.62	.05	2.71	3.31	.23	—	3.54	4.03	.13	—	4.16
Total	28.83	8.52	1.29	38.64	50.85	2.97	—	53.82	49.77	1.25	—	51.02
Dead branches	1.91	.82	.10	2.83	3.76	.18	—	3.94	3.22	.03	—	3.25
1000 stems/acre	*Plot 5*				*Plot 21*				*Plot 28*			
Foliage	4.90	.24	.18	5.32	9.48	—	.03	9.51	6.87	—	.02[1]	6.89
Cones	.30	—	—	.30	.51	—	—	.51	.19	—	—	.19
Stem wood	18.46	.77	2.34	21.57	31.64	—	.39	32.03	24.73	—	.30	25.03
Stem bark	2.87	.07	.35	3.29	4.46	—	.06	4.52	3.55	—	.05	3.60
Branch wood	3.14	.12	.39	3.65	6.22	—	.06	6.28	3.45	—	.07	3.52
Branch bark	2.29	.09	.09	2.47	4.36	—	.02	4.38	2.55	—	.02	2.57
Total	31.96	1.29	3.35	36.60	56.67	—	.56	57.23	41.34	—	.46	41.80
Dead branches	2.40	.08	.24	2.72	3.23	—	.04	3.27	2.41	—	.04	2.45
1500 stems/acre	*Plot 2*				*Plot 9*				*Plot 18*			
Foliage	6.83	—	.04	6.87	6.02	.11	.11	6.24	9.65	.02	—	9.67
Cones	.17	—	—	.17	.27	—	—	.27	.36	—	—	.36
Stem wood	29.72	—	.68	30.40	23.72	.54	1.75	26.01	34.75	.13	—	34.88
Stem bark	4.15	—	.09	4.24	3.85	.05	.24	4.14	4.96	.01	—	4.97
Branch wood	3.57	—	.09	3.66	3.18	.05	.26	3.49	6.04	.01	—	6.05
Branch bark	2.71		.01	2.72	2.39	.04	.07	2.50	4.47	.01		4.48
Total	47.15	—	.91	48.06	39.43	.79	2.43	42.65	60.23	.18	—	60.41
Dead branches	3.34	—	.04	3.38	2.23	.02	.36	2.61	4.78	.01	—	4.79
2000 stems/acre	*Plot 4*				*Plot 6*				*Plot 15*			
Foliage	6.42	—	.03	6.45	9.68	.10	.15	9.93	8.01	.01	.04	8.06
Cones	.34	—	—	.34	.29	—	—	.29	.26	—	—	.26
Stem wood	30.56	—	.05	30.61	39.38	.85	1.26	41.49	35.58	.10	.44	36.12
Stem bark	4.58	—	.10	4.68	5.44	.10	.14	5.68	5.16	.01	.06	5.23
Branch wood	3.16	—	.05	3.21	5.21	.07	.14	5.42	4.07	.01	.06	4.14
Branch bark	2.54	—	.02	2.56	3.88	.05	.04	3.97	3.12	.01	.02	3.15
Total	47.60	—	.25	47.85	63.88	1.17	1.73	66.78	56.20	.14	.62	56.96
Dead branches	3.16	—	.04	3.20	4.57	.08	—	4.65	3.87	.01	.01	3.89
3000 stems/acre	*Plot 3*				*Plot 8*				*Plot 19*			
Foliage	7.79	1.28	.03	9.10	7.86	.04	.13	8.03	7.67	—	.10	7.77
Cones	.29	—	—	.29	.39	—	—	.39	.17	—	—	.17
Stem wood	37.31	4.79	.55	42.65	38.42	.26	2.24	40.92	38.13	—	1.50	39.63
Stem bark	5.49	.48	.07	6.04	6.19	.02	.28	6.49	5.62	—	.21	5.83
Branch wood	3.81	.65	.05	4.51	3.75	.04	.27	4.06	3.76	—	.11	3.87
Branch bark	3.02	.46	.02	3.50	2.97	.03	.07	3.07	2.96	—	.04	3.00
Total	57.71	7.66	.72	66.09	59.58	.39	2.99	62.96	58.31	—	1.96	60.27
Dead branches	3.81	.14	.05	4.00	3.63	.01	.19	3.83	4.83	—	.07	4.90
5000 stems/acre	*Plot 7*				*Plot 12*				*Plot 22*			
Foliage	6.74	.02	.25	7.01	9.27	—	—	9.27	8.71	1.24	.07	10.02
Cones	.10	—	—	.10	.25	—	—	.25	.26	—	—	.26
Stem wood	35.10	.19	3.65	38.94	48.41	—	—	48.41	45.68	.68	1.03	47.39
Stem bark	4.74	.01	.59	5.34	6.66	—	—	6.66	6.74	.47	.16	7.37
Branch wood	3.05	.02	.51	3.58	4.48	—	—	4.48	3.75	.46	.13	4.34
Branch bark	2.48	.02	.14	2.64	3.60	—	—	3.60	3.00	.35	.06	3.41
Total	52.21	.26	5.14	57.61	72.67	—	—	72.67	68.14	6.20	1.45	75.79
Dead branches	3.87	.02	.17	4.06	5.74	—	—	5.74	5.79	.16	.03	5.98

[1]Includes pin cherry.

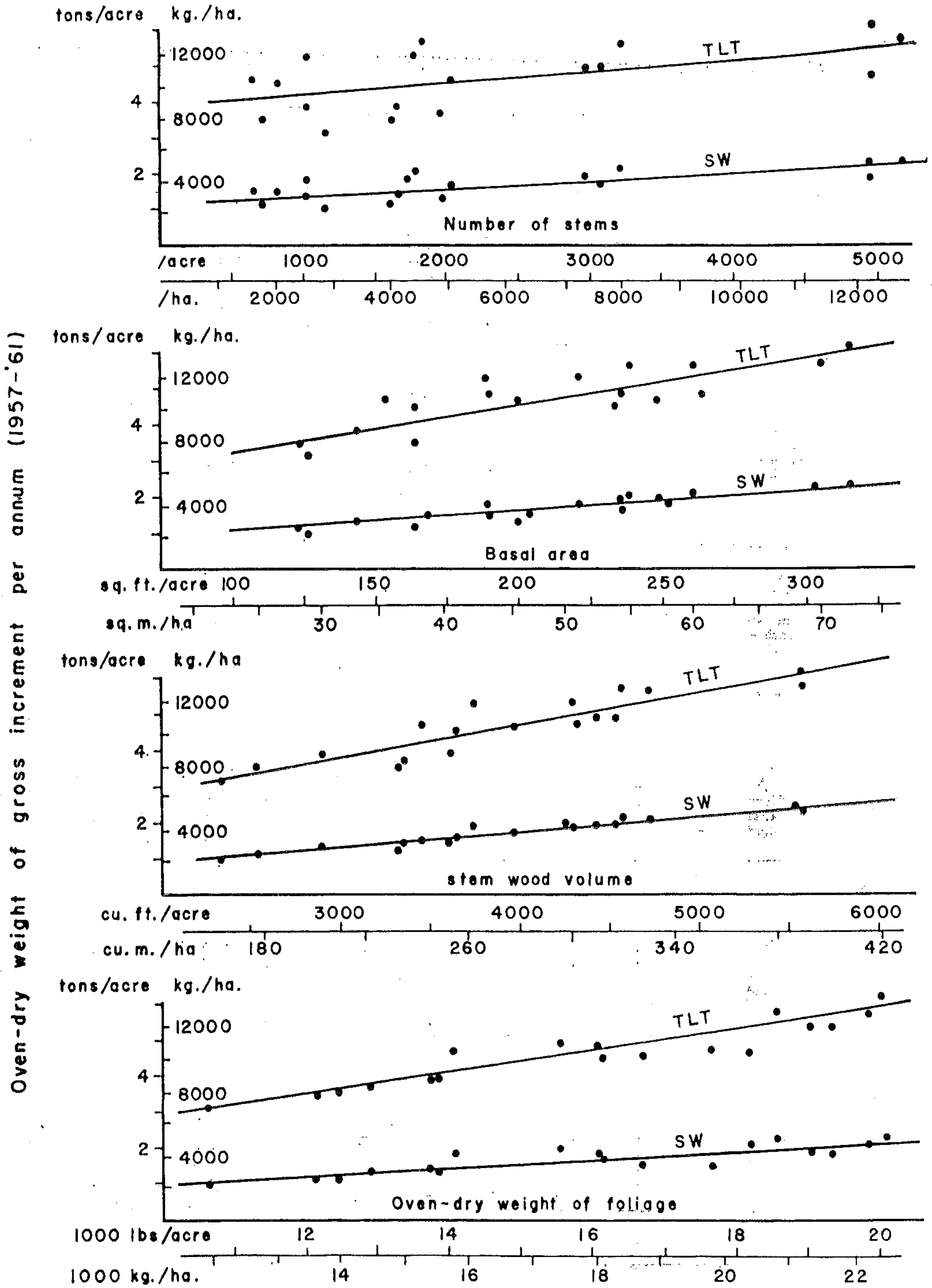

FIGURE 8. *Annual dry-weight increment (1957–1961) for all species plotted over: number of stems, basa area, stem wood volume, and oven-dry weight of foliage, for all species combined. Each point represents one plot, TLT = total living tree above ground and SW = stem wood only.*

TABLE 10. Distribution of gross periodic annual increment (1957-61) among the tree components.

Component	Number of stems per acre						Number of stems per acre					
	700	1000	1500	2000	3000	5000	700	1000	1500	2000	3000	5000
	tons/acre/yr.						percent of total					
						BALSAM FIR						
Foliage	1.84	1.84	1.95	2.09	2.02	2.14	47.9	46.3	46.7	45.6	42.9	41.9
Cones	.05	.07	.05	.06	.06	.04	1.3	1.8	1.2	1.3	1.3	.8
Stem wood	1.26	1.36	1.44	1.65	1.80	2.03	32.9	34.2	34.4	36.0	38.2	39.8
Stem bark	.14	.14	.14	.15	.16	.16	3.5	3.5	3.3	3.3	3.4	3.1
Branch wood	.32	.32	.34	.35	.37	.41	8.1	8.1	8.2	7.6	7.8	8.0
Branch bark	.23	.24	.26	.28	.30	.33	6.3	6.1	6.2	6.2	6.4	6.4
Total	3.84	3.97	4.18	4.58	4.71	5.11	100.0	100.0	100.0	100.0	100.0	100.0
						WHITE SPRUCE						
Foliage	.23	.03	.01	.01	.15	.15	53.5	60.0	50.0	50.0	48.4	55.6
Cones	—	—	—	—	—	—	—	—	—	—	—	—
Stem wood	.03	.02	.01	.01	.11	.08	30.2	40.0	50.0	50.0	35.4	29.6
Stem bark	.01	—	—	—	.01	.01	2.3	—	—	—	3.2	3.7
Branch wood	.04	—	—	—	.02	.02	9.3	—	—	—	6.5	7.4
Branch bark	.02	—	—	—	.02	.01	4.7	—	—	—	6.5	3.7
Total	.33	.05	.02	.02	.31	.27	100.0	100.0	100.0	100.0	100.0	100.0
						WHITE BIRCH						
Foliage	.02	.09[1]	.05	.08	.09	.11	50.0	56.2	55.5	66.7	52.9	47.8
Cones	—	—	—	—	—	—	—	—	—	—	—	—
Stem wood	.01	.05	.03	.03	.04	.07	25.0	31.2	33.3	25.0	23.5	30.4
Stem bark	—	—	—	—	.01	.01	—	—	—	—	5.9	4.4
Branch wood	.01	.02	.01	.01	.02	.03	25.0	12.6	11.2	8.3	11.8	13.0
Branch bark	—	—	—	—	.01	.01	—	—	—	—	5.9	4.4
Total	.04	.15	.09	.12	.17	.23	100.0	100.0	100.0	100.0	100.0	100.0
						ALL SPECIES						
Foliage	2.09	1.95	2.01	2.18	2.26	2.40	48.5	47.0	46.8	46.2	43.5	42.3
Cones	.05	.07	.05	.06	.06	.04	1.2	1.7	1.2	1.3	1.2	.7
Stem wood	1.30	1.43	1.48	1.69	1.95	2.18	32.4	34.2	34.5	35.8	37.5	38.9
Stem bark	.15	.14	.14	.15	.18	.18	3.5	3.3	3.3	3.2	3.5	3.8
Branch wood	.37	.34	.35	.36	.41	.46	8.6	8.1	8.2	7.6	8.0	8.1
Branch bark	.25	.24	.26	.28	.33	.35	5.8	5.7	6.0	5.9	6.3	6.2
Total	4.21	4.17	4.29	4.72	5.19	5.61	100.0	100.0	100.0	100.0	100.0	100.0

[1] Includes pin cherry.

Nowhere in Figure 8 is there any indication of deviation from the linear trend of production at either low or high densities. It is also apparent that number of stems per acre is not a good index of production (r^2 = .3191). This results from the failure of number of stems to account in any way for variation in species and size-class composition. Plots containing a larger number of birch trees, which tended to be much smaller than the average fir tree, were very low in production. This produced an erratic distribution in the lower densities. Basal area and volume both adjust for these smaller-than-average trees. The effect of species composition is apparent when annual production is examined in terms of pounds of total tissue produced per square foot of basal area as shown below.

Stems per acre	*Fir*	*Spruce*	*Birch*	*Average*
700	639	628	530	637
1000	602	428	576	606
1500	522	429	498	521
2000	513	481	463	512
3000	503	648	440	506
5000	472	546	467	474

In terms of production birch does not make as good use of its space in the stand as do the other two species. In this respect it must be recalled that birch is an intolerant species and that in the stands examined the trees occupied intermediate crown positions.

The distribution of increment by tree component indicates that the greatest proportion goes into foliage production (Tables 10, 11, 12). Foliage made up 48 percent of the fir increment at 700 stems per acre and 42 percent at 5000 stems per acre. The corresponding percentages for spruce are 53 and 56, for birch 50 and 48.

TABLE 11. Distribution of gross periodic annual increment (1957-61) by tree component.

Component	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
					tons/acre/year							
700 stems/acre	*Plot 13*				*Plot 26*				*Plot 27*			
Foliage	1.24	.45	.06	1.75	2.04	.18	—	2.22	2.24	.08	—	2.32
Cones	.04	—	—	.04	.06	—	—	.06	.05	—	—	.05
Stem wood	.88	.24	.03	1.15	1.44	.11	—	1.55	1.47	.05	—	1.52
Stem bark	.09	.03	—	.12	.16	.01	—	.17	.18	—	—	.18
Branch wood	.20	.07	.02	.29	.33	.03	—	.36	.42	.01	—	.43
Branch bark	.15	.05	—	.20	.24	.02	—	.26	.29	.01	—	.30
Total	2.60	.84	.11	3.55	4.27	.35	—	4.62	4.65	.15	—	4.80
1000 stems/acre	*Plot 5*				*Plot 21*				*Plot 28*			
Foliage	1.27	.08	.19	1.54	2.45	—	.03	2.48	1.78	—	.02[1]	1.80
Cones	.06	—	—	.06	.10	—	—	.10	.03	—	—	.03
Stem wood	.89	.05	.06	1.00	1.86	—	.01	1.87	1.33	—	.02	1.35
Stem bark	.08	—	.01	.09	.19	—	—	.19	.13	—	—	.13
Branch wood	.23	.01	.05	.29	.45	—	.01	.46	.29	—	.01	.30
Branch bark	.17	.01	.01	.19	.32	—	—	.32	.22	—	—	.22
Total	2.70	.15	.32	3.17	5.37	—	.05	5.42	3.[illegible]8	—	.05	3.83
1500 stems/acre	*Plot 2*				*Plot 9*				*Plot 18*			
Foliage	1.78	—	.04	1.82	1.56	.04	.11	1.71	2.51	.01	—	2.52
Cones	.03	—	—	.03	.05	—	—	.05	.07	—	—	.07
Stem wood	1.40	—	.02	1.42	1.09	.02	.06	1.17	1.84	—	—	1.84
Stem bark	.13	—	—	.13	.13	—	—	.13	.18	—	—	.18
Branch wood	.30	—	.01	.31	.26	.01	.03	.30	.48	—	—	.48
Branch bark	.23	—	—	.23	.19	—	.01	.20	.36	—	—	.36
Total	3.87	—	.07	3.94	3.28	.07	.21	3.56	5.44	.01	—	5.45
2000 stems/acre	*Plot 4*				*Plot 6*				*Plot 15*			
Foliage	1.67	—	.04	1.71	2.52	.03	.15	2.70	2.08	—	.04	2.12
Cones	.07	—	—	.07	.06	—	—	.06	.05	—	—	.05
Stem wood	1.33	—	.02	1.35	1.96	.02	.04	2.02	1.66	—	.02	1.68
Stem bark	.12	—	—	.12	.18	—	—	.18	.15	—	—	.15
Branch wood	.29	—	.01	.30	.43	.01	.02	.46	.33	—	.01	.34
Branch bark	.23	—	—	.23	.32	—	—	.32	.27	—	—	.27
Total	3.71	—	.07	3.78	5.47	.06	.21	5.74	4.54	—	.07	4.61
3000 stems/acre	*Plot 3*				*Plot 8*				*Plot 19*			
Foliage	2.02	.45	.03	2.50	2.04	.01	.14	2.19	1.99	—	.10	2.09
Cones	.06	—	—	.06	.08	—	—	.08	.03	—	—	.03
Stem wood	1.76	.34	.02	2.12	1.75	—	.06	1.81	1.88	—	.06	1.94
Stem bark	.15	.04	—	.19	.17	—	.01	.18	.16	—	.01	.17
Branch wood	.37	.07	.01	.45	.38	—	.03	.41	.37	—	.02	.39
Branch bark	.30	.05	—	.35	.30	—	.01	.31	.29	—	.01	.30
Total	4.66	.95	.06	5.67	4.72	.01	.25	4.98	4.72	—	.20	4.[illegible]
5000 stems/acre	*Plot 7*				*Plot 12*				*Plot 22*			
Foliage	1.75	.01	.26	2.02	2.41	—	—	2.41	2.26	.43	.06	2.75
Cones	.02	—	—	.02	.05	—	—	.05	.05	—	—	.05
Stem wood	1.70	.01	.17	1.88	2.33	—	—	2.33	2.07	.23	.04	2.34
Stem bark	.13	—	.02	.15	.18	—	—	.18	.18	.02	—	.20
Branch wood	.34	—	.06	.40	.48	—	—	.48	.41	.06	.02	.49
Branch bark	.28	—	.02	.30	.39	—	—	.39	.33	.05	.01	.39
Total	4.22	.02	.53	4.77	5.84	—	—	5.84	5.30	.79	.13	6.22

[1] Includes pin cherry.

TABLE 12. Gross periodic annual dry-weight increment, 1952-56.

Plot	Total tree				Stem wood				Branch wood			
	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
					tons/acre/year							
					700 stems/acre							
13	2.01	.63	.12	2.76	.78	.21	.04	1.03	.16	.05	.02	.23
26	3.47	.25	—	3.72	1.32	.09	—	1.41	.26	.02	—	.28
27	3.54	.09	—	3.63	1.26	.03	—	1.29	.30	.01	—	.31
					1000 stems/acre							
5	2.19	.10	.25	2.54	.78	.03	.06	.87	.19	.01	.05	.25
21	3.89	—	.05	3.94	1.56	—	.01	1.57	.33	—	.01	.34
28	2.92	—	.05	2.97	1.14	—	.02	1.16	.22	—	.01	.23
					1500 stems/acre							
2	3.14	—	.08	3.22	1.25	—	.03	1.28	.24	—	.01	.25
9	2.61	.07	.20	2.88	.96	.03	.06	1.05	.20	—	.03	.23
18	4.09	.01	—	4.10	1.52	—	—	1.52	.36	—	—	.36
					2000 stems/acre							
4	3.01	—	.06	3.07	1.18	—	.02	1.20	.23	—	.01	.24
6	4.28	.08	.20	4.56	1.66	.03	.06	1.75	.33	—	—	.33
15	3.73	.01	.07	3.81	1.50	—	.02	1.52	.28	—	.01	.29
					3000 stems/acre							
3	3.78	.58	.05	4.41	1.55	.23	.01	1.79	.30	.04	.01	.35
8	3.88	.02	.26	4.16	1.58	.01	.09	1.68	.30	—	.03	.33
19	3.87	—	.19	4.06	1.65	—	.06	1.71	.30	—	.02	.32
					5000 stems/acre							
7	3.42	.02	.45	3.89	1.48	.01	.15	1.64	.27	—	.06	.33
12	4.90	—	—	4.90	2.15	—	—	2.15	.39	—	—	.39
22	4.40	.37	.12	4.89	1.87	.15	.04	2.06	.33	.04	.02	.39

Converting mortality data from number of stems by diameter class to a dry weight basis estimates of mortality and net periodic annual increment (1957-61) are obtained (Table 13).

Increment for the period 1952-1956 bore the same general relationship to the present stand density as did that for the period 1957-1961. In general current growth was still increasing slightly in these stands, mostly in the fir component. White spruce increment increased to a lesser extent than fir, and white birch either remained level or decreased.

Discussion

The results show that the denser stands with their larger numbers of smaller crowns, are the highest producers of dry matter. Since the critical factor in explaining a theoretical drop in production at high density was thought to be the amount of respiring surface area

TABLE 13. Average annual above-ground gross increment, mortality, and net increment of total tree in tons per acre per year.

Stems per acre	Gross annual increment				Annual mortality[1]				Net annual increment			
	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
	tons/acre/year											
700	3.84	.43	.04	4.31	.13	—	—	.130	3.71	.43	.04	4.18
1000	3.97	.05	.16	4.18	.18	—	.001	.181	3.79	.05	.16	4.00
1500	4.18	.02	.09	4.29	.26	.001	.001	.262	3.92	.02	.09	4.03
2000	4.58	.02	.12	4.72	.32	.001	.001	.322	4.26	.02	.12	4.40
3000	4.71	.31	.17	5.19	.44	.007	.005	.452	4.27	.30	.17	4.74
5000	5.11	.27	.24	5.62	.49	.003	.005	.498	4.62	.27	.23	5.02

[1] This is periodic annual mortality and ignores any growth put on by dying trees after the beginning of the period (five years).

this factor was carefully analyzed. Both bole surface area and branch surface are found to increase with increased density as expected (Table 14, Fig. 9). Either this increase is not enough to produce an inefficient balance of nonphotosynthetic area to photosynthetic area or surface area is not a good measure of respiring tissue.

To check the surface area relationship further the number of square feet of stem, branch, and total surface area per pound of foliage were calculated by dbh class for each density. For a given diameter the amount of surface area per pound of foliage is independent of stand density but there is a marked increase in the ratio with decreasing stem size (Fig. 10b). Thus the nonphotosynthetic-photosynthetic area relationship suggests that the smaller trees should be less efficient, but this does not fit the fact. Alternately, it can be assumed that in branches the entire tissue respires rather than just the surface so the number of pounds of branch material per pound of foliage was calculated by diameter class. This indicates marked differences both with diameter and density (Fig. 10a) but there is a logical correlation to tree efficiency. The data are summarized in Table 15. It would appear that in branches, weight or volume is a better parameter of the respiring tissue than surface area when examining crown efficiency.

To carry the analysis a step further, the efficiency of various crown sizes was calculated from the original equations (Tables 2, 3 and 4) on the basis of the number of pounds of both total tissue and stem wood only produced per pound of foliage. It was found that for all three species the smallest crowns had a marked advantage on this basis (Fig. 11). Using cubic volume of wood produced per pound of foliage the results were similar but the initial drop was neither as pronounced nor as steep. The greater efficiency of volume production in small crowns is related to the higher form quotient of the supporting stems which in turn is explainable in terms of the growth sequence work of Duff and Nolan (1953). The greater efficiency of weight production in small crowns is attributable not only to the increased volume increment but also to the higher specific gravity found in the wood of smaller trees.

The mechanism which results in increased specific gravity in small trees is not known, but examination of the wood

TABLE 14. Stem and branch surface area per acre.

Plot	Stem surface area				Branch surface area				Total			
	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All	Fir	Spruce	Birch	All
	100 square feet/acre											
	700 stems/acre											
13	171	38	14	223	684	172	7	863	855	210	21	1086
26	302	16	—	318	1004	82	—	1086	1306	98	—	1404
27	260	8	—	268	1194	42	—	1236	1454	50	—	1504
	1000 stems/acre											
5	214	10	34	258	699	36	19	754	913	46	53	1012
21	504	—	5	509	1317	—	3	1320	1821	—	8	1829
28	294	—	12[1]	306	864	—	6[1]	870	1158	—	18[1]	1176
	1500 stems/acre											
2	402	—	10	412	994	—	4	998	1396	—	14	1410
9	309	10	31	350	878	21	15	914	1187	31	46	1264
18	448	3	—	451	1454	9	—	1463	1902	12	—	1914
	2000 stems/acre											
4	445	—	12	457	888	—	4	892	1333	—	16	1349
6	463	14	23	500	1208	33	9	1250	1671	47	32	1750
15	478	3	10	491	1127	4	5	1136	1605	7	15	1627
	3000 stems/acre											
3	589	49	11	649	1156	181	4	1341	1745	230	15	1990
8	573	7	41	621	1234	19	15	1268	1807	26	56	1889
19	547	—	29	576	1235	—	13	1248	1782	—	42	1824
	5000 st ms/a re											
7	596	6	69	671	1108	14	31	1153	1704	20	100	1824
12	817	—	—	817	1453	—	—	1453	2270	—	—	2270
22	760	58	29	847	1342	173	10	1525	2102	231	39	2372

[1] Includes pin cherry.

samples suggests they may contain a higher percentage of the heavier latewood. It might be inferred from this, that the controlling factors are operative while the earlywood is being laid down and limit its extent while leaving the amount of latewood relatively unaffected. Whatever the explanation it is clear that, in terms of cubic feet or pounds produced per pound of foliage, efficiency increases with decreasing crown size and from this it can be inferred that efficiency increases from dominant, through the codominant to the suppressed crown classes. Similar conclusions with respect to crown efficiency of individual trees were reached by Senda, *et al.* (1952) for *Pinus densiflora* and by Senda and Satoo (1956) for *Pinus strobus*. Since both of these studies indicated that fresh weight of foliage remained relatively constant across the spacings involved one would expect that production should have been higher in the denser stands. However, in their English

TABLE 15. Branch weight per pound of foliage and branch and stem surface area per pound of foliage by species and number of trees per acre.

Stems per acre	Dry-weight of branches per pound of dry foliage			Surface area per pound of dry foliage: Branch			Stem		
	Fir	Spruce	Birch	Fir	Spruce	Birch	Fir	Spruce	Birch
	lbs/lb			sq ft/lb					
700	1.06	1.21	3.94	6.79	7.23	5.66	1.73	1.57	11.85
1000	1.04	.91	2.74	6.78	7.70	5.21	2.39	2.15	9.36
1500	.99	.95	2.85	7.39	12.09	6.26	2.58	5.44	13.27
2000	.91	1.30	1.50	6.68	16.58	3.97	2.87	7.71	10.05
3000	.87	.89	2.49	7.77	7.65	6.05	3.67	2.15	15.20
5000	.82	.66	2.61	7.89	7.49	6.35	4.40	2.58	15.32

summary Senda *et al.* (1952) state, "...it is concluded that amount of wood produced by a young pine stand is not affected by stand density but the percentage of bole-wood in the produced wood is affected by density"; it increased with increasing density. With respect to the white pine study Senda and Satoo (1956) concluded that "...the amount of stem wood produced by unit weight of needle leaves was larger in the plots of higher densities, but over-density seemed not to be beneficial. The average of stem wood production per unit area in the last three years was larger in the plots of higher densities."

The picture becomes clearer when the percent distribution of total increment and standing crop among the tree components are examined (Fig. 11). In the smallest trees a much larger proportion of the total growth goes into stem wood, and a smaller proportion into foliage than in trees with larger crowns. While the present data provide no way of checking, it is postulated that these smaller crowns have a higher proportion of shade foliage. This foliage is known to be more efficient than sun foliage on a weight basis and in addition is structurally lighter (Clark 1961) which may partially explain why foliage represents a small percentage of the total increment and standing crop for small crowns. Coupled with the shade foliage relationship is the fact that balsam fir foliage has a very low light saturation point in photosynthesis (Clark 1961). Clearly the threshold of inefficiency is not crossed even in the densest stands or for the most suppressed trees.

Analysis of tree efficiency in terms of production per unit area of leaf surface (Watson 1952) was not possible in the present study but will be attempted in later work.

While the curves representing production per pound of foliage were similar in shape for the three species there were some noteworthy differences among them. On the basis of cubic feet of stem wood per pound of foliage small fir crowns are better producers than spruce. The lines cross at about 4 inches diameter breast height (balsam fir crown weight 4.7 pounds) beyond which spruce production is higher. Based on total dry-weight product per pound of foliage spruce is higher than fir across the entire range examined. Based on weight of stem wood product per pound of foliage the spruce is higher than fir in small crowns but its advantage disappears at about 5 inches diameter breast height (fir crown 9.7 pounds) beyond which point the two species are equal. This is explainable by

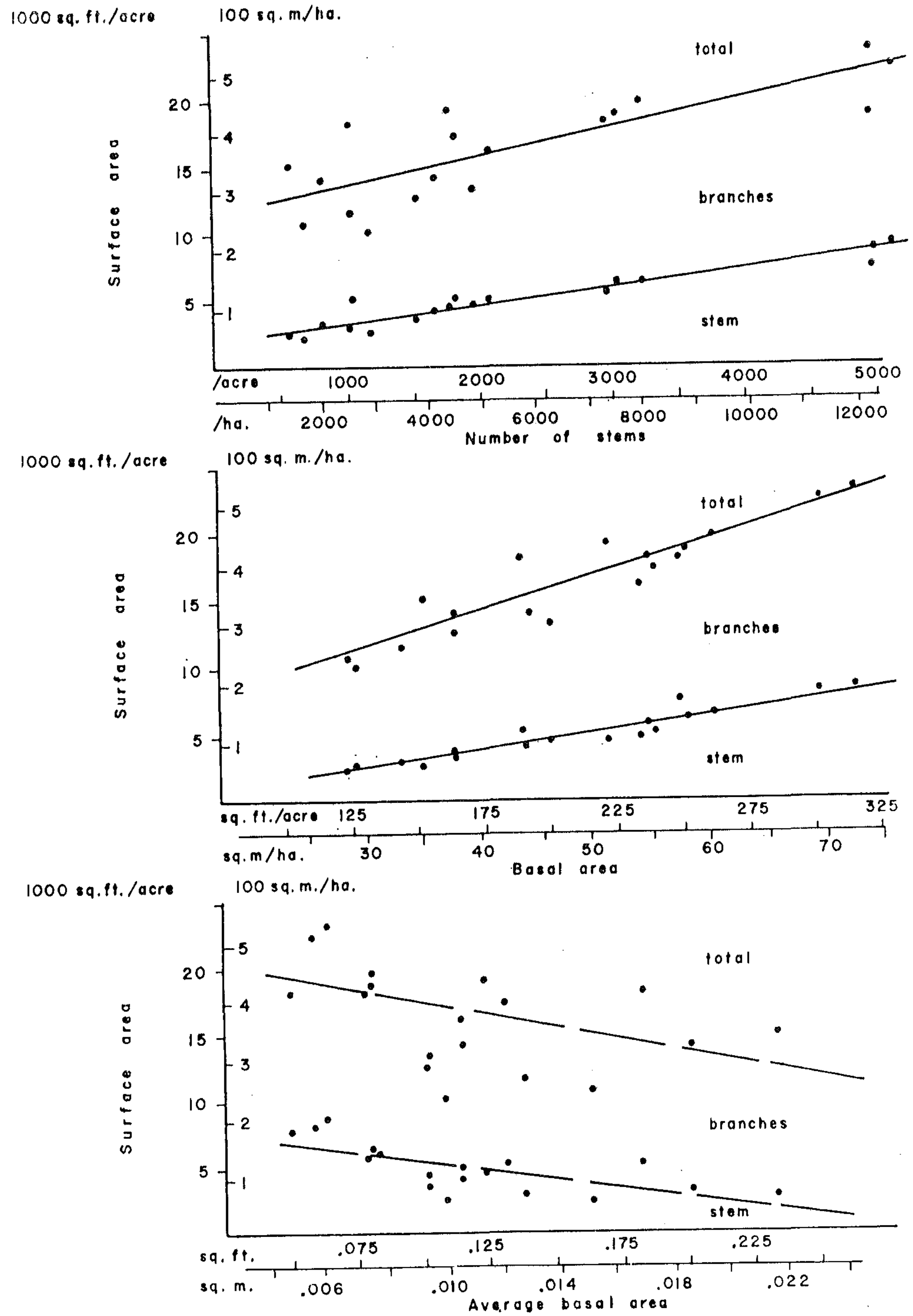

FIGURE 9. *Branch and stem surface area, for all species, over number of stems, basal area and average basal area.*

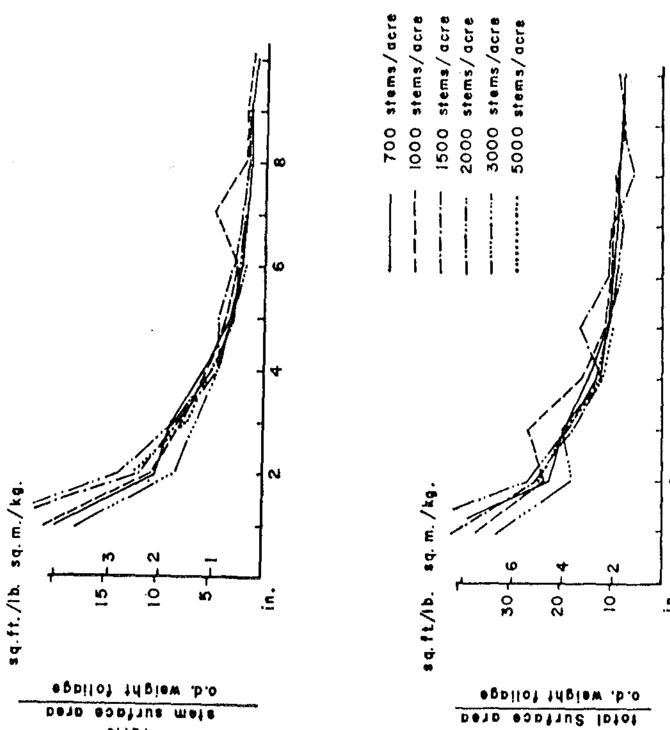

FIGURE 10b. *Stem and total surface area per pound of foliage by diameter class for balsam fir in each stand.*

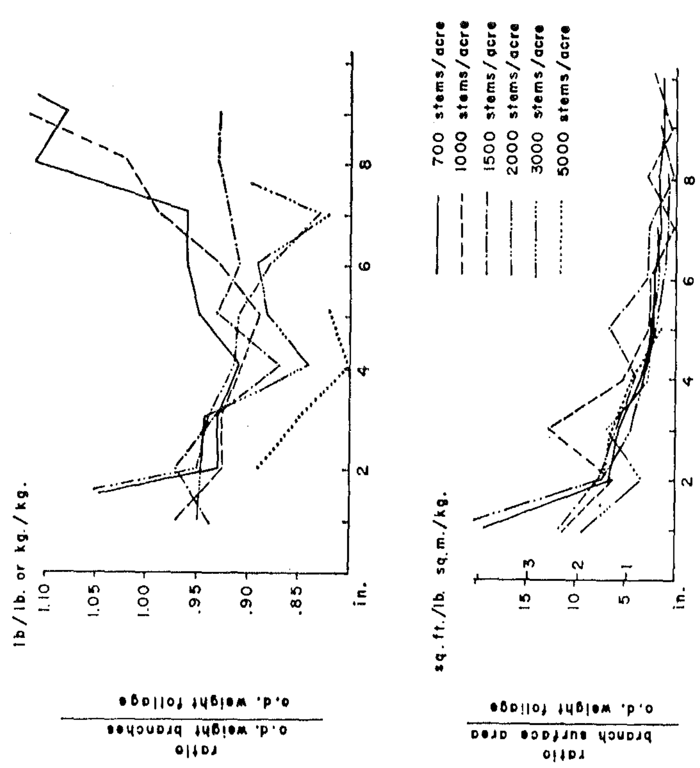

FIGURE 10a. *The oven-dry weight of branches (wood plus bark) and branch surface area per pound of foliage by diameter class for balsam fir in each stand.*

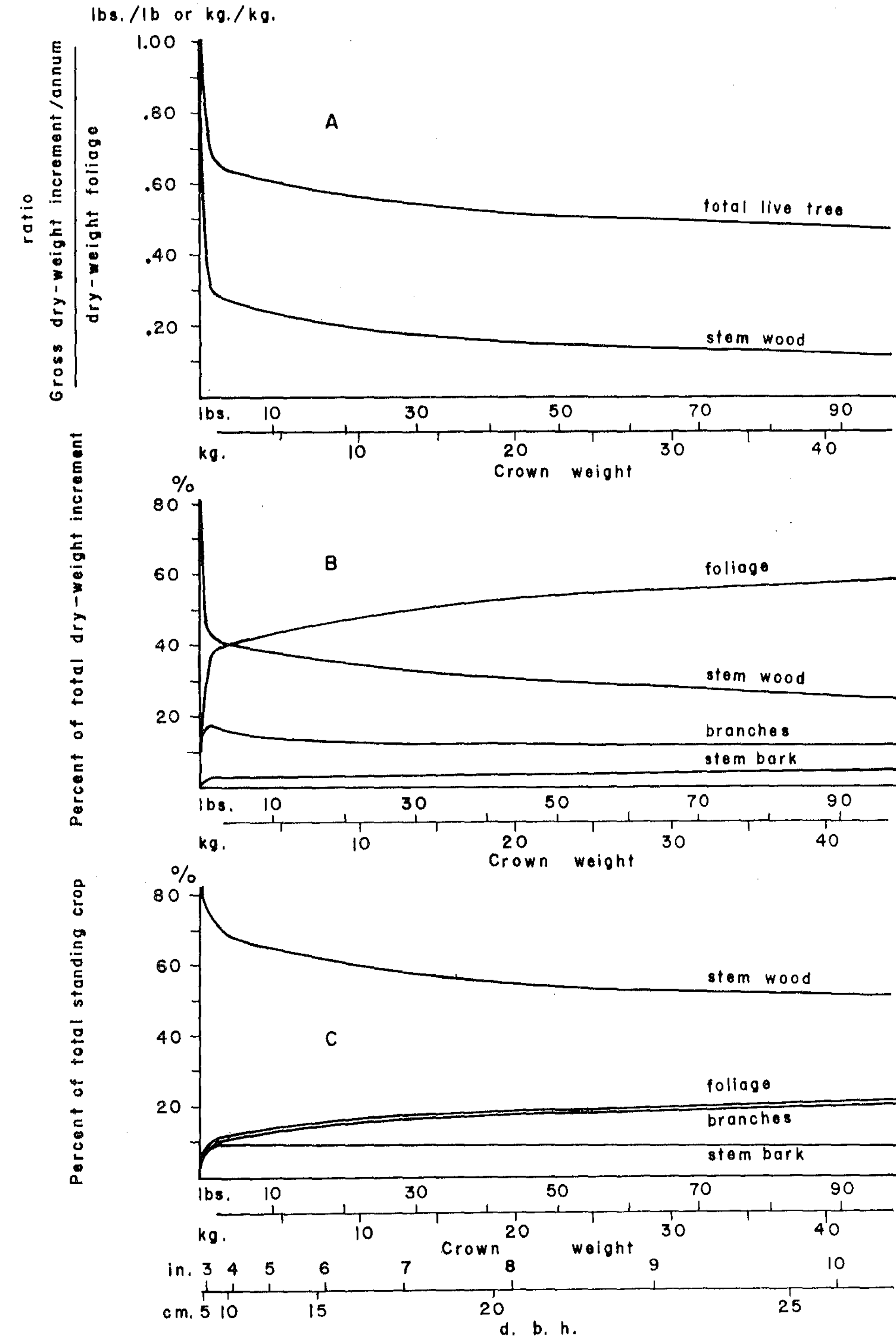

FIGURE 11. *A. Gross production of total tree and stem wood per pound of foliage over crown weight. B. The percentage distribution of dry-weight increment. C. The percentage distribution of standing crop over crown weight. Balsam fir only.*

the specific gravity curves (Fig. 5). The initial drop in production with increased crown size is much sharper for white birch which produces roughly three and one-half times as much weight (both of total living tissue and stem wood) per pound of foliage than either fir or spruce. The range of birch crowns examined was, of course, limited compared to that for fir and spruce.

It becomes clear that in these stands the critical feature of production is stand structure, in particular the relative proportion of trees of various crown sizes. There is thus the danger that the somewhat erratic distribution of number of stems over diameter associated with the small plots used in this study could be critical. It was found, however, that smoothing the number over diameter curve did not change the relative position of the various densities with reference to production but rather accentuated the trends already noted.

There appear to be three major possible explanations regarding the relationship of production to stand density indicated in this study. First, there exists the theoretical chance that the variations in density are reflections of variation in site and that production is merely indicating site differences. Considerable care was taken to eliminate this possibility when the study area was selected and it is unlikely that site differences are sufficient to cause the observed variations in productivity. Also, production varies inversely with the average height of dominants (age constant) which tends to refute this idea if not the concept of site index in tolerant species.

Secondly, the stand may not yet fully occupy the site in which case production is greatest in the stands which come closest to full occupancy. If this be the case, the increasing production with increasing density is itself an indication of understocking. Also the fact that current increment has not yet reached its peak could be cited as evidence that the stands are not yet fully closed. The relationship of current annual increment to mean annual increment suggests that the denser stands are closer to the point of culmination. The continued presence of the intolerant white birch and pin cherry in roughly equivalent proportions across the range of density may also be an indication of incomplete occupancy. Certainly both these species will disappear from the stands if present developmental trends continue.

The third possibility is that the stands have in fact reached full occupancy and there are physiological phenomena which operate to increase efficiency even while the stands get tighter. Certainly the present study did not include a sample plot that was clearly understocked, either in field observation or from examination of the compiled stand data. It may be that the primary response of fir and spruce to competition is in terms of crown length rather than crown diameter, thus making it possible to crowd more trees on an area while maintaining a physiologically equivalent or greater amount of foliage per acre. For instance, the ratio of length of live crown to total height of tree tended to be constant for a given diameter but to increase with increasing stem size, and hence with decreasing density on a stand basis, yet the base of the green crown was at essentially the same height in all densities. This could lead to a higher proportion of the more efficient shade foliage in the denser stand.

While it can be positively stated that the increment over density relationships must drop off sharply at low densities there is some question as to whether more open stands with structure and history similar to the ones examined actually exist. Observation leads to the conclusion that on average sites, such as the one examined, the advance growth in 1920 was universally abundant enough to produce stands of at least 600 stems per acre at 40 years of age. While this may mean the tree stand did not fully occupy the site in its early years, and thus account in part for the lower standing crop at low densities, it is difficult to imagine that these stands do not now fully occupy the site.

At the other extreme of density there is an absolute maximum of production. Whether this point lies short of the absolute maximum of density obtainable remains a moot point. Stands denser than 5000 stems per acre are extremely difficult to find and indeed stands in excess of 6000 stems per acre may not exist on this site. Because of the tolerant nature of balsam fir and its extremely low light saturation requirements, crown differentiation will always occur in such stands. Concomitant with differentiation is the natural thinning which reduces the number of stems per acre to a non-critical value. The few examples of true stagnation, or check, in fir stands found in the Green River Watershed are on extremely dry, overdrained, esker ridges and kame terraces.

It is of interest to speculate on what might result from thinning in immature stands of balsam fir. Since unit production rises with decreasing crown size and since thinning, especially from below, results in an increase in average crown size it follows that thinning will cause a reduction in current total fiber production per unit area. Part of this reduction results from the fact that the stand no longer fully occupies the site. This reduction is temporary and should disappear when the trees increase in size to the point where, for the number present, they again fully occupy the site—with a smaller number of larger individuals. A certain part of the reduction in increment, however, results from the fact that the larger crowns are somewhat less efficient and that the increased foliation as a result of the stand opening is largely in the form of less efficient sun foliage. The results of this study suggest that this reduction is continuing and would exist at least until the crowns had closed again to an extent proportional to that previous to thinning. This should not be construed as an indictment of thinning since there are economic factors which must also be considered.

The present study indicates that the most efficient production of dry matter is by the largest possible number of small crowns. However, there are certain qualifications attendant on this generalization: in the study area the principal species, balsam fir, is in its optimum climate on a near optimum site and is known to be remarkably shade tolerant; and the present estimates of production do not include the underground portion of the trees nor the shrubs and lesser vegetation.

Conclusions

The results of this study support the Möller hypothesis insofar as dry matter production is closely related to the amount of foliage. However, Möller's assumption that the amount of foliage is constant for all densities does not apply in this case. There is a weak but significant tendency towards increasing amount of foliage with increasing density. This is associated with increased production across the range of density examined. Similarly the results of the study do not conform to the Assmann hypothesis. It must be concluded, therefore, that for stands of the type discussed here and possibly for those of other tolerant coniferous species neither of these two theories are valid generalizations of the productivity-stand density relationship. Two of the more important problems which must be examined before an acceptable generalization can be developed are establishment of a biologically meaningful measure of stand density and a study of the physio-ecological relationships which result in the phenomenon called tolerance.

Summary

Eighteen plots were established in natural 38 to 45-year-old balsam fir–white spruce–white birch stands of 700, 1000,

1500, 2000, 3000 and 5000 stems per acre. A total of 101 fir, 14 spruce, 24 birch and 1 pin cherry were felled and analyzed to determine the distribution of dry matter in the above-ground tree components: foliage, cones, stem wood, stem bark, branch wood, branch bark and dead branches. Current periodic annual increment was also determined by component for each felled tree and the data were applied to the standing trees. The principal findings are:

1. The relationships of such factors as: stem height, form and volume, stem weight, crown weight, weight of branches, and the increment of these factors, to stem diameter at breast height are independent of stand density.
2. Average specific gravity of stem wood decreases exponentially with increasing stem diameter at breast height but, for a given diameter, is independent of stand density.
3. Total dry-weight of foliage per acre and current annual increment of cubic volume and of dry weight all increase linearly with increasing stand density.
4. As a corollary to 3, small crowns produce more tissue per pound of foliage than large crowns. This is thought to result from a combination of the low light saturation point of photosynthesis in balsam fir, the high proportion of shade needles in small crowns, and the favorable distribution of dry matter among tree components in small trees.
5. Spruce crowns are slightly more efficient than fir in production per pound of foliage. White birch crowns produce roughly three times as much dry matter per pound of foliage as either spruce or fir. However, because of differences in crown size the number of pounds produced per square foot of basal area is greatest for balsam fir followed by spruce and birch.
6. Neither the Möller nor the Assmann hypotheses of stand production are acceptable generalizations in stands consisting of highly tolerant species.

Sommaire

Dix-huit placeaux ont été délimités dans des peuplements naturels comprenant des sapins baumiers, des épinettes blanches et des bouleaux blancs de 38 à 45 ans; la densité des peuplements s'établissait à 700, 1000, 1500, 2000, 3000 et 5000 sujets à l'acre. On a abattu 101 sapins, 14 épinettes, 24 bouleaux et un cerisier de Pennsylvanie, afin de procéder à des analyses et de déterminer la teneur en matière sèche de toutes les parties aériennes des arbres, c'est-à-dire le feuillage, les cônes, le bois de la tige, l'écorce de la tige, le bois des branches, l'écorce des branches et les branches mortes. On a aussi déterminé la croissance annuelle de chaque partie de chaque arbre, et les données recueillies ont servi à l'étude des arbres vivants. Cette étude a permis de faire les constatations suivantes:

1. Le rapport entre la hauteur, la conformation et le volume de la tige, le poids de la tige, le poids de la cime, le poids des branches et l'accroissement annuel de tous les facteurs ci-dessus, d'une part, et le diamètre du tronc à hauteur de poitrine, d'autre part, est indépendant de la densité du peuplement.
2. Le poids spécifique moyen du bois de la tige décroît selon une exponentielle de l'accroissement du diamètre à hauteur de poitrine; toutefois, ce poids spécifique, pour un diamètre donné, est indépendant de la densité du peuplement.
3. Le poids anhydre des feuilles, à l'acre, et l'accroissement annuel du volume et du poids anhydre augmentent en proportion directe de l'accroissement de la densité du peuplement.
4. Comme corollaire à l'alinéa 3, les petites cimes produisent plus de tissu végétal par livre de feuillage que les grosses cimes. Ceci serait dû, croit-on, à l'effet combiné du faible degré de saturation lumineuse de la photosynthèse chez le sapin baumier, de la forte proportion d'aiguilles ombragées dans les petites cimes et de la répartition plus favorable de la matière sèche entre les diverses parties des arbres de petite taille.

5. La cime de l'épinette blanche produit un peu plus de matière sèche par livre de feuillage. La cime du bouleau blanc produit à peu près trois fois autant de matière sèche par livre de feuillage que la cime de l'épinette ou du sapin. Toutefois, en raison des différences de volume des cimes, le nombre de livres de matière sèche produites par pied carré de surface terrière est le plus élevé chez le sapin baumier, l'épinette blanche et le bouleau blanc venant ensuite.
6. Ni l'hypothèse de Möller ni celle d'Assmann, sur le calcul de la production de matière ligneuse, ne sont applicables aux peuplements d'essences nettement sciaphiles.

Literature Cited

Assmann, E. 1950. Grundflachen und Volumzuwachs der Rotbuche bei verschiedenen Durchforstungsgraden. Forstw. Centr. 69: 256–286.

———. 1953. Bestockungsdichte und Holzerzeuzung. Forstw. Centr. 72:69–101.

———. 1961. Waldertragskunde. Organische Production, Structur, Zuwachs und Ertrag von Waldbestanden. BLV Verlagsgesellschaft Munchen, Bonn Wien, 490 pp. see pp. 222–239 on he effect of different thinning intensities on yield.

Baskerville, G. L. 1962. Production in forests. Canada Dept. of Fo es·ry, Maritimes Resion, Fredericton, N. B. 85 pp. mimeo.

Clark, J. 1961. Photosynthesis and respiration in white spruce and balsam fir. State Univ. Coll. of For. Syracuse, N. Y. Tech. Pub. 85. 72 pp.

Duff, G. H. and N. J. Nolan. 1953. Growth and morphogenesis in Canadian forests species. I. The controls of cambial and apical activity in *Pinus resinosa*. Can. Jour. Bot. 31:471–513.

Hirai, S. 1955. Studies on the weight growth of forest trees, V. *Pinus strobus*. Bull. of Tokyo Univ. For. 48:221–235, English summary p. 234.

Iwaki, H. 1958. The influence of density on the dry matter production of *Fagopyrum esculentum*. Jap. Jour. Botany 16:210–226.

Kira, T., H. Ogawa and N. Sakazaki. 1953. Intraspecific competition among higher plants. I. Competition-yield-density inter-relationships in regularly dispersed populations. Jour. Inst. Polytech., Osaka City Univ. 4(D):1–16.

Kittredge, J. 1944. Estimation of amount of foliage of trees and stands. Jour. For. 42:905–912.

Kuroiwa, S. 1960. Ecological and physiological studies on the vegetation of Mt. Shimagare. IV. Some physiological functions concerning matter production in young *Abies* trees. Bot. Mag. Tokyo. 73:133–141.

Langmaid, K. 1963. Soil survey of the Andover-Plaster Rock area of New Brunswick. Canada Dept. of Agr., Research Institute, Fredericton, N. B. In press.

Loucks, O. L. 1962. A forest classification for the Maritime Provinces. Proc. Nova Scotia Inst. of Sci., Halifax, N. S. 25:85–167.

Madgwick, H. A. I. 1962. Studies on the growth and nutrition of *Pinus resinosa*. Unpub. Ph. D. Thesis. St. Coll. of For., Syracuse, N. Y. 111 pp.

Möller, C. M. 1946. Untersuchungen uber Laubmenge, Stoffverlust und stoffproduktion des Waldes. Det. forst. Forsøg. i Dannmark. 17:1–287.

———.1947. The effect of thinning, age and site on foliage, increment and loss of dry matter. Jour. For. 45:393–404.

———. 1954. The influence of thinning on volume increment. In "Thinning Problems and Practices in Denmark." State Univ. Coll. of For., Syracuse, N. Y. World For. Bull. 1 pp. 5–44.

———, D. Müller, and J. Nielsen. 1954a. Respiration in stem and branches of beech. Det. forst. Forsøg. i Danmark. 3:273–301.

———, D. Müller, and J. Nielsen. 1954b. Graphic presentation of dry matter production in European beech. Det. forst. Forsøg. i Danmark. 21:327–335.

Monsi, M. 1960. Dry matter reproduction in plants. I. Schemata of dry matter reproduction. Bot. Mag. Tokyo. 73:81–90.

Morris, R. F. 1948. How old is a balsam tree? For. Chron. 24:106–110.

Ovington, J. D., and W. H. Pearsall. 1956. Production ecology. II. Estimates of average production by trees. Oikos. 7:202–205.

Ovington, J. D. 1956. The form, weights and productivity of tree species grown in close stands. New Phytol. 55:289–304.

———. 1957. Dry matter production by *Pinus sylvestris*. Annals of Bot. 21:288–314.

———, and H. A. I. Madgwick. 1959. The growth and composition of natural stands of birch. I. Dry matter production. Plant and Soil 10:271–283.

ROWE, S. 1959. Forest regions of Canada. Canada Dept. North. Affairs and Nat. Res., Forestry Branch Bull. 123. 71 pp.

SATOO, T., NAKAMURA and S. SENDA. 1955. Materials for the studies of growth in stands. I. Young stands of Japanese red pine of various density. Bull. of Tokyo Univ. For. 48: 65–90. English summary pp. 89–90.

———, R. KUNGUGI and A. KUMEKAWA. 1956. Materials for the studies of growth in stands. III. Amount of leaves and production of wood in aspen (*Populus davidiana*) second growth in Hokkaido. Bull. of the Tokyo Univ. For. 52:33–51. English summary p. 51.

SENDA, S., N. KENTARO, S. TAKAHARA and T. SATOO. 1952. Some aspects of growth in stands (a preliminary report). An analysis on pine stands of different spacing. Bull. of Tokyo Univ. For. 43:49–57. English summary p. 56.

———, and T. SATOO. 1956. Materials for the study of growth in stands. II. White pine (*Pinus strobus*) stands of various densities in Hokkaido. Bull. of Tokyo Univ. For. 42:15–31. English summary pp. 29–31.

SWAIN, J. M. and F. C. CRAIGHEAD. 1924. Studies on the spruce budworm. Part I. A general account of the outbreaks and injury and associated insects. Canada Dept. of Agr. Bull. N. 37 N. S.

VINCENT, A. B. 1962. Development of balsam fir thickets in the Green River watershed following the spruce budworm outbreak of 1913–1919. Canada Dept. of For. Tech. Note 119. 20 pp.

WATSON, D. A. 1952. The physiological basis of variation in yield. Advances in Agron. 4:101.