Primary Production and Distribution of Produced Dry Matter in a Plantation of *Cinnamomum camphora**

—Materials for the studies of growth in stands. 7.—

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Contents

I. INTRODUCTION

Dry matter production of a plantation of *Cinnamomum camphora* (Lauraceae) in the Tokyo University Forest In Tiba was analysed on the same line as the previous papers.[40~45] It is very important to compare various aspects of dry matter production of different types of forest ecosystems as a basis for a better understanding of growth of forest trees. Many works have been made on the biomass and production of forests of conifers and deciduous broad-leaved forests since the work of BOYSEN JENSEN and MÜLLER[2], and considerable number of papers were already published. However, when the field work of the present study was made in 1956, works on the forests of evergreen broad-leaved trees were not yet published, partly because such forests are not common in the countries of Europe and North America where forest sciences are well developed. In the last few years, considerable number of works on biomass and production of evergreen broad-leaved forests have been published. On tropical forests, works on various forest types in Thailand[14, 30, 31, 32], on a tropical rain forest in Côte D'Ivoir[23], on montane rain forests[28, 29] and mangroves[4] in Puerto Rico were published. On evergreen broad-leaved forests of temperate zone, works in Osumi Peninsura in southern Japan were published[12, 15, 52], but all these works were made on mixed forests consisted of many species. As for somewhat pure stand, works on natural forests of *Castanopsis cuspidata*[10, 11, 46, 49, 51] and works

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on natural forests of *Cameria japonica*[37] were published and the last three of them[10, 11, 37] were summarized by the authors themselves along with other materials[9]. These natural forests are also not so simple as plantations in structure and in species composition. However, studies on even-aged pure stand have not been made except works dealing with very young plantations of *Acacia mollissima*[47, 50] which is an exotic species of special nature. In most of these works, merely biomass and production of tree layer were estimated but detailed analysis was not made. It is desirable to work with forests of simple nature as the first step of this kind of works.

The author wishes to appreciate with thanks the assistance given by Mr. Y. KASUYA in the field works.

II. THE PLANTATION

The plantation of *Cinnamomum camphora*, in which the present work was made, located in the section b, compartment 17, of the University Forest. The place is called Oppara. The approximate longitude and latitude are 140°09'E and 35°09'N. Altitude is about 200 m above sea level. According to the record from 1944 to 1953 of the meteorological observatory of the University Forest at Kiyosumi, about 5 km south of the plantation, monthly mean temperature was highest in August (25.4℃) and lowest in February (4.5℃), and annual precipitation was about 2300 mm. This plantation located in a little inland and natural vegetation around the plantation contained more deciduous

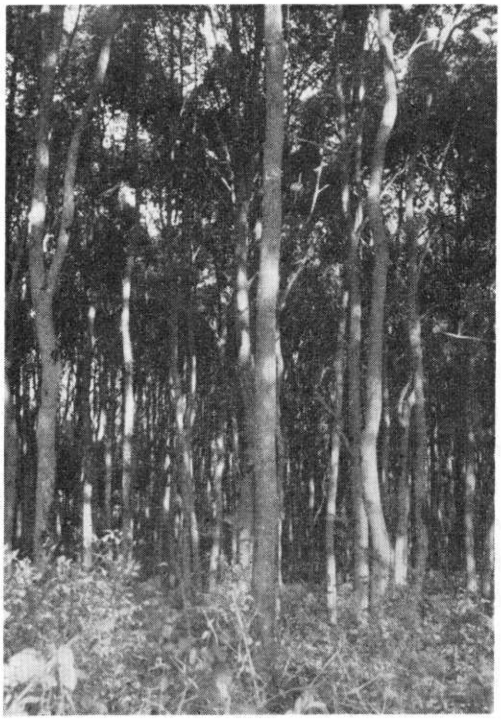

Fig. 1. The stand of *Cinnamomum camphora*.

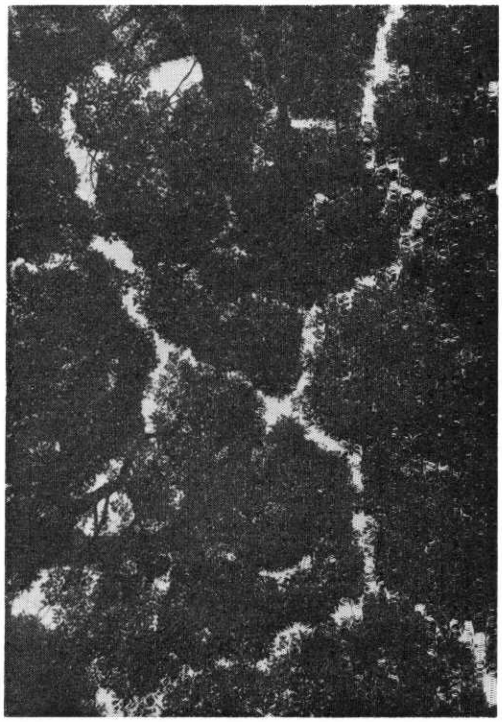

Fig. 2. Crown canopy of the stand of *Cinnamomum camphora*.

elements than in Kiyosumi. The plantation was on a flat hill of diluvium and site quality was ranked as medium.

C. camphora trees were planted in 1910 under the protection of *Pinus thunbergii* trees which had been planted aforehand in 1907, to avoid cold damage, and then pines were gradually removed and the plantation was changed into a pure stand of *C. camphora.* Still at the time of the field work, some of the planted *P. thunbergii* trees and natural *P. densiflora* trees which invaded at the time of planting remained in some parts, but most part of the plantation was a pure stand of *C. camphora.* The study was made on a part of pure stand. Thinning was not made for a long years before the field work. The forest is shown by the photograph of Fig. 1. Foliage distributed only in the upper part of the canopy. Between the foliage of each tree there was a gap of nearly the same width, and crown of different trees did not intermingle each other, as shown by the photograph of Fig. 2. The sample plot covered an area of 0.97 hectare. The outline of the stand is presented in Table 1, and frequency distribution of diameter breast high is shown by Fig. 3.

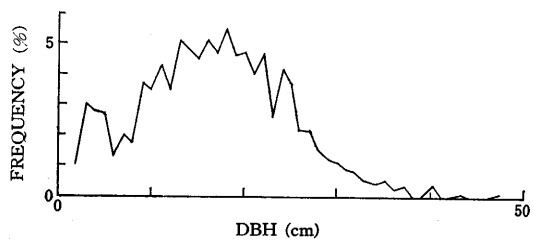

Fig. 3. Percentage distribution of diameter breast high.

Table 1.

Age	D. B. H. (cm)	Height (m)	Basal area (m^2/ha)	Number of trees/ha
46	18.2	16.6	32.35	1,250

III. METHOD

Field work was carried out in July, 1956. At the time of the field work, leaves of *C. camphora* developed fully but growth of the current season was not yet completed. Of all trees in the sample plot, diameter breast high was calipered to the nearest centimeter, and 15 sample trees were selected according to the URLICH-II method. After felling each sample tree, height was measured and positions of branches were recorded. When, in the crown canopy, the main stem was not to be clearly distinguished, strongest one in the direction of trunk was assumed as stem. The height-diameter curve of sample trees is shown by Fig. 4. All leaves were immediately stripped off, weighed, mixed thoroughly, and samples of 20~30 g were taken. Dry weight and area of the leaf samples were determined in the laboratory, to obtain the basis of conversion of fresh weight into dry wight and area. Dry weight was determined by drying the samples at 85℃ for 48 hours and area was determined by means of dot-counting method[25]. All of current year shoots were cut off and weighed, and then mixed thoroughly and samples of 20~30 g were taken. Dry weight of them were determined in the laboratory by drying the

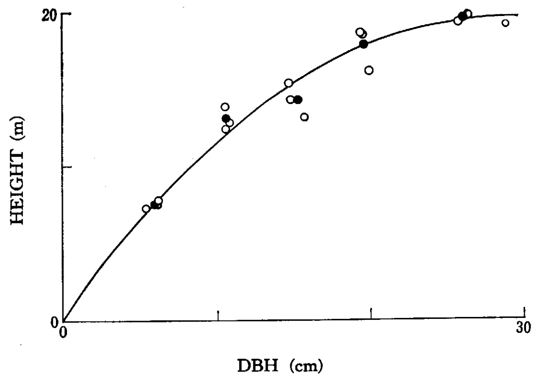

Fig. 4. The relation between the tree height and diameter breast high of sample trees. open circles: sample trees, filled circles: mean of each diameter class.

samples at 85℃ for 72 hours, and volume was determined by replacing water, to obtain the basis of conversion of fresh weight into dry weight and volume. All branches older than one year were cut off and separated into three classes by diameter: below 1 cm, from 1 to 5 cm, and above 5 cm, (if any). They were weighed separately. From branches below 1 cm, samples of 25~85 g were taken and their relative growth rate of cross sectional area for the latest one year, for 1955, was determined.

From branches between 1 and 5 cm, from 2 to 10 discs, depending on the size of the sample tree, were taken and weighed separately, and the relative growth rate of cross sectional area for the latest two years, for 1954 and 1955, was determined. From these growth rates increment of whole branches below 5 cm was estimated. For branches above 5 cm in diameter, discs were taken from all branches at an intervals of 1 m, weighed and increment for the latest two years, for 1954 and 1955, was determined in the method similar to stem analysis. These samples and discs were weighed immediately after taking and dry weight and volume of them were determined afterward, to obtain the basis for conversion of fresh weight into volume and dry weight and also volume into dry weight. Discs from stems were taken at the height of 0 m (ground level), 0.3 m, 1.3 m above ground, from breast height to the lowest branch they were taken at every 2 m, and within the crown at every 1 m. From these discs volume growth of stem was determined by means of stem analysis. Volume was converted into dry weight and fresh weight using the conversion factor determined on the discs which were treated as the discs from branches. Bulk density of discs averaged 0.585.

Biomass of undergrowth was determined by five sample plots of 1×1 m. All plants in the plots were clipped off and dry weight and area of leaves and dry weight of other parts were determined for each species. Of woody plants, increment in woody parts was determined by means of stem and branch analysis, on some subsamples.

IV. BIOMASS

1. Tree layer

A. Estimations

Two methods were used for the estimation of the standing crop of the tree layer. One is principally the same as the method presented by KITTREDGE[16] for the estimation of leaf mass of forest stand. This method can be used not only for the estimation of the amount of foliage leaves but also for the estimation of the amount of other parts[40, 42, 43, 44]. The estimation of the amount of parts of trees per hectare were made by the following way: determining the regression equation representing the allometric relations between diameter breast high and amount of the parts of the sample trees, calculating the amount for each diameter from the equation, multiplying the amount per tree with the number of trees per hectare of corresponding diameter, and summing up the products.

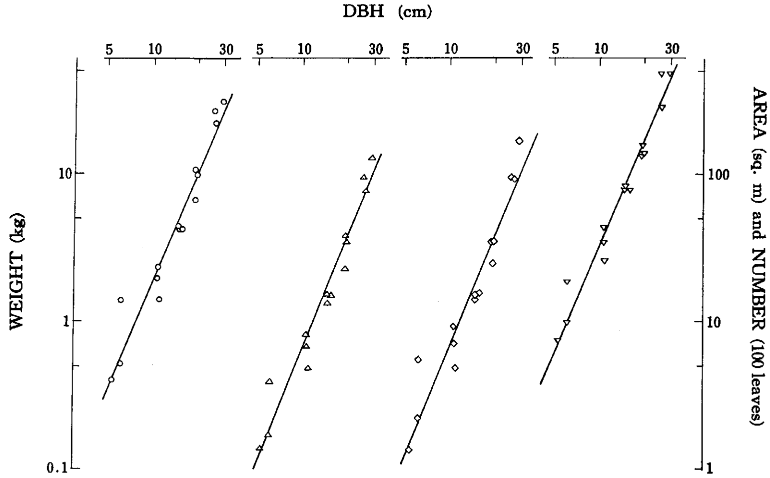

Fig. 5. The relations between diameter breast high and amount of foliage leaves of sample trees.
circles: fresh weight, triangles: dry weight, squares: area, inverted triangles: number.

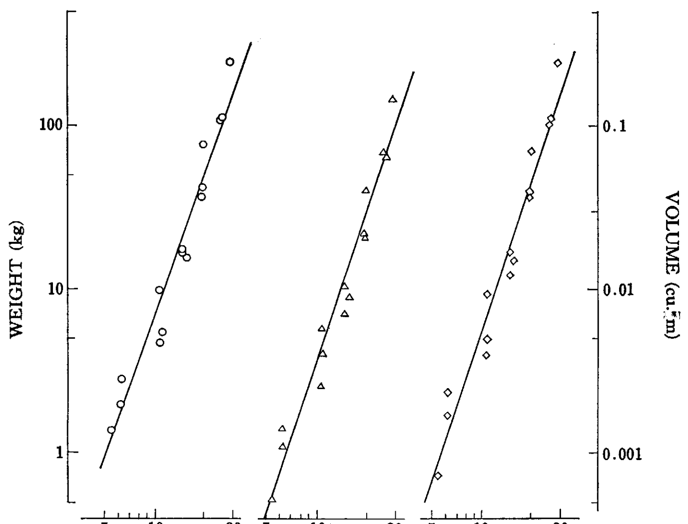

Fig. 6. The relations between diameter breast high and amount of branches of sample trees.
circles: fresh weight, triangles: dry weight, squares: volume.

The relations between the diameter breast high (D cm) and the amount of part of trees (W) are shown by Figs. 5~9, and expressed by the equation

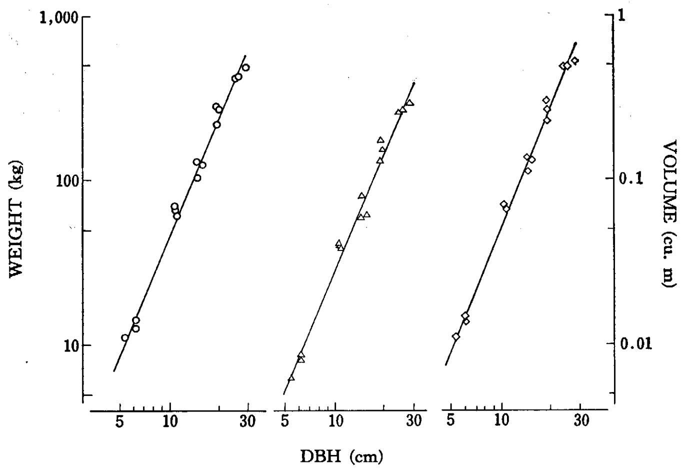

Fig. 7. The relations between diameter breast high and mass of stems of sample trees. See the explanation of Fig. 6.

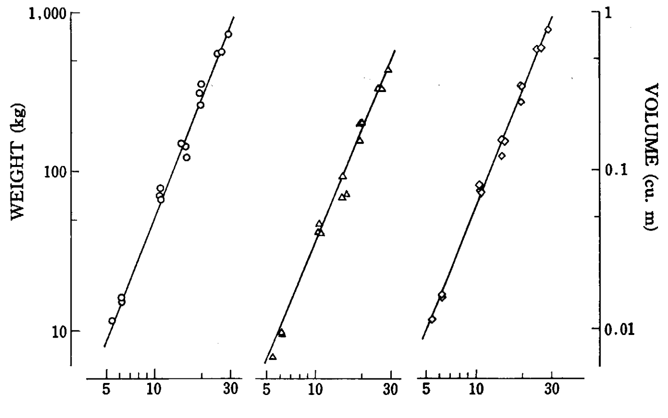

Fig. 8. The relations between diameter breast high and mass of non-photosynthetic systems of sample trees. See the explanation of Fig. 6.

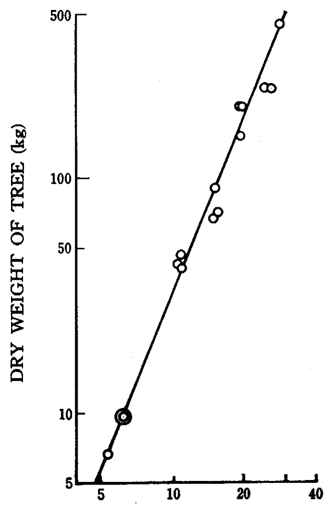

Fig. 9. The relation between diameter breast high and dry weight of sample trees.

$$\log W = b \log D + a \quad \cdots\cdots (1)$$

where a and b are constants. The constants for the amounts of parts of trees and whole trees are determined by means of least square and presented in Table 2. By means of the equation (1) and the constants in Table 2, the amount per tree for each diameter were calculated, with the frequency distribution of diameter shown by Fig. 3, the amount for 1 hectare of the stand were estimated and presented in Tables 3~5.

Table 2. Constants for the equation log $W=b$ log $D+a$ (1) for biomass estimation where D is D. B. H. in cm and W is quantity per tree.

W		Unit	b	a	Corresponding text figure
Leaf	Fresh weight	kg	2.4283	−2.1580	5
	Dry weight	kg	2.5386	−2.7451	5
	Area	m^2	2.4732	−1.6316	5
	Number		2.4089	+1.0968	5
Branch	Fresh weight	kg	2.8881	−2.0770	6
	Dry weight	kg	3.0604	−2.5244	6
	Volume	dm^3	3.0622	+0.6719	6
Stem	Fresh weight	kg	2.4221	−0.7584	7
	Dry weight	kg	2.3820	−0.9383	7
	Volume	m^3	2.4158	−3.7433	7
Non-photosynthetic systems	Fresh weight	kg	2.5031	−0.7784	8
	Dry weight	kg	2.4836	−0.9850	8
	Volume	m^3	2.5226	−3.7649	8
Total dry weight of tree		kg	2.4840	−0.9763	9

Table 3. Amount of leaves per hectare

Method	Fresh weight (kg)	Dry weight (kg)	Area (m^2)	Number
Equations in Table 2	11044.43	4073.03	42753.43	18332686
Ratio of cross sectional area	11854.67	4537.14	48834.15	18846030
	(11.0–11.9t)	(4.1–4.5t)	(4.3–4.9ha)	(18–19×10^6)

Table 4. Amount of branches and stems per hectare

Method		Equations in Table 2	Ratio of cross sectional area
Fresh weight (t)	Branches	56.466	64.294
	Stems	272.550	255.296
	Branches+Stems	329.016	319.590
	Branches & Stems (direct)	334.746	——
Dry weight (t)	Branches	35.034	37.379
	Stems	156.993	150.812
	Branches+Stems	192.027	188.191
	Branches & Stems (direct)	195.641	——
Volume (m^3)	Branches	55.305	61.169
	Stems	324.637	270.526
	Branches+Stems	379.942	331.686
	Branches & Stems (direct)	366.603	——

The other method is multiplying the sum of the amount of parts of sample trees with the ratio of cross sectional area of all trees in the stand (32.3496 square meter per hectare) to the sum of cross sectional area of sample trees (0.3492 square meter). The amounts thus estimated are presented in Tables 3~5.

The estimates by the two methods resulted slight differences. Estimates by the first method were smaller for the amount of leaves and branches and larger for the amount of stem than the estimates by the second method. The estimates for the amount of non-photosynthetic parts and for whole tree were also larger by the first method of which most parts were consisted of stem.

Table 5. Biomass of the tree layer above ground (t/ha)

Method		Leaves	Branches	Stem	Total
Equation in Table 2	Amount	4.073	35.034	156.993	196.100
	Percentage	2.1	17.9	80.0	100
Ratio of cross sectional area	Amount	4.537	37.379	150.812	192.728
	Percentage	2.4	19.4	78.2	100

B. Leaf biomass

Among these estimates, the amount of stem is an accumulation of increment for many years and the amount of branches is easily affected by stand density[41,45], but amount of leaves are not affected by many factors[21], and can be compared with other stands. Leaf biomass of this stand was, as shown by Table 3, 11.0~11.9 metric tons per hectare in fresh weight, 4.1~4.5 tons per hectares in oven-dry weight, 4.3~4.9 as leaf area index or 18.3–18.8 millions in number. For the purpose of comparison, values of leaf biomass of evergreen broad-leaved forests were collected from publications and shown in Table 6. The value for this stand is not so large as compared with others, even when the leaf biomass of the undergrowth is taken into account.

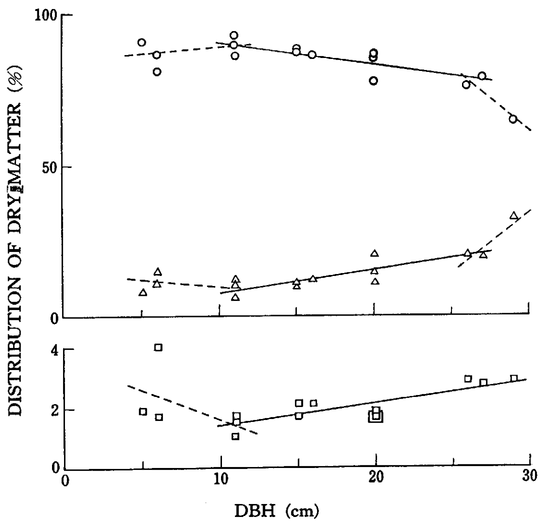

Fig. 10. Distribution of biomass into parts of trees in relation to diameter breast high. Circles: stem, triangles: branches, square: leaves.

C. The percentage distribution of dry matter within the tree layer.

As shown by Table 5, of biomass of the tree layer, about 2% was leaves, about 18~19% was branches and 78~80% was stems. However, among individual trees, the percentage distribution was different by tree size such as diameter, height and amount of leaves per tree. As shown by Fig. 10, in the range of diameter breast high between 10 and 26.5 cm, percentage of stem decreased

Table 6. Leaf biomass of evergreen broad-leaved forests

	Locality	Tree layer		Undergrowth		Reference
		Dry weight t/ha	Leaf area index	Dry weight t/ha	Leaf area index	
Tropical forest	Belgian Congo	6.5	—	—	—	1
Tropical rain forest	Côte D'Ivoir	2.5	3.2	—	0.5	23
Tropical forest	Ghana	7.0	—	—	—	27
Lower montane rain forest	Puerto Rico	8.1	6.4	—	—	29
do.	do.	7.3	13.9	—	—	28
Red mangrove	do.	5.4	—	—	—	4
do.	do.	7.8	—	—	—	4
"Wolkenwald"	Venezuela	—	1.5	—	0.4	53
"Quebradawald"	do.	—	4.4	—	1.8	53
Tropical rain forest	Thailand	8.2	—	—	—	14
Evergreen gully forest	do.	14.5	12.1	—	—	30
Tropical rain forest	do.	7.7	10.7	0.6	1.6	31
do.	do.	8.2	11.4	0.3	0.9	31
do.	do.	7.8	10.8	0.6	1.5	31
Dry evergreen forest	do.	11.8	—	—	—	32
do.	do.	8.9	—	—	—	32
Castanopsis cuspidata forest	Japan	10–20	5–9	—	—	10
do.	do.	12.4	—	—	—	10
do.	do.	6.1	—	—	—	10
do.	do.	10.9	—	—	—	10
do.	do.	11.0	9.7	—	—	9
do.	do.	9.9	9.5	—	—	9
do.	do.	6.4	5.5	—	—	9
do.	do.	6.0	5.2	—	—	9
do.	do.	8.4	7.2	—	—	9
do.	do.	7.4	8.0	—	—	46
do.	do.	7.4	8.0	—	—	49
do.	do.	11.4	12.5	—	—	51
Camellia japonica forest	do.	7.5	6.2	—	—	9
do.	do.	7.1	5.6	—	—	9
do.	do.	7.6	6.8	—	—	9
do.	do.	7.3	—	—	—	37
do.	do.	6.0	5.4	—	—	37
do.	do.	6.0		—	—	37
do.	do.	7.4		—	—	37
Acacia mollissima plantation	do.	9.9	9.7	—	—	47
do.	do.	8	—	—	—	50
Quercus-Rapanaea mixed forest	do.	8.8	6.9	—	—	9
do.	do.	12.0	9.4	—	—	9
do.	do.	9.9	7.7	—	—	9
Quercus-Camellia mixed forest	do.	7.1	7.5	—	—	9
do.	do.	5.9	7.0	—	—	9
do.	do.	6.3	6.8	—	—	9
do.	do.	6.4	6.2	—	—	9
Distvilium racemosum & others	do.	11.4	8.8	—	—	12
do.	do.	11.4	8.8	—	—	15
do.	do.	8.9	—	—	—	15
Machilus-Shiia type	do.	10.1–13.1	7.3–9.6	—	—	15
Shiia, Lithocarpus & others	do.	8.7	7.6	—	—	52
Lithocarpus, Machilus & others	do.	13.6	10.6	—	—	52
Machilus, Distylium & others	do.	11.1	8.2	—	—	52

(significant at 1% level) and percentage of branches increased (significant at 5% level) with increasing diameter. Percentage of leaves increased with diameter (significant at 1% level) among trees larger than 10 cm of diameter. In the other diameter ranges, the trends were not significant. Fig. 11 shows the percentage distribution of the three parts in relation to height of the trees. If smallest trees, 7~8 m in height, were excluded, with increase of height percentages of branches and leaves increased (significant at 5% level) and percentage of stem decreased, but the trend for stems was not statistically significant. With increase of leaf area per tree, percentages of leaves and of branches in total tree biomass increased and the percentage of stems decreased. These trends were statistically significant (1% level). In short, it may be said that the percentages of branches and of leaves were larger and the percentage of stem was smaller in larger trees, *i. e.*, larger trees had more crown in relation to the size of stem than smaller trees.

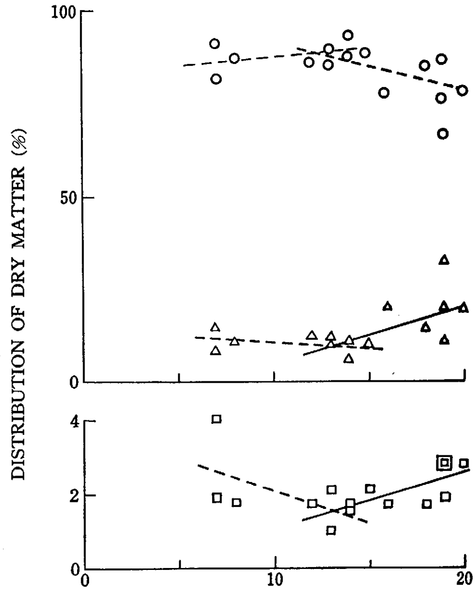

Fig. 11. Distribution of biomass into parts of trees in relation to height of trees. See the explanation of Fig. 10.

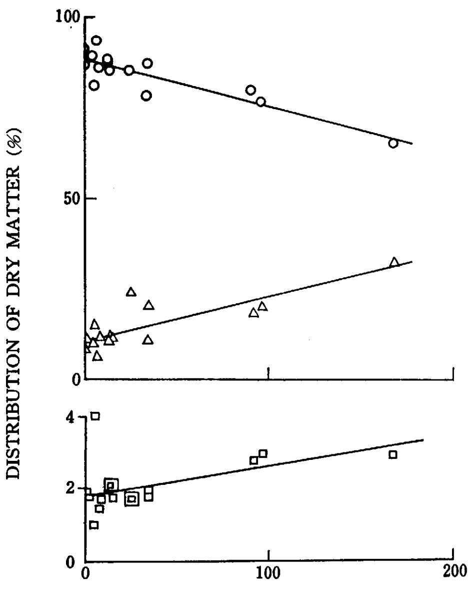

Fig. 12. Distribution of biomass into parts of trees in relation to leaf area. See the explanation of Fig. 10.

2. Undergrowth.

The undergrowth consisted of very abundant species: in five sample plots of 1 meter square, there were 25 species of woody plants, 13 species of herbacious plants, and 16 species of vines. Important member of these 54 species are shown in Table 7. Biomass of the undergrowth per 1 square meter is shown by Table 8.

3. Biomass of the ecosystem.

Table 9 sums up the biomass of this ecosystem, which amounted to about 200

Table 7. Important species of undergrowth

1. Frequency	5:	*Rosa buergeri, Trachelosperum asiaticum, Oplismenus undulatifolius* var. *japonicus*
	4:	*Hedera rhombes, Akebia trifoliata, Bladhia japonica, Dioscorea japonica*
	3:	*Lindera umbellata, Prunus incisa, Acer crataegifolium, Rhus ambigha.*
2. Number per sq. m	50<	*Rosa buergerii, Trachelosperm asiaticum,*
	50–40:	*Oplismenus undulatifolius* var. *japonicus,*
	40–30:	*Bladhia japonica*
	10–5:	*Hedera rhombes*
3. Dry weight per sq. m	20<	*Rosa buergeri*
a. dry wt. of leaves	10–5g:	*Quercus serrata, Deutzia crenata, Prunus incisa, Castanea crenata, Dioscorea japonica*
	5–3:	*Bladhia japonica, Trachelosporum asiaticum, Oplismenus undulatifolius* var. *japonicus, Lindera umbellata, Pteridium aquilinum, Aucuba japonica*
b. dry wt. above ground	40g<	*Castanea crenata, Prunus incisa, Deutzia crenata*
	40–30:	*Rosa buergeri, Quercus serrata*
	20–10:	*Dioscorea japonica, Bladhia japonica*
	10–5:	*Aucuba japonica, Lindera umbellata, Oplismenus undulatifolius* var. *japonicus, Tracheloperum asiaticum, Rhododendron kempferi, Weigela coraeensis, Rosa polyantha, Akebia trifoliata, Lonicera gracilipes* var. *glabra*

Table 8. Biomass of undergrowth per sq. m

	Number of species	Number of plants	Fresh weight (g)	Dry weight			Leaf area sq. m
				C* (g)	F* (g)	Total (g)	
Woody species:							
above 50 cm	4.2	10.8	719.2	168.06	46.82	214.88	0.669
below 50 cm	4.4	85.8	185.4	25.40	26.90	52.30	0.384
Herbacious spp.	3.4	54.2	85.0	0.36	20.20	20.56	0.505
Vines	7.4	80.2	217.2	37.20	20.40	57.60	0.272
Total	19.4	231.0	1206.8	231.02	114.32	345.34	1.830
Maximum	22	373	1673	438.4	153.2	591.6	2.241
Minimum	16	126	742	112.4	59.1	226.6	0.852

* C: non-photosynthetic system, F: photosynthetic system

metric tons per hectare and 98% of it was tree layer. Leaf biomass was 5.2 metric tons per hectare of which 80% belonged to the tree layer. Leaf area index of this stand was 6.1, of which 80% belonged to the tree layer. In total biomass, undergrowth could be neglected, but in leaf biomass, undergrowth which is rather neglected in many of the studies of the same nature as the present one, is too large to be neglected.

Table 9. Biomass

	Dry weight (t/ha)					Leaf area index
	Leaves	Branches	Stems	Stems and branches	Total	
Tree layer (A)	4.073	35.034	156.993	193.027	196.100	4.275
Undergrowth	1.143	—	—	2.310	3.453	1.830
Total	5.216			195.337	199.553	6.105
Percentage of tree layer	78.1	—	—	98.3	98.3	70.0
Tree layer (B)	4.537	37.379	150.812	188.191	192.728	4.883
(Undergrowth)	1.143	—	—	2.310	3.453	1.830
Total	5.680	—	—	190.501	196.181	6.713
Percentage of tree layer	79.9			93.5	98.2	72.7

V. NET PRODUCTION

1. Tree layer

Dry matter production by the tree layer was estimated separetely as leaves, branches and stems, but estimation of the production as roots was not made, because of the difficulty involved and limited time.

A. Leaves

Every year in late April or in early May, new leaves unfold and old leaves are shed, thus this tree species renews its leaves annually and has leaves produced in one year. As new leaves had already fully developed in July when sampled, dry weight of leaves in Table 2 was assumed as annual production. However, though the leaves seemed to be mature when sampled, it is possible that there is some further increases of the weight of leaves with lapse of time. This might result underestimate of leaf production, though some parts of the matter in leaves could be recovered before they are shed. There are also possibility of underestimate by not measuring leaves already shed or grazed by larvae of insects, but damaged leaves were not found and there was not any serious cause to lose leaves.

B. Branches and stems.

Dry matter production as stem was estimated by converting the mean of volume increment for 1954 and 1955 into dry weight with bulk density of wood for each tree. Volume increment was determined by means of stem analysis. For the estimation of dry matter production as branches, different methods were used for different parts of branches. Branches consisted of two parts: new shoots which contain only the products of the current year and older branches which contain the products of the current year as well as products of the past one to several years. Dry weight of the current year shoots was assumed as the annual production, though there is possibility of underestimate due to further growth of them. For the older branchs less than 5 cm in diameter, relative growth rate of samples was determined for each size class of branches, and dry weight of the corresponding size class of branches was multiplied by it and the product was assumed as dry matter production of each size class. Dry matter production as branches larger than 5 cm in diameter was determined in the same way as stem, piece by piece.

Dry matter production as stems and branches per unit area was estimated by two methods which are the same as those in the estimation of biomass. The relations between diameter breast high of sample trees (D cm) and growth of branches and stems (W) are shown by Figs. 13~16, and expressed by the equation (1). Constants in the equation (1) are shown in Table 10 for each part and for different expressions of growth. With the equations and the stand table showing the distribution of diameter, dry matter production and volume increment were estimated and shown in Table 11. Table 11 also shows the estimates with the value for sample trees and the ratio of cross sectional area of all trees in one hectare of stand to sample trees. For all estimates, the estimation with the ratio of cross sectional area resulted larger value than with allometric

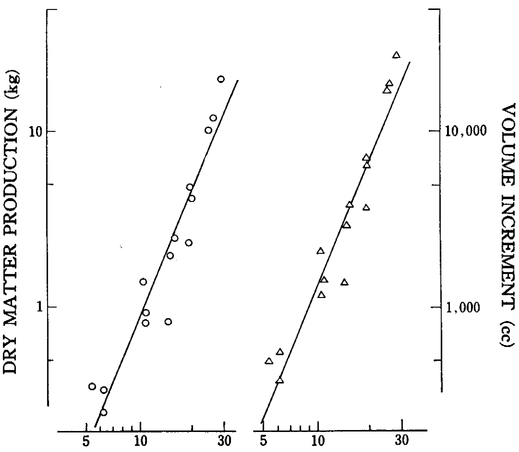

Fig. 13. Increment in stems in relation to diameter breast high of sample trees. circles: dry matter, triangles: volume

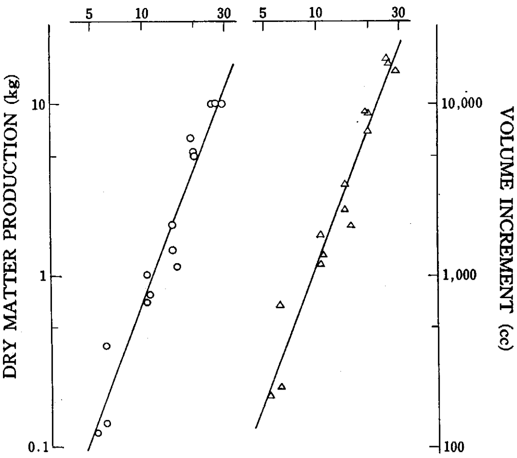

Fig. 14. Increment in branches in relation to diameter breast high of sample trees. See the explanation of Fig. 13.

Table 10. Constants of the equation, $\log W = b \log D + a$, for estimation of production, where D is diameter breast high in centimeter and W is the quantity per tree.

		Unit	a	b	Corresponding text figure
Branch	Volume	cc	2.3931	+0.7144	14
	Dry matter	g	2.3671	+0.5685	14
Stem	Volume	cc	2.6685	+0.3864	13
	Dry matter	g	2.6577	+0.1590	13
Non-photosynthetic systems	Volume	cc	2.5281	+0.8718	15
	Dry matter	cc	2.3775	+0.8367	15
Whole tree		g	2.5256	+0.8205	16

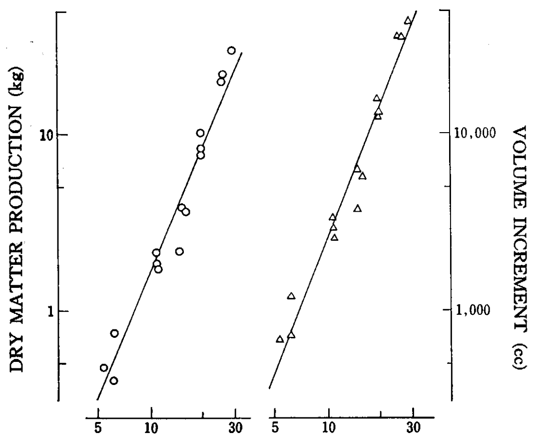

Fig. 15. Increment in woody tissues in relation to diameter breast high of sample trees. See the explanation of Fig. 13.

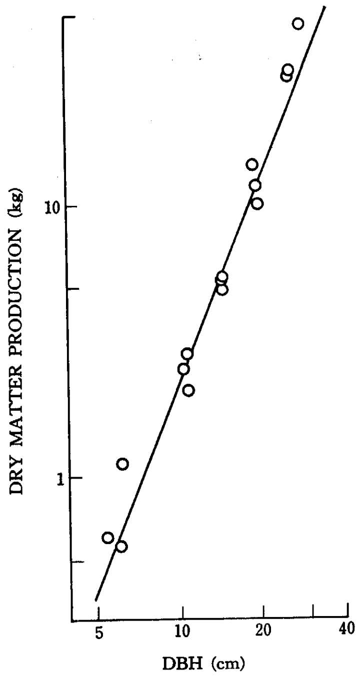

Fig. 16. Dry matter production in relation to diameter breast high of sample trees.

Table 11-A. Increment of woody tissues (aboveground only) m^3/ha

Method	Branches	Stems	Branches +Stems	Branches & Stems
Equations in Table 10	7.451	8.225	15.676	16.104
Ratio of cross sectional area	8.673	8.207	16.880	—

Table 11-B. Dry matter production (aboveground only) kg/ha

Method		Equations in Table 10	Ratio of cross sectional area
Tree layer	1. Leaves	4073.03	4537.14
	2. Branches	4864.45	5740.85
	3. Stems	4700.81	4736.43
	4. Branches+Stems (2+3)	9565.26	10477.28
	5. Branches & Stems (direct)	9312.26	—
	6. Total (1+2+3)	13638.29	15014.42
	7. Total (1+5)	13385.39	—
	8. Total (direct)	14268.19	—
Undergrowth	9. Leaves	1143.2	
	10. Non-photosynthetic systems	480.4	
	11. Total (9+10)	1623.6	
Total	12. 6+11	15261.9	16638.0
	13. 7+11	15010.0	—
	14. 8+11	15891.8	—

relation, though the difference was slight. Dry matter production by the aboveground parts of the tree layer was estimated as 13.4~15 tons per hectare. Volume increment in the stems was estimated as 8.2 cubic meters

2. Undergrowth

Undergrowth was very complicated in its composition and estimation of dry matter production by them is very difficult, and so in many cases it is neglected or given up. However, as shown by Table 9, it has considerable amount of leaves and production by them cannot be neglected. Life span of leaves of evergreen member of undergrowth is not known, but it was assumed that their leaves are renewed annually. All of herbaceous plants were counted as the products of the current year. From the measurements of samples, it was assumed that one tenth of woody parts of woody plants higher than 50 cm and one third of woody parts of those lower than 50 cm and vines were considered as the products of the current year. The estimate of dry matter production by undergrowth amounted to 114.32 g of leaves and 48.04 g of woody parts per square meter, in total 162.36 g per square meter or 1.62 tons per hectare. Net production as the aboveground parts of this ecosystem was estimated as 15.1~16.6 tons per hectare, as shown by Table 12.

Table 12. Annual net production (t/ha)

	Tree layer	Undergrowth	Total
Leaves	4.1– 4.5	1.1	5.2– 5.6
Non-photosynthetic systems	9.3–10.5	0.5	9.9–11
Total	13.4–15.0	1.6	15.1–16.6

Dry matter production as roots and other subterranean parts were not estimated. If it is one fifth of the production as stem and branches, as assumed by many authors, it may be 1.9~2.1 tons per hectare, and net production by this ecosystem may be 17~19 tons per hectare per annum.

3. The efficiency of solar energy utilization.

Knowing the annual amount of the solar radiation reaching the surface of a plant community and energy content of the primary production of the plant community, the over-all efficiency of the solar energy utilization for the production of organic matter can be calculated if respiratory activity is excluded. Estimation of the efficiency of energy conversion by forest ecosystems was made recently by many authors[3,6,7,23,34,35,46,47,48]. MÜLLER and NIELSEN[23] reported an efficiency of 0.8% of visible light for a tropical rain forest. They also reported a high efficiency of 4.6% for *Eucalyptus saligna* which was calculated from the data of FAO. According to HELLMERS and BONNER[7], the efficiency of agricultural crops ranges from 2 to 2.2%, of the visible light regardless of kind of crop and locality. TADAKI[47] obtained a high efficiency of 1.3% for whole year and 1.9% for the growing season of the total incident solar energy by a plantatoin of *Acassia mollissima* in Japan. These values are equivalent to about 2.9 and 4.2% of the visible light, respectively.

The total solar and sky radiation on a horizontal surface in Tokyo, which is the nearest observatory to the site of the present study, for the year previous to the field work, from April 1955 to March 1956, was 90.417×10^8 Cal., according to the Geophysical Review published by Japan Meteorological Agency, Tokyo. Assuming that 1 g of dry matter is equivalent to 4 Cal., (according to the measurements by OVINGTON and HEITKAMP[35], it ranged from 3.317 to 5.180 Cal.), the net production of this ecosystem was converted into energy:

tree layer: 13.4~15.0 t=53.6-60.0$\times10^6$ Cal.
undergrowth: 1.62 t=6.5$\times10^6$ Cal.
in total: 60.1~66.5$\times10^6$ Cal.

These values are equivalent to 0.66~0.74% of the total incident solar energy for a year and 1.00~1.11% of the total incident solar energy of the growing season (April-October). Photosynthesis in the wintertime in this climate is very slight and sometime exceeded by respiration[24]. Assuming that the visible light of 4000~7000 Å is 45% of the total indicent light, as MÜLLER and NIELSEN[23] did (44.3% according to BRAY[3]), the efficiency is 1.47~1.64% for a whole year and 2.22~2.47% for the growing season. The latter value is very close to the value calculated by HELLMERS and BONNER[7] of *Pinus silvestris*[33] and *Fagus silvatica*[21].

VI. DISTRIBUTION OF PRODUCED MATTER WITHIN THE ECOSYSTEM

Yield of timber by a forest ecosystem depends not only on the photosynthetic efficiency or gross production and net production, but also on the percentage of distribution of the net production into stemwood. Therefore, to know the reason why the timber yield is large in some case and small in the others, and to improve the silvicultural practices, information on the distribution of produced matter into parts of ecosystem is very important.

1. Distribution into parts of the ecosystem.

Pattern of the distribution or distribution ratio of net production into the parts was induced from Table 11. Distribution ratio differed slightly by the method of estimation of net production, as shown by Table 13. Of 15.1~16.6 tons per hectare of the annual

Table 13. Distribution of produced matter (%)

Method of estimation of increment		Within woodland		Within tree layer			Within woody tissues of tree layer	
		Tree layer	Under-growth	Stems	Branches	Leaves	Stems	Branches
Ratio of cross sectional area		90.2	9.8	31.6	38.2	30.2	45.3	54.7
Equations in Table 10	1*	89.4	10.6	34.5	35.6	29.9	49.1	50.9
	2*	89.2	10.8	—	—	—	—	—
	3*	89.8	10.2	—	—	—	—	—

*1: estimating each part separately, 2: estimating leaves and others separately, 3: estimating as total, from the equations.

net production of the ecosystem (aboveground) about one tenth was distributed into the undergrowth and about nine tenth were distributed into the tree layer. This ratio, of course, differes by the penetration of light through the crown canopy which is different with species and age of trees.

Of 13.4~15.0 tons per hectare of annual net production as aboveground parts of the tree layer, about 30~35% were distributed into stems, about 35~40% into branches, and about 30% into leaves. The distribution into stem was only one third of production of the tree layer excluding the roots, and it becomes far less if roots and undergrowth were taken into account. The distribution ratio within the tree layer varies with tree species and silvicultural practices. Mean of distribution ratios of twelve stands of four coniferous species and of five stands of three broad-leaved species were shown tentatively in a table in a previous paper[39]. The distribution ratio into leaves is not so much different from the average, but the one into stem is smaller and the one into branch is larger than average, though the mean value in the table in the previous paper is based on a few examples and more data are needed. From the viewpoint of forestry in which prodution of stemwood is the objective, this stand is not efficient, more than one half of produced non-photosynthetic system was branches. Only one third of net production made stemwood, of which still some more parts are discarded as waste. If we consider a forest ecosystem as a factory of timber, "production cost" of this "factory" is very high.

2. Distribution in relation to the size of tree.

The pattern of distribution was related to the size of trees, as it is very important, especially in the selection of trees in thinning, to know the size class having highest distribution into the stems. As the dimensions of trees, leaf area per tree was used along with diameter and height which are used very often and easier to measure. Leaf area represents the dominance of trees in the crown canopy better than diameter and height, though it is not possible to measure for the practical purposes.

A. Relation to diameter.

The upper half of the figure 17 shows the relation of distribution ratio into each part to diameter breast high. For the

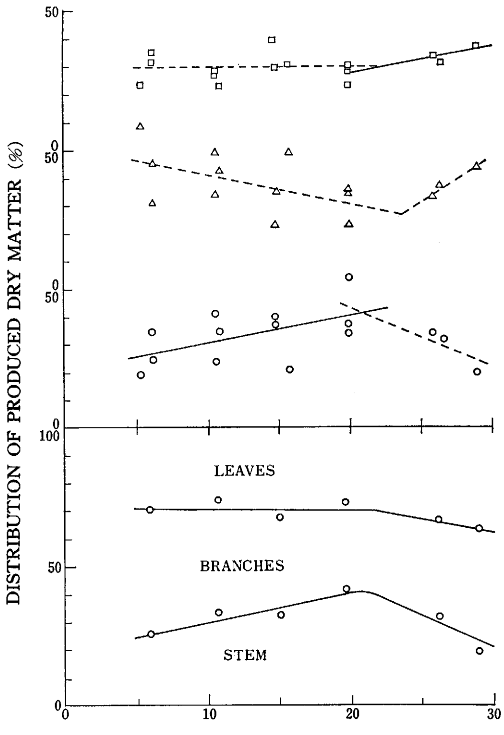

Fig. 17. Distribution of produced dry matter into parts of trees in relation to diameter breast high.
circles: stem, triangles: branches, squares: leaves.

diameter ranges where linear relation is observed, regressions were determined. In the figure, solid lines represent significant regressions and broken lines mean insignificant. Up to 20 cm of diameter, with increase of diameter breast high, distribution into the stem increased significantly, distribution into the branches seemed to decrease though insignificant, but distribution into the leaves was not affected by the diameter. Above this limit, distribution into the leaves increased significantly with increase of diameter, but the distribution into the stem and branches did not show significant trends, though it seems that distribution into the branches increased and distribution into the stem decreased. Lower half of the figure shows the pattern of distribution derived from the above results. As the sample trees could be divided into six diameter classes, mean values of each class are shown. From this figure, it can be seen that the influence of stem diameter on distribution ratio is less on the leaves and larger on the stems and branches; it seems that there is an optimum range of diameter for higher distribution into the stems.

B. Relation to tree height.

Sample trees can be divided into three height classes: lower or dominated tree class which consisted of three trees of height between 7.1 and 7.6 m, medium or intermediate tree class which consisted of seven trees of height between 12.2 and 16.0 m, and higher or dominant tree class which consisted of five trees of height between 18.2 and 19.3 m. The distribution ratio of the three classes are shown in Table 14. The distribution into the stem is larger in the higher tree class and the distribution into the branches was higher in the lower tree class, but distribution into the leaves was not much different with tree class. However, among the trees of the higher class, distribution into the stem decreased with increasing diameter or leaf area.

Table 14. Distribution of produced dry matter within tree in relation to height

	Height (m)		Distribution (%)		
	Mean	Range	Stem	Branches	Leaves
Lower	7.4	7.1- 7.6	28.1	42.5	29.4
Medium	13.9	12.2-16.0	33.0	38.0	29.1
High	18.9	18.2-19.3	35.4	34.3	30.3

C. Relation to leaf area of tree.

Upper half of Fig. 18 shows the relation of the distribution ratio into each part to the leaf area of tree. As in the case of diameter, solid lines represent the significant regressions and broken lines mean that regressions are statistically not significant. Among trees with more than about 20 square meter of leaf area, with increasing leaf area the produced dry matter distributed significantly more into leaves and significantly less into stems. Distribution into the branches seems to increase with increasing leaf area, though the regression was not significant. Among trees with leaf area less than about 40 square meter, with increasing leaf area, distribution into the stem increased significantly and distribution into the branches decreased significantly, but the influence of leaf area on the distribution into the leaf was not clear. The lower half of Fig. 18 shows the pattern of the distribution into each part derived from the above result. Trees were divided into five classes by their leaf area and the mean value of each class are also shown by circles. It may be said that the distribution into the leaves increased with increase of leaf area of tree, and tree with leaf area of about 36 square meter has the highest distribution into the stem and lowest distribution into the branches. As the average leaf area per tree in this stand was 34 or 39 square meters, depending on the method of estimation, trees with average leaf area had highest distribution to the stem.

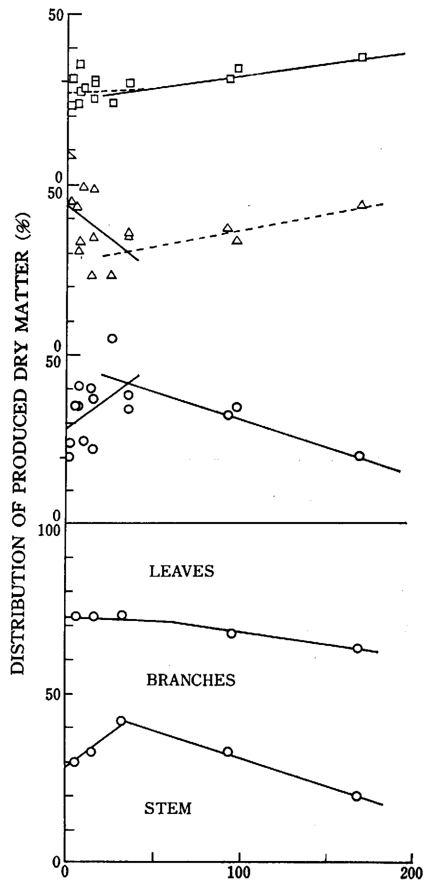

Fig. 18. Distribution of produced dry matter into parts of trees in relation to leaf area. See the explanation of Fig. 17.

Diameter breast high of trees with about 36 square meters of leaf area was a little over 19 cm, as shown by Fig. 5. Tree with diameter breast high of 19 cm, or 20 cm from Fig. 17, has a height of 18 m as shown in the height-diameter curve of Fig. 4. Tree height of 18 m belongs to the higher tree class in Table 14. From these interrelationships, it may be said that highest distribution ratio into the stem is found in trees of upper layer of the crown canopy having relatively less leaf area and diameter. Among trees of upper layer of the canopy, trees with relatively larger diameter and more leaves and branches have lower distribution ratio into the stem. If we consider these trees as "wolf trees" in thinning practice, "wolf trees" could be defined ecologically as "trees with larger crown which can produce more dry matter but the distribution ratio of produced dry matter into the stem is lower".

The pattern of distribution found here is somewhat different from the one found in the stand of *Populus davidiana*[40] and in a young stand of *Pinus densiflora* (unpublished). In these cases, in trees with less leaves and smaller diameter, produced dry matter distributed more into stems and less into branches and leaves. On this subject more informations are needed.

VII. THE RELATION BETWEEN DRY MATTER PRODUCTION AND AMOUNT OF LEAVES

In Fig. 19, the increment of dry matter in stem, leaves and branches of sample

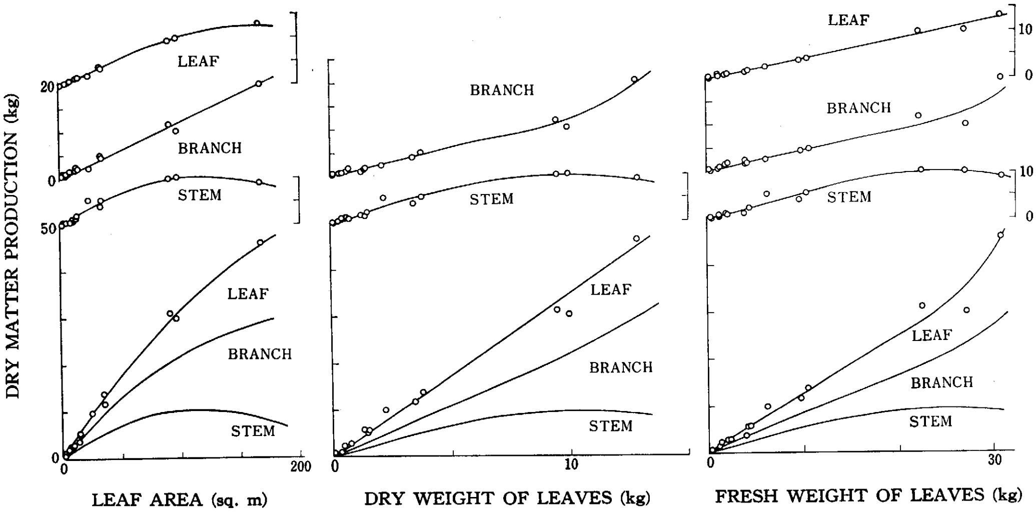

Fig. 19. Dry matter production and amount of leaves.

trees are related to the amount of leaves. Though the increment of dry matter increased with increase of leaves, the pattern of the increase differed by part of tree. With increase of leaves, the increment of dry matter in stems increased less than proportion to the amount of leaves, and in branches more than proportion to the amount of leaves, though the increment of dry matter of total aboveground parts was fairly proportional to the amount of leaves. This difference in pattern of dry matter increment by parts of tree reflects the different distribution ratio of trees of different size. This relation may be described also in another way. Table 15 shows the coefficients of variation in the dry matter increment per unit leaf. Irrespective of the expression of the amount of leaves, the coefficient of variation was largest for the increment of stem and smallest for the increment of total aboveground parts per unit leaf. This means that increment of dry matter in whole aboveground parts is fairly proportional to the amount of leaves but increment of dry matter as stem is not proportional to the amount of leaves, reflecting the differences in distribution ratio.

Table 15. Coefficient of variation of efficiency of leaves expressed as dry matter production per unit leaf

Base	Stem	Stem+Branch	Stem+Branch +Leaf
Area	40.2 (100)	27.4 (68)	21.3 (53)
Dry weight	37.0 (100)	22.2 (60)	15.8 (43)
Fresh weight	37.7 (100)	23.2 (62)	8.6 (23)

Dry matter production per unit amount of leaves, or net assimilation rate in British terminology, is shown in Table 16. Net assimilation rate was calculated with two methods; one is by dividing the value of net production in Tables 11a and 12 by the amount of leaves in Table 3, another is by determining the slope of lines passing through

Table 16. Net assimilation rate

Base	From the value for stand		Regression of amount of leaves and production
	From equations in Table 10	Cross sectional area	
Leaf area g/m	319- 334	307	338
Fresh weight g/kg	1212-1292	1275	1198
Dry weight g/kg	3262-3505	3309	3509

the origin, as the relations of dry matter production as whole aboveground part to the amount of leaves in Fig. 19 are nearly linear. There were little differences between the estimates of the two methods. Net assimilation rate per year was 1200~1300 g per 1 kg in fresh weight of leaves, 3300~3500 g per 1 kg in dry weight of leaves, and 310~340 g per 1 square meter of leaves. These values are smaller than the value for *Betula verrucosa*[36] (0.48 kg/sq. m=0.24 kg/sq. m both side) and similar to or a little less than the value for *Acacia mollissima* (3000-4000 g/kg[50] and 3000 g/kg[47]). The difference in net production between this stand and *Acacia* stands are chiefly due to the difference in the amount of leaves but not to the efficiency of leaves. Presuming that *Betula verrucosa* has leaves for six months, OVINGTON and MADGWICK[36] presented net assimilation rate per week as 18 g per square meter. As *Cinnamomum camphora* tree has leaves throughout the year, net assimilation rate per week was 6~7 g per square meter, a fairly high value considering the adverse conditions for photosynthesis in the winter. NEGISI *et al*[26] measured seasonal change of net assimilation rate of open grown young plants of pollar clones for 2 season in a nursery, reporting the value of net assimilation rate ranging from about 0.1 to 0.9 g per 10 days per square decimeter. These values are equivalent to and 63 g per square meter per week. These large values may be attained by the favorable conditions in light and soils in nursery beside the character of the tree species. KUSUMOTO[17] calculated the annual net production by leaves of *Cinnamomum camphora* from the measurements of photosynthesis and respiration of leaves in laboratory conditions and from change of light intensity and temperature throughout the year, and presented a value of 1.39 kg CO_2 per 50 square centimeter of leaves. Converting this value into dry matter by multiplying with 0.614, annual net production by 1 square meter of leaves becomes 170.7 kg. Even if the respiration by stems and branches were substracted from this value, net assimilation rate may be far larger than the value in this study. This large difference may be caused chiefly by the mutual shading of leaves in stand and favorable water supply in the laboratory conditions.

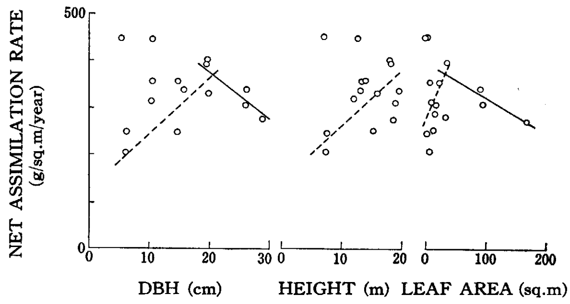

Fig. 20. Net assimilation rate in relation to the size of trees.

Fig. 20 shows the relations between net assimilation rate and size or dominance of trees expressed by diameter breast high, height, and leaf area per tree. Solid lines in the figure show that regressions are significant, and the broken lines show that regressions are significant only when they were determined for 13 trees, excluding two trees with exceptionally high net assimilation rate. Thus, among trees with diameter larger than 15 cm and with leaf area larger than 20 square meter net assimilation rate decreased with increasing size of trees, while among the trees with diameter smaller than 20 cm and leaf area smaller than 40 square meter net assimilation rate increased with size of trees if two exceptional trees were omitted. Highest net assimilation rate was attained at the diameter of 20 cm and leaf area of 30 square meters. These dimensions correspond to the dimensions of trees with highest distribution ratio of dry matter into the stems. With increase of height net assimilation rate increased, if two exceptional trees were neglected. Net assimilation rate was compared among trees of three height classes. As shown by Table 17, if the amount of leaves expressed with fresh weight, net assimilation rate of trees of the upper layer was highest and the lower layer was lowest; if amount of leaf is expressed by dry weight there was no difference in net assimilation rate among the three classes; and if amount of leaves is expressed as leaf area, trees of lower class showed lower net assimilation rate but there was little difference between the upper two classes. These differences are due to the difference in the characters of leaves by layer as shown by Fig. 21; leaves of trees of lower layer have higher water content and smaller weight per unit area or larger specific leaf area, showing characters of shade leaves.

Stemwood increment per unit amount of leaves, which is seen in many publications, was determined from Tables 3 and 11, and shown in Table 18. These values were a little higher than shade tolerant conifers which have very large quantity of leaves and

Table 17. Net assimilation rate in relation to tree height

	Height (m)		Net assimilation rate		
	Mean	Range	Per leaf area (g/sq.m)	Per fresh weight (g/kg)	Per dry weight (g/kg)
Lower	7.4	7.1– 7.6	298	1132	3523
Medium	13.9	12.2–16.0	341	1221	3517
High	18.9	18.2–19.3	342	1564	3505

Table 18. Stemwood production per unit leaf

Basis	Method of increment estimation			
	Equations in Table 10		Cross sectional area	
	Volume (cc)	Dry weight (g)	Volume (cc)	Dry weight (g)
Leaf fresh weight (kg)	745	400	692	400
Leaf dry weight (kg)	2019	1154	1809	1054
Leaf area (sq. m)	192	110	168	97

lower than shade intolerant conifers and other broad leaved trees[38]. If trees of three height classes are compared, the efficiency of leaves to produced stemwood was highest in the trees of the upper layer and lowest in the trees of the lower layer, irrespective of the expression of the amount of leaves, as shown by Table 19. The highest efficiency of leaf to produce stemwood of the trees of the upper layer is chiefly due not to higher net assimilation rate but to higher distribution ratio of produced dry matter into the stem: net assimilation rate in the trees of the upper layer was not higher than in the trees of the intermediate layer except when amount of leaves is expressed by fresh weight (Table 17), but distribution ratio of dry matter to the stem was highest in the trees of the upper layer (Table 14).

Table 19. Stemwood production per unit area in relation to tree height

	Height (m)		Stemwood production		
	Mean	Range	Per leaf area cc/sq.m	Per fresh weight cc/kg	Per dry weight cc/kg
Low	7.4	7.1– 7.6	123	472	1508
Medium	13.9	12.2–16.0	193	687	1977
High	18.9	18.2–19.3	217	841	2236

VIII. GROSS PRODUCTION

1. Loss of dry matter through respiration.

As respiration was not measured at all, some estimations were made by using published data.

A. Respiration by leaves.

A–1. Tree layer

KUSUMOTO[18] measured respiration of leaves of many evergreen broad-leaved trees, and for *Cinnamomum camphora* presented values as 0.801 mg CO_2 per 50 square centimeter per hour for sun leaves and 0.454 mg CO_2 per 50 square centimeter per hour for shade leaves. He[19] also determined the temperature-respiration curves for many evergreen broad-leaves and for *C. camphora* presented a formula

$$y=0.7t^2+1.8t+2$$

where t is temperature in ℃ and y is respiration rate. As the temperature, records from the observatory of the University Forest located at Kiyosumi, about five kilometers south of the stand, are available. With monthly mean temperature from April 1955 to March 1956, the value presented by KUSUMOTO[18] was adjusted and monthly values of respiration by unit amount of leaves were calculated, and multiplied with the amount of leaves per hectare. The value for CO_2 was converted into the value for dry matter by multiplying the value for CO_2 with 0.614, assuming that starch is decomposed.

The value of respiration by KUSUMOTO[18] was given for sun and shade leaves separately, but the amount of leaves for the present study is given only as total amount of leaves. Because sun and shade leaves are rather a nature of leaves changing continuously by the degree of shading in the crown canopy, it may not be possible to divide all leaves in the canopy clearly into sun and shade leaves. As it was not possible to estimate the amount per hectare of sun and shade leaves separately, MÜLLER and NIELSEN[23] assumed that, in a tropical rain forest, all trees over 15 m of height have only sun leaves and other lower trees have only shade leaves, and estimated the respiration loss of the stand. TADAKI[46] assumed that half of the leaves of a *Castanopsis cuspidata* forest is shade leaves and estimated the respriation loss.

Two methods were used here.

A-1-1 Assuming that maximum (110 g/sq.m) and minimum (71 g/sq.m) of the leaf weight per unit area of the sample trees represent sun and shade leaves respectively, and the values of respiration presented by KUSUMOTO[18], which were presented as value per unit area, were converted into values per unit dry weight. The values of respiration per unit dry weight of sun and shade leaves thus converted were 1.450 mg CO_2 per g per hour and 1.275 mg CO_2 per g per hour and the difference between sun and shade leaves became very little. The mean of these two values, 1.363 mg CO_2 per g per hour was assumed as representing the mean respiration rate of leaves. Loss of dry matter through respiration of leaves was estimated with this value, monthly mean temperature at Kiyosumi, and amount of leaves per hectare, and shown in Table 20.

Table 20. Loss of dry matter through respiration of leaves (t/ha/year)

<table>
<tr><th>Method</th><th>1</th><th>2</th></tr>
<tr><td>Tree layer</td><td>15.22</td><td>17.53</td></tr>
<tr><td>Undergrowth</td><td colspan="2">2.91</td></tr>
<tr><td>Total</td><td>18.13</td><td>20.44</td></tr>
</table>

A-1-2. Water content (dry weight basis) and dry weight per unit area of leaves of sample trees showed close relation with their diameter breast high, height, and amount of leaves per tree, as shown by Fig. 21. For the relation to diameter breast high (D cm) and height (H m), which were fairly linear, regression equations were determined as follows:

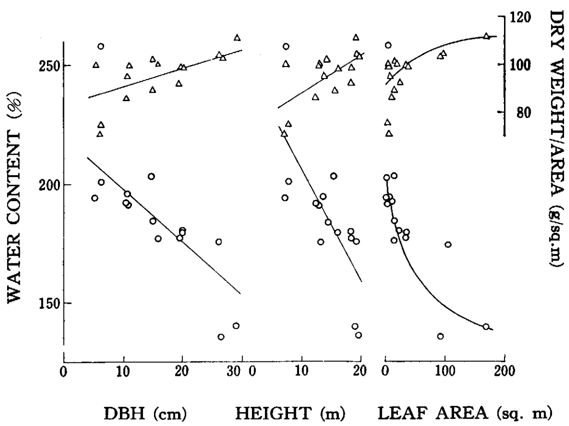

Fig. 21. Water content (circles) and weight per unit area (triangles) of leaves in relation to size of trees.

For leaf water content (WC %):

$WC = 220.3 - 2.219D$, significant at 1 % level

$WC = 251.9 - 4.669H$, significant at 1 % level

For dry weight per unit area (LW g/sq. m):

$LW = 0.83 + 0.0075D$, significant at 5 % level

$LW = 0.72 + 0.0162H$, significant at 1 % level.

With increasing height and diameter water content decreased and leaf weight per unit area increased. These trends means that larger trees have more sun leaves. Diameter and height of trees having leaves of mean values of water content and dry weight per unit area were determined by means of these equations. Such trees were determined as having 14 cm of diameter breast high and 14 m of height from the equation for leaf water content, and 15 cm and 14 m from the equation for leaf weight. From the height-diameter curve in Fig. 4, trees with height of 14 m have a diameter breast high of 14 cm. As these values agreed very well, it was assumed that all trees above 15 cm of diameter have only sun leaves and those below 14 cm of diameter have only shade leaves, and with the equation in Table 2 and frequency distribution of diameter, the amounts of sun and shade leaves per one hectare were estimated as 38382 and 3516 square meters, respectively. Loss of dry matter through respiration of leaves was estimated with the respiration of sun and shade leaves presented by KUSUMOTO[18], monthly mean temperature at Kiyosumi, and the amount of sun and shade leaves per hectare and shown in Table 20.

The value of loss of dry matter through respiration of leaves estimated with these two methods did not differ so much. By one method it was estimated as 15.2 tons per hectare per year and by another method it was estimated as 17.5 tons. These values are very close to the value of a tropical rain forest[23] and a little lower than the estimates for a mixed evergreen broad-leaved forest[12] (24.1 t) and for *Castanopsis cuspidata* forest[46] (23.7 t).

A-2. Undergrowth

As undergrowth consited of many species, mainly of evergreen species, mean value (0.29 mg/50 sq. m. hr.) of respiration rate of shade leaves of many evergreen broad-leaved species presented by KUSUMOTO[18] was used, and dry matter loss was estimated using the temperature at Kiyosumi and leaf area per hectare, and shown in Table 20.

Loss of dry matter through respiration of the whole mass of the leaves of this ecosystem was estimated as 18~20 tons per year.

B. Respiration by non-photosynthetic system.

B-1. Tree layer.

KUSUMOTO[19] presented a value of respiration of "stem" of *Cinnamomum camphora*, but he did not specify the size of the "stem." As it is possible that his "stem" was small one, his data can not be used here as the basis of calculation. KIMURA[12] used the values of respiration of *Fagus sylvatica* in June by MÖLLER *et al*[21]. He estimated annual respiration by multiplying the value of June with 7.64, though the reason why 7.64 was used is not clear. This conversion factor by KIMURA was also used here. 0.614 was used for converting the figure for CO_2 into dry matter instead of 0.546 which was used by MÖLLER *et al*[21].

Two methods were used here.

B-1-1. From the values in Table 6 of MÖLLER *et al*[20], values of annual respiration per tree were plotted against diameter breast high on a double logalithmic paper, as

KIMURA[12] did. As they show a linear relationship, a regression equation was determined and respiration of tree of diameter of every centimeter was calculated. With the frequency distribution of diameter in Fig. 3, loss of dry matter through respiration of non-photosynthetic system was estimated as 14.44 tons per hectare per year.

B-1-2. The values in Table 5 of MÖLLER *et al*[20] were plotted and the relation between respiration and diameter of sample was made into a smooth curve, and with this curve values of respiration of each diameter of sample was made. With these values and the volume of woody tissues of each diameter class shown in Table 21, respiration per 1 hectare of the stand was made, and with the conversion factor loss of dry matter per year per hectare of the stand was estimated. As respiration rate of current year shoots, the value for sun leaves by KUSUMOTO[18] was used after converting it into dry weight basis. Dry matter loss per year thus estimated was 15.6 tons per hectare, and did not differ so much from the value estimated with another method.

Table 21. Amount per hectare of woody tissues of different diameters

Diameter (cm)	Volume (m^3)	Fresh weight (t)
Current year	1.498	2.572
0- 1	4.071	3.337
1- 5	27.630	25.896
5-10	50.346	47.645
10-15	58.807	55.256
15-20	75.751	71.814
20-25	66.763	62.675
25-30	36.589	34.665
30-35	8.667	8.111
35-40	6.397	5.983

KIMURA[12] estimated annual respiration loss by non-photosynthetic system including root of an evergreen broad-leaved forest as 28.3 tons per hectare. MÜLLER and NIELSEN[23] estimated annual respiration loss by non-photosynthetic system without root of a tropical rain forest as 18.5 tons per hectare. These values are larger than the value estimated here.

B-2. Undergrowth.

For biomass of non-photosynthetic system of undergrowth (2.31 tons per hectare) the same method as the second method for the trees was applied, assuming that respiration rate is the same as branches of 0~1 cm in diameter. Loss of dry matter by respiration of non-photosynthetic system (aboveground) was estimated as 0.06 tons per hectare.

B-3. Mathematical method for estimation of respiration by non-photosynthetic system.

MONSI[22] described the dry matter production by plants and plant communities by a simple equation

$$P=F(a-r)-Cr' \qquad \text{(A)}$$

where P is production of dry matter, F is amount of leaves, C is amount of non-photosynthetic system, a is photosynthetic rate, r and r' are respiration rates of leaves and non-photosynthetic system, respectively. Equation (A) is written as

$$\frac{P}{F}=(a-r)-\frac{C}{F}r' \qquad \text{(B)}$$

or $$\frac{P}{C}=\frac{F}{C}(a-r)-r' \qquad \text{(C)}$$

In these equations, as P, F and C had been measured for each sample tree. P/F is the same thing as net assimilation rate and the importance of C/F ratio is pointed out by IWAKI[8]. When P/F against C/F or P/C against F/C are plotted on a section paper, linear relations are expected and by the slope and the intercept $(a-r)$ and r' can be determined. KIRA *et al*[13] applied the equation (C) on northern coniferous forest, and some others used this method without any criticism. The author independently applied the equation (B) on young seedlings of three pine species of North America and obtained fairly reasonable value for $(a-r)$ and r'.

When the equations (B) and (C) were applied to this stand, as shown by Fig. 22 and 23, fairly good linear relationships were established between P/F and C/F, and between P/C and F/C. Slopes and intercepts were determined by means of least square as

$$\frac{P}{F}=2.311+0.233\frac{C}{F} \quad \cdots\cdots\cdots\cdots \text{(B}'\text{)}$$

and

$$\frac{P}{C}=2.883\frac{F}{C}+0.115 \quad \cdots\cdots\cdots\cdots \text{(C}'\text{)}$$

The slopes were highly significant for both cases, and the difference of $(a-r)$ and r' determined for the two equations may not be too large. However, in both cases, r', respiration by non-photosynthetic system, which can never be negative, was determined as negative. In case of *Picea glehnii* in Fig. V-2 of KIRA *et al*[13], the trend may be similar to the result obtained here. Even when the value for the tree groups of largest and smallest diameter in this stand are omitted, the trend did not alter. This rather

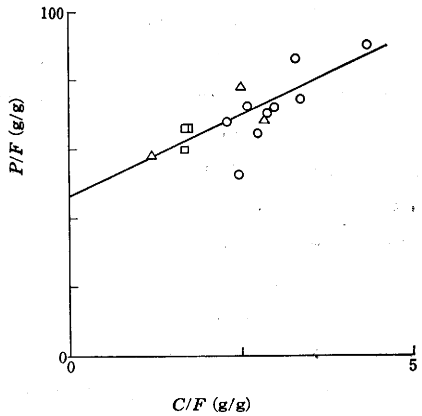

Fig. 22. Graphic presentaion of equation (B). See the text.

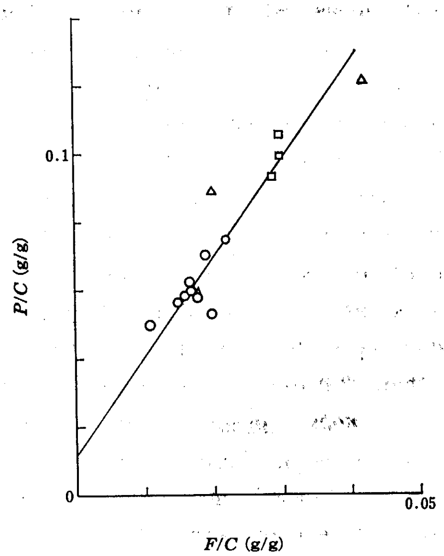

Fig. 23. Graphic presentation of equation (C). See the text.

sophisticated method can not be used for this stand. This result may perhaps due to the fact that values of $(a-r)$ and r' have systematic relations with P/F, C/F, P/C, or F/C, and that r', or respiration by non photosynthetic tissue, is not proportional to the volume and weight of the tissues[20].

2. Gross production.

Sum of net production (aboveground only) in Tables 11 and 12 and loss of dry matter through respiration of leaves in Table 20 and non-photosynthetic system (aboveground only) makes annual gross production (aboveground) per hectare (Table 22). For estimation of gross production, materials of different accuracy were used: net production was directly measured and accuracy is high; among respiration loss, respiration by leaves was estimated with the value by measurement on *C. camphora* by KUSUMOTO[18] and with some assumptions, so that accuracy is not so high as net production but higher than the value of respiration loss of non-photosynthetic system which were estimated with many assumptions, though the estimates by the two methods agreed fairly well in both cases. Thus, the accuracy of estimation of the gross production may be the same as the loss by respiration of non-photosynthetic system. Annual gross production (aboveground) per hectare was suggested as 48~53 tons. If gross production as roots was assumed as one fifth of the aboveground parts, as many authors did, annual gross production of this stand per hectare may be suggested as 57~63 tons which is a little less than 73.0 tons of a mixed evergreen broad-leaved forest[12] and more than 45.3 tons of a *Castanopsis cuspidata* forest (evergreen)[46] and 52.5 tons of a tropical rain forest[23]. However, among these values, accuracy of estimation is highest in the value for a tropical rainforest[23], as they made direct measurement as much as possible, and the others include many assumptions. Percentage of respiration loss in gross production was about 68% which is very close to 75% in a tropical rain forest[23] and 72% in a mixed evergreen broad-leaved forest[12], and higher than 52% of a *Custanopsis* forest[46].

Table 22. Annual gross production

Accuracy		1	2	3	4	5
Net production above ground	Tree layer	13.4–15.0				
	Undergrowth	1.62				
	Total	15.0–16.6				
Loss through leaf respiration	Tree layer		15.2–17.5			
	Undergrowth			2.9		
	Total			18.1–26.4		
Loss through respiration of non-photosynthetic system	Tree layer				14.4–15.6	
	Undergrowth				0.06	
	Total				14.5–15.7	
Gross production (above ground)					47.6–52.9	
Gross production						57.1–63.2

IX ABSTRACT

Of a 46-year-old pure stand of planted *Cinnamomum camphora* (Lauraceae) (evergreen), biomass, net production, pattern of distribution of produced matter within ecosystem, efficiency of leaves to produce organic matter were studied for the aboveground parts of tree layer and undergrowth.

Estimation of biomass and production was made with two methods: ratio of cross-sectional area of sample trees and the stand, and allometric relations to diameter breast high and distribution of diameter breast high of the stand, but the results by the two methods did not differ too much.

Biomass of the above-ground parts per 1 hectare of this ecosystem was about 196~200 metric tons, of which 193~196 tons belonged to the tree layer and about 3.5 tons to consist the undergrowth. Of the biomass of the tree layer, about 2% were leaves, about 18~19% were branches and about 78~80% were stems. However, among individual trees it may be roughly said that trees with larger diameter, height and leaf mass consisted of higher percentages of leaves and branches and lower percentage of stem. Leaf biomass per 1 hectare of the ecosystem consisted of 11.0~11.9 tons of the tree layer in fresh weight, 4.1~4.5 tons of the tree layer and 1.1 tons of the undergrowth in ovendry weight, and 4.3~4.9 of the tree layer and 1.8 of the undergrowth in leaf area index. Undergrowth may not be so important in the total biomass, but it can not be neglected in leaf biomass of the ecosystem. Leaf area index of this ecosystem was 6.1~6.7 which is not so large compared with other evergreen broad-leaved forests.

Net production (aboveground only) per hectare per annum was estimated as 15.0–16.6 tons which was equivalent to 0.7% of the total incident solar energy in energy content and 1.5~1.6% of the incident energy that can be utilized for photosynthesis. If the net production was compared to the incident solar energy during the growing season (April–October), the efficiency was 1.0~1.1% of the total incident energy and 2.2~2.5% of the energy that can be utilized for photosynthesis. The tree layer contributed nine tenth of the net production and the undergrowth one tenth, 1.62 tons. Of 13.4~15.6 tons of net production by the tree layer, about 30~35% distributed into the stems, about 35~40% into the branches and about 30% into the leaves. Only one third of net production made the growth of stem which was equivalent to 8.2 cubic meter in volume. However, of individual trees, pattern of distribution of produced matter was different with the size of trees: distribution to the stem was highest and to the crown was lowest in trees belonging to upper layer of the crown canopy but having smaller diameter and leaf mass; among larger trees of the upper layer distribution to leaves and branches increased and distribution to the stem decreased with increase of diameter and leaf mass; among smaller trees and trees of lower layers distribution to leaves and branches increased and distribution to the stem decreased with decreasing dimensions.

Efficiency of leaves to produce organic matter, or net assimilation rate in British terminology, was estimated with two different methods, but the difference of the result

by methods was very little. Net assimilation rate per annum was 1200~1300 g per 1 kg in fresh weight of leaves, 3300~3500 g per 1 kg in dry weight of leaves, and 310~340 g per 1 square meter of leaves. These values were far less than isolated young plants. Among individual trees, net assimilation rate was highest in trees in upper layer of the canopy with medium diameter and leaf mass.

The amount of leaves and non-photosynthetic systems of this forest was combined with published data on respiration, and annual consumption of organic matter through respiration was calculated. Gross production was suggested as 48~53 tons per hectare per annum, aboveground parts only.

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* in Japanese with English summary, ** in Japanese only

クス植栽林における物質の生産と分配（摘要）

——林分生長論資料 7——

教授 佐藤大七郎

これまでの 報告と おなじ 考えかたで，ほぼ おなじ 方法 に よって，東京大学 千葉県演習林 に 植えられた 46年生の クス の 純林に ついて，林木 と シタバエ の 地上部 だけ に ついて，物質 の 現存量，純生産量，生産された 物質 の 生態系 の なかでの 分配，物質生産量 と 葉の量 との 関係 に ついて しらべ，粗生産量 をも 推定した。

現存量 および 生産量 を，胸高断面積 の 比 および 胸高直径 に 対する 相対生長関係 を つかって 推定したが，ふたつの 方法 の 結果 の あいだ には あまり チガイ は なかった。

この クス林 の 1 ha あたりの 地上部 の 現存量 は およそ 196～200 t で，そのうち 上木の クス は 193～196 t，きわめて おおくの 種類 から できている シタバエ は およそ 3.5 t で あった。上木 の 現存量 の うち，およそ 2% が 葉，18～19% が 枝，78～80% が 幹 だった。しかし，ひとつひとつの 木 に ついて みれば おおづかみに いって，直径 が おおきく，樹高 が たかく，おおくの 葉 を つけている 木 ほど，現存量 の うちで 枝 と 葉 の しめる ワリアイ が おおく，幹 の ワリアイ が ちいさかった。

1 ha あたりの 葉 の 量 は，生重量では クス が 11.0～11.9 t，絶乾重量 では クス が 4.1～4.5 t， シタバエ が 1.1 t，葉面積指数 は クス が 4.3～4.9， シタバエ が 1.8 で あった。現存量 としては 生態系 の なか で わずかな ワリアイ を しめる に すぎない シタバエ も，葉 の 量 では けっして 無視 する こと が できない。生態系 としての 葉面積指数 は 6.1～6.7 だった。この アタイ は，おおくの 常緑広葉樹林 に くらべて けっして おおいとは いえない。

地上部 だけ に ついて しらべた 1年 1ha あたりの純生産量 は 15.0～16.6 t でこの アタイ は，太陽 からの 入射全エネルギーの およそ 0.7%，可視部の 1.5～1.6% に あたり，4～10 月の，いわゆる 生育期間 だけ に ついて みれば 入射全エネルギーの 1.0～1.1%，可視部の 2.2～2.5% に あたる。この 純生産量 の うち，およそ 9割 の 13.4～15.6 t が 上木 の クス，およそ 1割 の 1.62 t が シタバエ に よる 生産 で あった。およそ 13.4～15.6 t の 上木 の 生産量 の うち，およそ 30～35% が 幹，35～40% が枝，およそ 30% が 葉 であった。幹 の 生長量 の 8.2 m^3

は 純生産量の 1/3 に すぎない。しかし，ひとつひとつの 木に ついて みれば，生産物 の 分配の モヨウ は 木 の おおきさ に よって ことなって いた。幹 への 分配率 は，林冠 の 上層を しめる 木 の うちで，わりあい 胸高直径 が ちいさく，葉 の 量 も すくない もの で もっとも たかく，それよりも おおきな 木 では 直径 や 葉 の 量 が おおきいほど，それよりも ちいさな 木 では 葉 の 量 や 直径 が ちいさいほど 幹 への 分配率 が ひくく 葉 や 枝 への 分配率 が たかかった。

葉 が 乾物 を 生産する 能率，いわゆる 純同化率 (net assimilation rate) を 二つの 計算法 で もとめたが，計算法 による チガイ は すくなく，1年あたりの 純同化率 は，葉 の 生産量 1 kg あたり 1,200～1,300 g, 絶乾重量 1 kg あたり 3,300～3,500 g, 片面面積 1 m² あたり 310～340 g で，孤立状態 の もの よりも はるかに すくなかった。純同化率 は ひとつひとつの 木 の おおきさ に よって ことなり，林冠の 上層 を しめる 木 の なかで，直径 と 葉 の 量 が あまり おおきくない 木 で もっとも おおかった。

葉 や 非同化系 の 呼吸率 を 文献 から もとめ，ここで しらべた 葉 と 非同化系 の 量 と 気象記録 を つかって，呼吸 に よる 年間 の 有機物 の 消費量 を 試算して，この 生態系 の 地上部 だけ の 粗生産量 を 試算した ところ，1年 1 ha あたり 48～53 t となった。

APPENDIX 1. Stand Table

DBH	*n*	DBH	*n*	DBH	*n*	DBH	*n*	DBH	*n*
1	0	11	52	21	49	31	10	41	0
2	14	12	42	22	57	32	9	42	0
3	37	13	62	23	31	33	6	43	1
4	34	14	58	24	50	34	5	44	0
5	33	15	55	25	44	35	6	45	0
6	16	16	62	26	26	36	3	46	0
7	24	17	57	27	26	37	4	47	1
8	21	18	67	28	18	38	0	48	0
9	45	19	56	29	14	39	0	49	0
10	42	20	57	30	13	40	5	50	0
								Total	1,212

area: 0.97 ha

APPENDIX 2. Sample trees

	Diameter breast high (cm)	Height (m)	Biomass									Increment			
			Stem			Branch			Leaf			Stem		Branch	
			Volume (1000cc)	Fresh wt. (kg)	Dry wt. (kg)	Volume (1000cc)	Fresh wt. (kg)	Dry wt. (kg)	Fresh wt. (kg)	Dry wt. (kg)	Area (sq. m)	Volume (1000cc)	Dry wt. (kg)	Volume (1000cc)	Dry wt. (kg)
1	5.4	7.1	10.8	10.2	6.30	0.719	1.35	0.525	0.400	0.136	1.36	0.200	0.117	0.485	0.353
2	6.2	7.4	14.6	13.9	8.50	1.77	2.00	1.09	0.520	0.173	2.30	0.233	0.136	0.381	0.387
3	6.2	7.6	13.5	12.6	7.90	2.34	2.85	1.43	1.40	0.391	5.50	0.667	0.390	0.541	0.343
4	10.6	12.2	69.7	68.0	40.8	9.08	9.60	5.61	2.30	0.788	9.16	1.17	0.683	2.08	1.40
5	10.6	13.7	68.3	64.9	40.0	3.96	4.70	2.59	1.95	0.662	6.96	1.72	1.01	1.13	0.808
6	10.9	12.7	64.8	61.0	37.9	4.95	5.40	4.06	1.40	0.481	4.83	1.28	0.749	1.36	0.913
7	14.8	15.4	109	101	59.1	11.7	16.3	7.00	4.10	1.35	14.1	2.38	1.39	1.34	0.794
8	14.9	14.1	136	129	79.6	16.9	17.2	10.3	4.40	1.55	15.1	3.38	1.98	2.81	1.86
9	15.8	13.0	134	125	60.5	14.5	15.4	8.81	4.20	1.52	15.3	1.90	1.11	3.80	2.50
10	19.5	18.5	302	282	177	35.9	38.4	22.1	10.6	3.82	35.3	8.90	5.21	6.86	4.79
11	19.7	18.2	236	212	127	34.6	42.8	20.5	6.30	2.25	24.5	9.03	5.28	3.53	2.26
12	20.0	16.0	268	269	156	68.1	76.4	40.7	9.70	3.48	35.2	6.82	3.99	6.32	4.22
13	25.9	19.3	485	450	265	103	109	69.6	27.3	9.95	97.7	18.4	10.1	16.9	9.82
14	26.5	19.6	491	459	268	108	110	64.0	22.5	9.51	92.0	17.0	9.95	18.6	11.5
15	29.0	18.9	517	484	293	245	242	145	31.0	12.9	168	15.5	9.07	27.5	20.1