

Production and Distribution of Dry Matter in Forest Ecosystems*

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In forestry, in which production of timber is the most important objective, most of the practice is closely connected with growth of trees. Hence, throughout the history of the sciences of forestry, studies of tree growth was one of the most important subjects, but the studies were mostly confined to the mathematical treatments of growth of stems, and biological considerations were rather neglected. However, timber is only a part of products of tree as a living entity, and trees are merely a part of forest as an ecosystem. For the better understanding of the process involved in timber production, studies of the dry matter production by forest ecosystem as its basic process is necessary¹⁾.

Estimation of dry matter production by ecosystems can be made by two methods. One is made by measuring increase of dry weight of each component of the ecosystems and summing them up. The other is made by estimating the photosynthesis, or gross production, of ecosystem by function and structure of photosynthetic system and reducing the consumption by respiration, as contrived by MONSI and SAEKI²⁾. According to KIMURA's study³⁾ on mixed evergreen forest, the estimates by these two methods agreed each other very closely. However, as the study by the second method, which is more theoretical, is not yet sufficiently made for forest ecosystems, this paper deals mainly with the first method.

A part of solar energy incident upon the forest ecosystems is used for photosynthesis of green plants in them. A part of photosynthate is consumed by respiration of photosynthetic system, a part of the surplus is consumed by the respiration of non-photosynthetic system, a part is reproduced into new tissues, and the remainder is used afterwards. The produced matter which was not consumed by respiration, (and sometimes by other organisms), is accumulated in the forest ecosystems, and can be measured as dry matter. Dry matter accumulated in the forest ecosystems is distributed mainly into trees and undergrowth. A part of dry matter accumulated by tree is reproduced as photosynthetic system and the remainder as non-photosynthetic system, such as stems, branches, roots, bark, seeds, etc. Of these components, quantities of bark, seeds, etc. are very little and can be neglected in most cases of forest. In Table 1 is shown the distribution of produced dry matter into stem, branches, and leaves as well as into undergrowth as the mean of 12 stands of 4 species of conifers and 5 stands of 3 species of broad-leaved trees, which are so far available. As the distribution is affected by many factors such as species and structure of stand, this table is not shown as repre-

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Table 1. Distribution of Net Production

	Distribution within trees (per cent)			Distribution to undergrowth (per cent)	Net production in forest (t/ha)
	Stems	Branches	Leaves		
Coniferous, mean of 12 range	55.3 45.9—68.5	15.2 7.0—28.5	28.5 11.1—40.3	9.7 0—19.2	13 8.7—16.6
Broad leaved, mean of 5 range	49.5 34.5—64.3	19.0 10.1—35.7	31.5 24.8—35.9	9.4 2.5—29.3	9 6.1—14.0

senting both groups, but to give a sort of general idea. In forests of shade intolerant species and of older ages, distribution to undergrowth is larger. Nevertheless, of the dry matter produced by forest ecosystems, distribution into the stem was less than one half in many cases, and the actual utilization as timber may be far less.

From forester's point of view, of production by forest ecosystems, production by tree is of prime importance, and the distribution of the produced matter into stemwood makes timber yield. The distribution into other parts is considered as "costs" to continue production; leaves are indispensable in production, branches are necessary for proper arrangement of photosynthetic system or making up an efficient productive structure, roots are necessary for intake of water and minerals, and so forth. Thus, yield of timber by a forest depends not only on the total quantity of matter produced by forest ecosystem, but also on the distribution of the produced matter into the stemwood. Only through the studies of dry matter production and distribution of produced matter into parts of forest ecosystems, we can find out the reason why timber yield is high in some case and low in the other, and establish the way of improving the silvicultural practices. It may be possible to increase timber yield either through increase of dry matter production itself or through control of its distribution into the components of ecosystems. Since 1950, we have carried out studies of dry matter production and distribution of forest ecosystems of various species, of different silvicultural treatment, and on various site qualities and localities⁴⁻⁹). Of the results of these studies along with other unpublished materials, figures on biomass are presented already in one of the tables in the recent review by OVERTON¹⁰). Here will be presented the problems in estimation of biomass and of production, quantity of leaves, and production and distribution of dry matter.

Regardless of the method used for the estimation of dry matter production, estimation of the quantity and production of the parts of forests per unit area is the first step. In one method, quantity of leaves as the producer and quantity of non-photosynthetic system as the consumer is indispensable. In the other method, estimation of increase of dry weight of each component is essential. There are many methods of estimation, but three methods have been used most frequently. One of them is cutting all trees in the plot, measuring the quantity of each component of the fallen trees, and summing

Table 2. Quantity of Needle Leaves Determined by Different Methods

Tree species	Age	Clear cutting		Mean dbh cm	Quantity of leaves (t/ha) in dry weight		
		Area m ²	Number trees		Clear cutting	dbh-leaves equation	Average trees
<i>Pinus densiflora</i>	13	20	13	7.2	4.56	4.99	4.37
<i>Chamaecyparis obtusa</i>	28	—	—	9.2	—	13.8	11.5
do.	28	—	—	8.2	—	11.1	9.9
do.	28	—	—	8.3	—	11.6	12.1
<i>Cryptomeria japonica</i>	43	32	14	15.4	17.82	18.42	18.27
do.	12	37	22	7.4	16.78	16.94	16.45

them up. The second method is cutting trees of average diameter breast high induced from the basal area of the plot, with or without stratification of the diameter class, measuring the quantities, determining the mean value, and multiplying it with the number of trees in the plot or with the ratio of cross sectional area. The third method is cutting the trees selected randomly as to cover the whole range of diameter of the trees in the plot, measuring the quantities, determining the equation showing the relations between diameter breast high and the quantities, calculate the quantity for each diameter by means of the equation, multiplying it with the number of trees of corresponding diameter, and summing up the products for the whole stand. By the first method, we can determine the biomass and production of roots as well, but as it is too labor-consuming to work with a large sample plot, and a small plot results errors however the value for the plot itself is correct, this method is not so frequently used. This method requires clear cutting however small the area is, and under many circumstances clear cutting is not allowed. This method is used for the estimation of biomass and the production by undergrowth and natural regenerations. The second method is very simple, but sometimes it is not easy to get sufficient number of "average" trees. The third method is rather complicated, but there is no difficulty in sampling trees. This method may be useful in establishing reference materials for non-destructive plots, though with limitations. Table 2 shows the estimates of the quantity of leaves by these three methods on the same plots. The second method is apt to give lower values and the third is apt to give higher values, compared with clear cutting. These methods inevitably give underestimates of production, because loss of produced matter, such as shedding of leaves and consumption by defoliating insects, is neglected. To adjust these losses, continuous observations on litter and frass fall are desirable.

The third method was first proposed by KITTREDGE¹¹⁾ for the estimation of the quantity of leaves on unit area of forest stand. The method is based on the fact that when leaf weight and diameter of individual trees are plotted on a double logarithmic paper the trends are linear so that they can be represented by a simple regression equation. By this method the quantity of leaf per unit area can be estimated as fresh

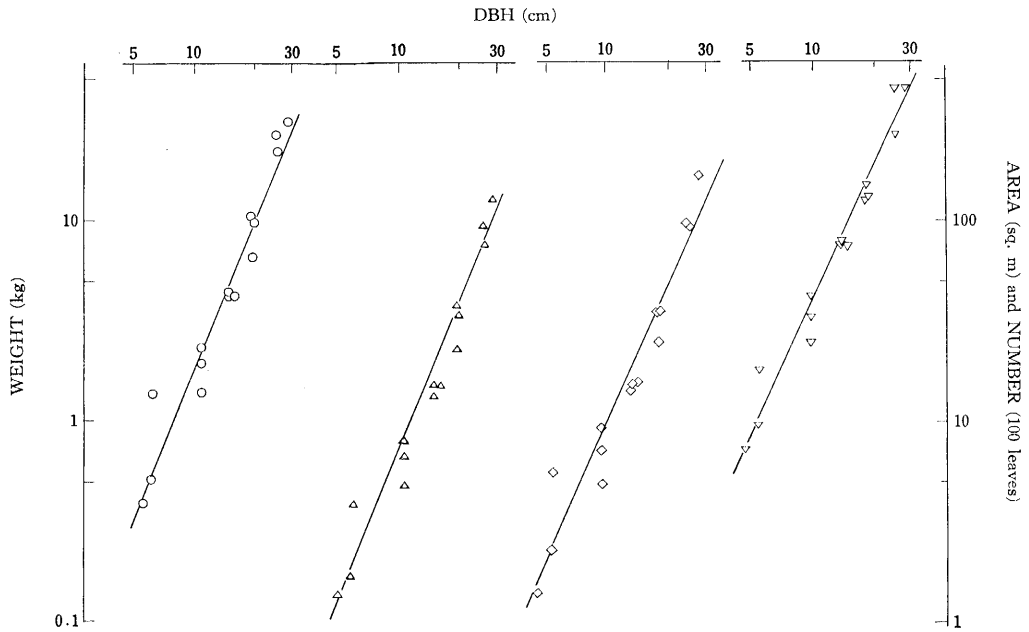


Fig. 1. Relations between quantities of leaves and diameter breast high of trees in a *Cinnamomum camphora* stand. ○ fresh weight, △ dry weight, ◇ area, ▽ number

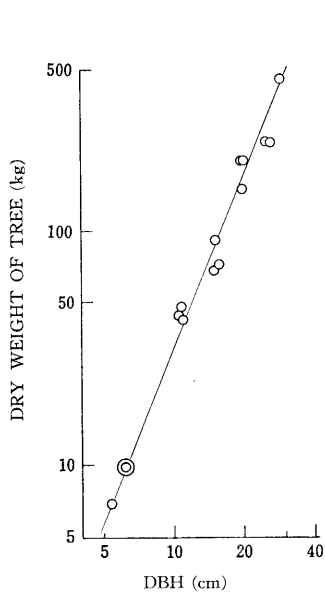


Fig. 2. Relation between dry weight of above-ground parts of tree and diameter breast high of trees in a *Cinnamomum camphora* stand.

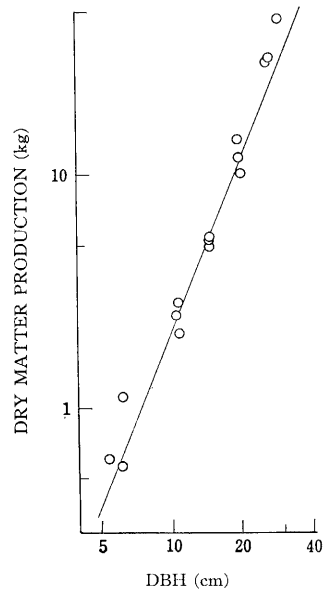


Fig. 3. Relation between dry matter production (above ground) and diameter breast high of trees in a *Cinnamomum camphora* stand.

weight, dry weight, area, and number, as shown by Fig. 1. This method was proved to be very useful and the principle of the method was found to be applicable also for the estimation of the mass and increment of branches, stems, and whole trees in volume,

weight, and surface area^{4,6)}. In Fig. 2 and 3, the relations between dry weight and dry matter production per tree and diameter breast high of trees in a *Cinnamomum camphora* plantation is shown. Instead of diameter, other measures of stem, such as volume or its substitutes and cross sectional area, can be used.

However, there is a question whether the equation determined for a particular stand of a species could be applied for other stands of the same species or not. The stand table giving the number of trees of each diameter is, perhaps, the simplest of the characteristics of the forest stand to be obtained by field measurements and it is secured without destruction of stands, while the determination of the equation requires a time-consuming job of cutting, separating, and measuring of each component of trees on sufficient number of sample trees. It will be very convenient if such quantities are estimated without determining the equation separately of each stand, especially when handling with permanent plot for the studies of circulation of matter in which cutting of trees is not allowed. However, application of the equation determined for a particular forest stand to other stands is very erroneous¹²⁾. Fig. 4 shows the relation between diameter breast high and dry weight of leaves of *Cryptomeria japonica*, of 28 stands from 5 localities, ranging from 5-years-old to about 200-years-old*. As seen from the figure, variation was very large, for example, the quantity of leaves of trees having a diameter breast

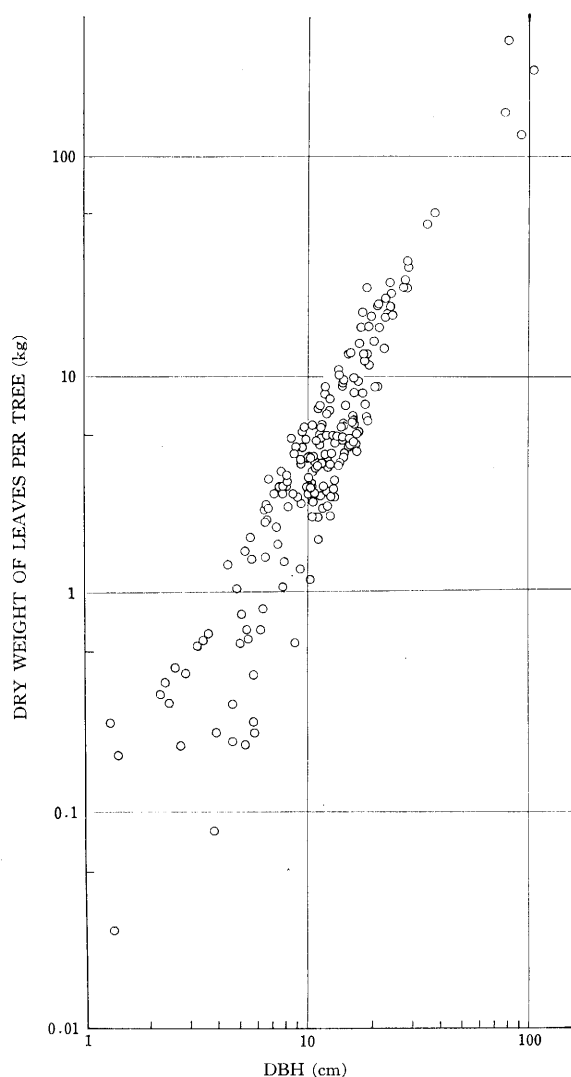


Fig. 4. Oven-dry weight of leaves of *Cryptomeria japonica* in relation to diameter breast high.

* Most of the materials of *Cryptomeria japonica* and *Larix leptolepis* are based on the data collected by the working group, "Joint Study of 4 Universities on Productivity of Forest", in which the present author took part. Thanks are due to the member of the group.

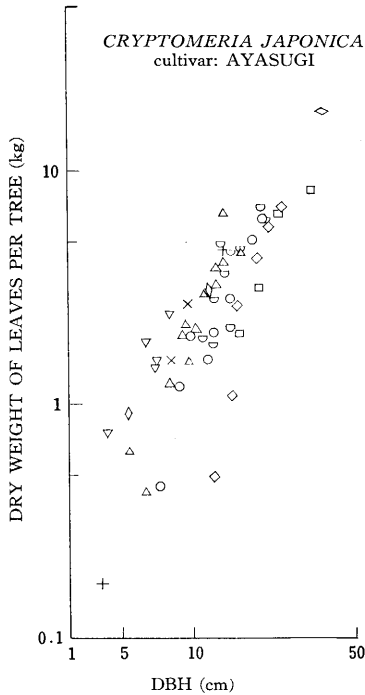


Fig. 5. Relation between oven-dry weight of leaves and diameter breast high of stands of a cultivar of *Cryptomeria japonica*. Different symbols mean different stands.

high of 10 cm ranged from about 300 g to 6000 g. Accordingly, application of an equation for one stand to another can result large error, and the equation for the whole sample is also meaningless. This was true even within a group

of stands made of the same race within the same locality. Fig. 5 shows the relation for a cultivar of *Cryptomeria*, Ayasugi, propagated only by cuttings, in Kikuti, Kumamoto, Japan. In the figure, values for different stands are shown with different symbols. However, for each stand, of course, good linear regression was established (Fig. 6) and estimates of the quantity of leaves using the regression equation were fairly correct. This fact found for *Cryptomeria japonica*, which is moderately shade tolerant species, was also true for *Larix leptolepis* which is extremely light demanding (Fig. 7) and *Thujaopsis dolabrata* which is extremely shade tolerant (Fig. 8). Despite the difference in the regression equations, the quantity of leaves per unit area thus estimated did not differ so much (Fig. 8). The difference in the constants of regression equations is partly

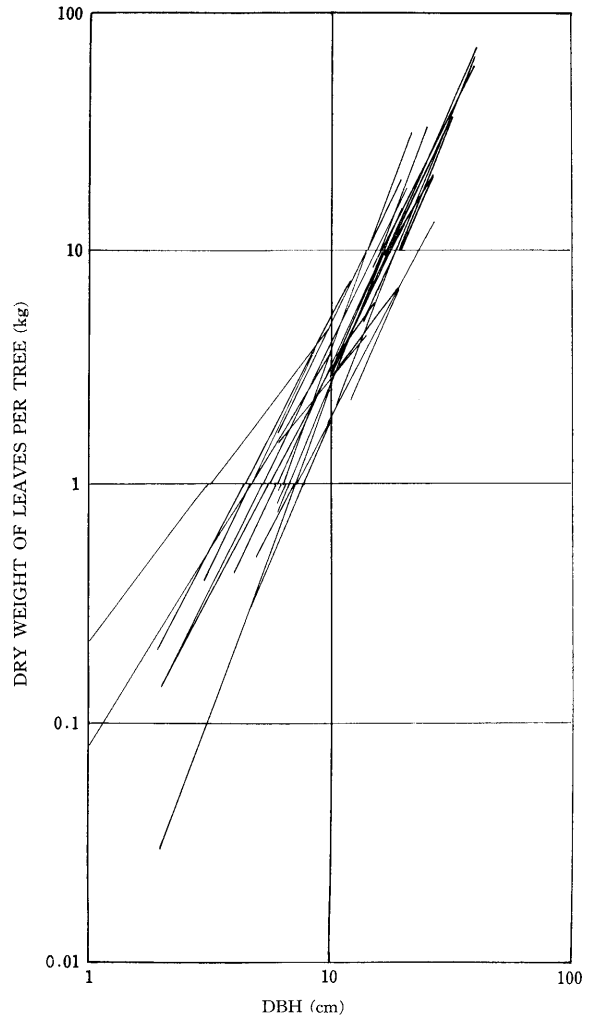


Fig. 6. The regression lines for the relations between oven-dry weight of leaves and diameter breast high. Each line represents a stand. The same materials as in Fig. 1.

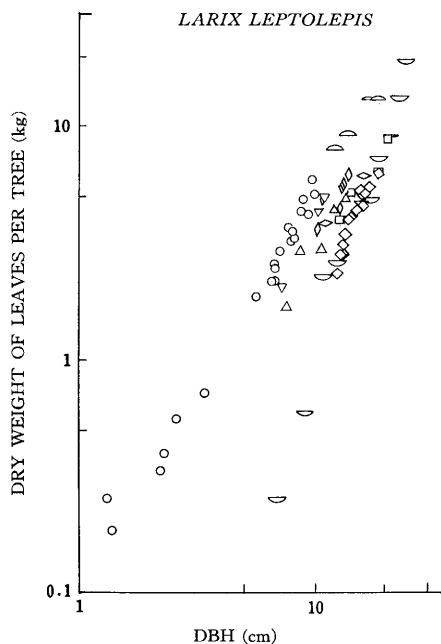


Fig. 7. Quantity of leaves in relation to diameter breast high, *Larix leptolepis*. Different symbols mean different stands.

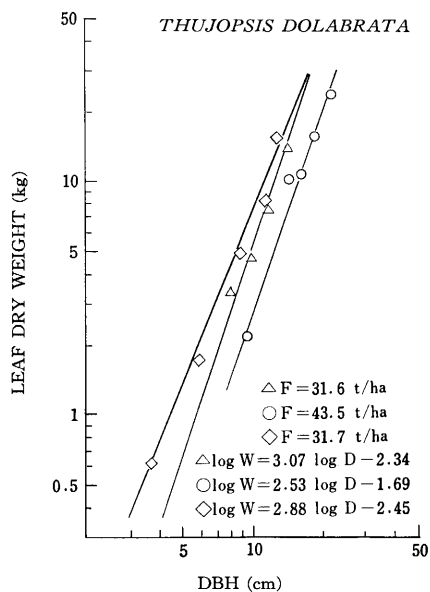


Fig. 8. Regressions of leaf dry weight to diameter breast high of three stands, *Thujopsis dolabrata*.

compensated by the pattern of frequency distribution of diameter which is another factor determining the quantity of leaves per unit area of forest stand.

The constants of the regression equation were found not to be related to height, mean diameter, number of trees per hectare, age, and race, but they were closely related to competition among trees in the stand. The constants of the equation increased with increase of competition. Table 3 shows examples of a spacing experiment of *Pinus densiflora*⁵⁾ and a thinning experiment of *Zelkova serrata*⁷⁾. This trend means that the difference of leaf weight due to a given difference of diameter increases with increasing competition. Discussions on this subject were published already¹²⁾. These differences in the constants of regression equation are, perhaps, due to the following fact: the quantity of leaves on a tree consists of the products of the latest one to a few years as older leaves were already shed, and so it reflects a few years' history of the tree, while diameter of stem, either at breast height or at elsewhere, reflects longer history of the tree than that of the leaves, and the effects of the living conditions of the recent years are reflected as only a small part of it, because diameter at breast height or other heights is an accumulation of diameter growth since the tree reached the corresponding heights. In this respect, the use of diameter of stem close to or at the base of crown, which has nearly the same history as the lowest branches, appears to be better for this purpose, but the measurement of the diameter of such higher places

Table 3. Values of the slopes (b) and the elevations (a) in the relation between leaf weight per trees (W kg) and diameter breast high (D cm) expressed by the regression equation $\log W = b \log D - a$, for stands of different density of the same age on the same site qualities.

Original spacing or thinning	Number of trees per hectare	Average D.B.H. by basal area (cm)	Rate of natural thinning (%)	Slope (b)	Elevation (a)
<i>Pinus densiflora</i> of different spacing, 13 years old.					
2m	2462	11.9	1.5	1.86	1.21
1.5	4099	9.6	7.8	2.46	1.88
1	7411	7.1	25.5	3.21	2.55
0.5	12806	5.6	68.0	3.28	2.54
whole samples				2.79	2.19
<i>Zelkova serrata</i> , thinning experiment, 32 years old.					
thinned	1273	14.0	...	2.03	1.82
not thinned	2600	12.8	...	2.49	2.28
whole samples				2.27	2.09

is not practical in the field study, and making up of a stand table of diameter distribution is indispensable for the estimation of the quantity of leaves and other components of a stand by this method.

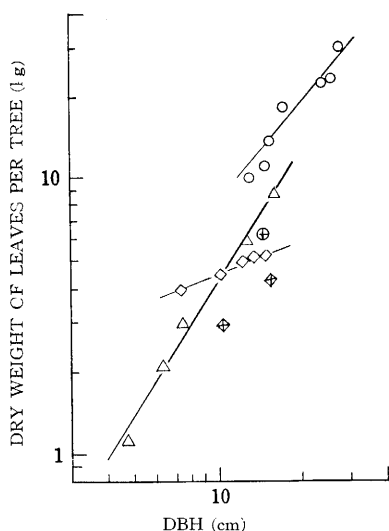


Fig. 9. The relation between the quantity of leaves and the diameter breast high of mean diameter induced from basal area of stands of three types of commercially managed forests of *Cryptomeria japonica*. Circles: Akita, Triangles: Yosino, Squares: Kumamoto. Symbols with cross: stands with exceptional density.

The relation established by KIT-TREDGE¹¹⁾ is for individual trees within a stand, but this relation is not confined to such a case. Similar relation exists between the quantity of leaves and diameter of trees of mean diameter, induced from basal area, of stands of comparable nature. Logarithm of leaf weight of average trees of stands is linear proportional to logarithm of diameter breast high of average trees, as in the case of the relation for individual trees within a stand. Examples based on the data of experiments of particular nature were shown in a previous report¹²⁾. This relation held true also in groups of commercially managed forests of *Cryptomeria japonica*. The slope of the equation reflected the difference in the principles of management, or types of forestry (Fig. 9). It was found to be

possible to estimate the quantity of leaves of stands belonging to the same principles of management by determining the diameter of average trees from basal area of stand, calculating the quantity of leaves of such trees from the equation showing the relation between the quantity of leaves and diameter of average trees of the stand, and multiplying it with the number of trees per unit area of the stand. However, care should be taken to exclude the exceptional stands by comparing with the course of decrease of number of trees in the corresponding yield table. This method may be applicable to other measures of stand, but it is on the way of study.

The relation between leaf weight and diameter of trees was expressed by equations of the same form for both the relation of individual trees within a stand and for the average trees of different stands of comparable nature. However, the slopes of the equation for the relation between stands were always smaller than the slope for the relation within stands (Fig. 10). The difference of the two cases may, perhaps, be due to the fact that, the dominance of average trees is similar among the stands, while the individual trees within a stand include dominant as well as suppressed trees. The dominant trees have more leaves than in proportion to the diameter, and the suppressed trees have less leaves than in proportion to the diameter, while among average trees there is less skewness of such a nature in the relation between the quantity of leaves and diameter breast high, which increased with increasing competition.

Some examples of dry matter production of forest ecosystems of Japan are presented in Table 4. Because of the difficulty of measurements, information on the production of roots is very few. Information on production of branch, of which measurement is rather labor-consuming, and of undergrowth, which is often neglected, is also limited. In some tree species, it is very difficult and erroneous to distinguish leaves of current year from those of the previous years, in some season. Data on dry matter production are not so abundant as those on biomass.

Dry matter production of forest ecosystem depends on the quantity and efficiency of leaves. The quantity of

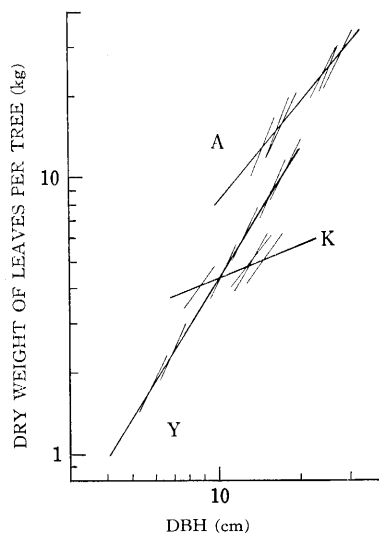


Fig. 10. The slope of the regression of the amount of leaves to diameter breast high of the relation within and between stands of *Cryptomeria japonica*. A: Akita, Y: Yosino, K: Kumamoto. Thick lines: between stands, thin lines: within each stand. Only a part of the regression lines for the relation within each stand are shown to avoid the complexity of the figure.

Table 4. Dry Matter Production in Various Forest Ecosystems (t/ha)

Species	Locality	Age	Trees					Under-growth	Total
			Stem	Branches	Leaves	Roots	Total		
<i>Picea abies</i>	Hokkaido	46	5.67	1.29	4.69	...	11.65	1.25	13.00
do.	do.	47	8.04	0.98	3.37	...	12.39	1.62	14.01
do.	do.	46	5.70	1.17	4.54	...	11.41	1.36	12.77
do.	do.	45	4.31	0.84	2.19	...	7.34	1.39	8.73
do.	Titibu	37	6.09	1.19	6.00	...	13.28	(+)	13.28
<i>Abies sacharinensis</i>	Hokkaido	26	6.70	3.82	2.88	...	13.40	(+)	13.40
<i>Larix leptolepis</i>	Hokkaido	21	7.89	3.66	4.90	2.83	19.28	0.16	19.44**
							16.45		16.61
<i>Pinus densiflora</i>	Tiba	*15	6.78	2.54	4.24	1.30	14.86	(+)	14.86**
							13.56		13.56
do.	do.	13	6.93	0.71	2.37	...	10.01	2.11	12.22
do.	do.	13	5.72	1.14	2.04	...	8.99	2.11	11.01
do.	do.	13	6.35	1.75	2.33	...	10.33	2.11	12.54
do.	do.	13	6.98	3.50	2.44	...	12.92	2.11	15.03
<i>Betula maximowiczii</i>	Hokkaido	*47	2.90	1.09	2.17	...	6.16	0.16	6.32
do.	do.	*47	3.65	0.98	2.59	...	7.22	0.29	7.51
do.	do.	*44	2.83	0.95	1.76	...	5.54	0.53	6.07
<i>Populus davidiana</i>	do.	*40	5.62	0.88	2.17	...	8.74	3.63	12.37
<i>Cinnamomum camphora</i>	Tiba	52	4.70	4.86	4.07	...	13.64	1.62	15.26

* Natural forest, others are plantation

** Including the production of roots

leaves of tree layer of closed stands tends to approach a maximum value specific to the species. This was recognized already by MÖLLER¹³⁾ in his extensive work. He reported that the quantity of leaves per unit area of closed forest stand is not affected by site quality, age, thinning, and so on. We also reported that quantity of leaves per unit

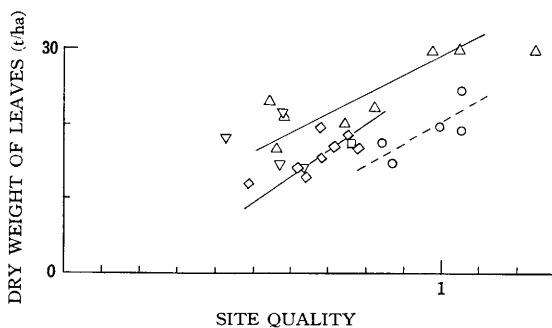


Fig. 11. Oven-dry weight of leaves per unit area of stand of *Cryptomeria japonica* in relation to site quality. Circles: Yosino, Triangles: Akita, Squares: Kumamoto. Other symbols, such as inverted triangles, represent other groups of stand of which regression was not determined because of insufficient numbers of plots.

area of closed stand is not affected by difference of density due to original spacing^{5, 6)} or to strength of thinning⁸⁾. Quantity of leaves of many commercially managed forests of *Cryptomeria japonica*, being fully closed and having many dead branches, was tried to relate to the number of trees per unit area, the ratio of actual density to calculated maximum density, age, and height, but no consistent trend was found with them. However, quantity of leaves had close connection with site

quality which is expressed by the ratio of actual height to the height at the same age of tree in the yield tables made for each region (Fig. 11). The quantity of leaves was larger in better sites. For two localities, Akita and Kumamoto, regression coefficients were significantly positive, and in another locality, Yosino, the regression coefficient was positive but insignificant, probably because of insufficient number of the plots. For other localities, number of plots was not large enough to determine regression. This trend does not agree with the result by MÖLLER¹³⁾ on beech, but KITTREDGE¹¹⁾ stated that the quantity of leaves is larger on better sites. Further studies are needed on this subject.

From the data published by many authors and also from our unpublished data, shade tolerant and intolerant species of conifers and broadleaved trees were selected and quantities of leaves per hectare of them are shown in Table 5. The table shows that forests of the same species have similar values even when planted in quite different localities, and that forests of different species of similar ecological characters also have similar values.

MONSI and SAEKI²⁾ found that light intensity in a given point in herbaceous and grass communities (I) relative to light intensity in the open (I_0) is expressed as a function of total leaf area (F) per unit area of ground above the point and the relation is shown as

$$\frac{I}{I_0} = e^{-KF}$$

where K is a constant dependent on the nature of leaves, such as transmissibility to light and arrangement, and e is the base of natural logarithm. This relation was true for crown canopy of forests, such as *Pinus densiflora*⁵⁾ and *Chamaecyparis obtusa*⁴⁾, even when the quantity of leaves was expressed by weight of leaves. In case of *Chamaecyparis obtusa* stand, which is shown by Fig. 12, K was 0.388. The equation is written as

$$F = -\left(\frac{1}{K}\right) \log_e \frac{I}{I_0}$$

Table 5. Quantity of Leaves (t/ha) in Dry Weight

<i>Fagus sylvatica</i>		<i>Fagus crenata</i>		<i>Betula verrucosa</i>	
EBERMEYER	3.3	YAMADA	2.9—3.1	OVINGTON	2.5
BOYSEN JENEN & MÜLLER	3.1	OHMASA	2.8	<i>Betula ermanii</i>	
MÖLLER	2.5			4 Univ.	2.4
BURGER	3.2			<i>Betula maximowiczii</i>	
BURGER	3.2			SATOO	2.2
BURGER	3.2			SATOO	2.6
				SATOO	1.8
<i>Picea abies</i>		<i>Pinus densiflora</i>		<i>Pinus sylvestris</i>	
MÖLLER	12	SATOO	4.6	BURGER	5
BURGER	15—20	SATOO	4.8	AMILON	4.9
BURGER	15.5	SATOO	5.1	TIRÉN	5
SATOO	14.7	SATOO	5.8	OVINGTON	5.1—10.5
SATOO	18.6	SATOO	5.3	<i>Pinus banksiana</i>	
SATOO	16.9	SATOO	5.2	ADAMS	4.0
SATOO	14.4	SATOO	5.1	ADAMS	4.0
SATOO	24.6	SATOO	5.4	ADAMS	5.6
		SATOO	4.6	ADAMS	5.8
		YAMASINA	4.5	HANSEN	6

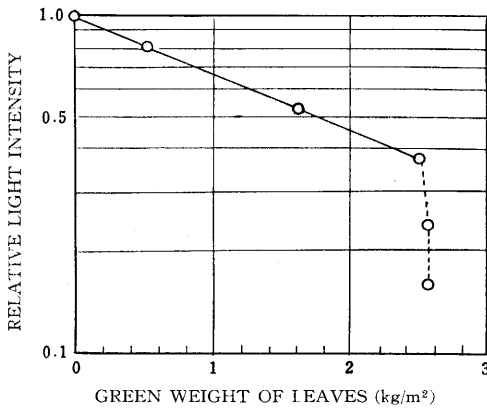


Fig. 12. Extinction of light through crown canopy of a *Chamaecyparis obtusa* stand. Abscissa is cumulative amount of leaves from the top.

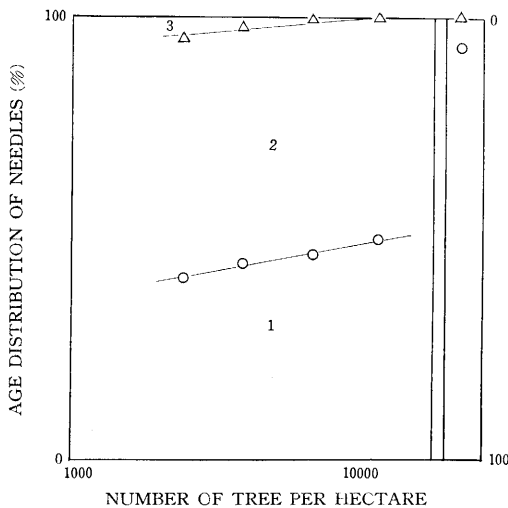


Fig. 13. Age composition of needles of *Pinus densiflora* stands. Below circle: current year needle, above triangle: 3-years-old needles, and 2-years-old needles in between.

synthetic activity due to leaf age is well known.

The efficiency of leaves to produce dry matter can be affected by many factors, some factors affect the photosynthetic activity, for example, it is well known that supply of water and minerals affects photosynthesis. The quantity of non-photosynthetic system also affects accumulation of dry matter through consumption of matter by respiration. Thus, if the quantity of leaves is fairly uniform among the forests of the same or ecologically similar species, it does not necessarily mean that dry matter production by them is uniform. For example, dry matter production and quantity of leaves

In this equation, extinction coefficient, K is, perhaps, relatively constant for a given species as it reflects the nature of leaves, and I/I_0 may also be relatively constant at the bottom of crown canopy of a given species, as the minimum light intensity for survival of leaves of a species is in a very narrow range. Then F_{max} , amount of the whole body of leaves per unit area of ground when I/I_0 is the relative light intensity at the bottom of the crown canopy, may be relatively constant. This is also substantiated by the following fact. Among the stands of *Pinus densiflora* of similar age having similar total quantity of leaves per unit ground area, there was large difference in age composition of leaves (Fig. 13). In case of stands of different densities there was a systematic trend in age composition, and in another nearby stand, which was investigated several years later, almost all leaves consisted of the current year leaves. This suggests that when large quantity of new leaves was produced, older leaves are shaded by them and cannot survive the lack of light. The different age composition can result different photosynthetic activities of the crown canopy and subsequent dry matter production. Difference in photo-

per unit area of plantations of *Picea abies* of different site quality are compared in Table 6. Dry matter production is less in the stands of lower site quality, though the quantity of leaves was not less in poorer sites. Thus, dry matter production was not proportional to the quantity of leaves, and so dry matter production by unit quantity of leaves for unit time interval, or net assimilation rate in British terminology, differed considerably and was less in poorer sites. But the variation in the efficiency of leaves to produce dry matter was not so large as in the efficiency of leaves to produce stemwood. It seems that, on poorer sites, produced matter was used in higher proportion for maintaining the crown canopy and surplus to supply stem was not so much as on the better sites, or, "cost" to produce timber was higher. Here the problem of distribution of produced matter into parts of trees becomes of practical importance. One of the case where the distribution of produced matter is of practical importance is the relation to stand density. As shown by Fig. 14, the efficiency of leaves to produce stemwood decreased with decreasing stand density, in all of four examples available, of which one is a thinning experiment of *Pinus strobus*⁸⁾ and the others are spacing experiments of

Table 6. Dry Matter Production and Quantity of Leaves (t/ha)

Picea abies

Locality	Site quality	(A) Quantity of leaves	(B) Dry matter production	(B)/(A)	Stem wood production per unit leaf
Hokkaido	A	18.50	12.39	0.67	0.49
	B	14.70	11.65	0.79	0.39
	B	14.37	11.41	0.79	0.40
	C	16.91	7.34	0.43	0.26
Titibu	—	24.64	13.28	0.54	0.25

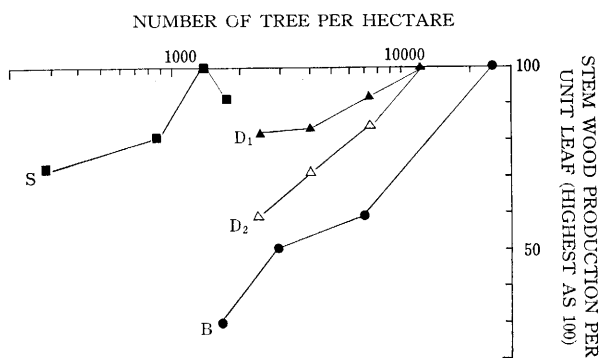


Fig. 14. Efficiency of leaves to produce stemwood.
S: A thinning experiment of *Pinus strobus*.
D₁ and D₂: Spacing experiments of *Pinus densiflora*.
B: A spacing experiment of *Pinus banksiana*.

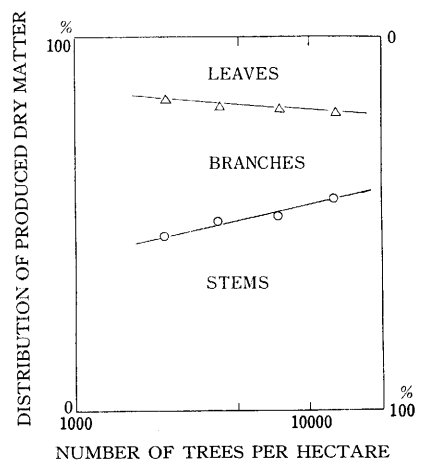


Fig. 15. Effect of stand density on the pattern of distribution of produced matter into components of stands of *Pinus densiflora*.

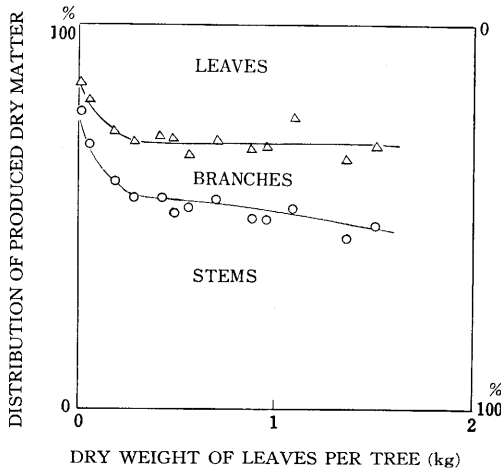


Fig. 16. Pattern of distribution of produced matter into components of trees in relation to the dominance of trees expressed as the quantity of leaves per tree, *Pinus densiflora*.

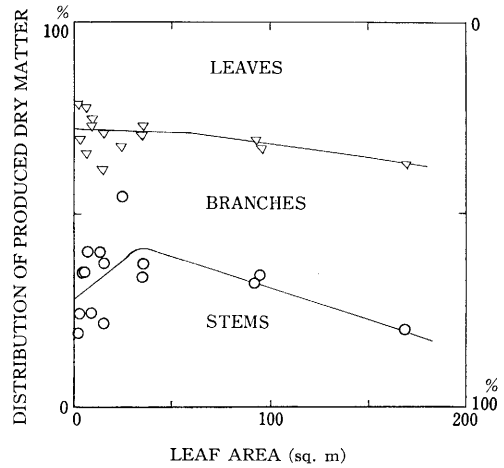


Fig. 17. Pattern of distribution of produced matter into components of trees in relation to the dominance of trees expressed as the quantity of leaves per tree, *Cinamomum camphora*.

Pinus densiflora^{5,9)} and *P. banksiana*¹⁴⁾. In one of them, production of branchwood was estimated and the distribution can be compared. As seen in Fig. 15, distribution to branch increased and to stem decreased with decreasing density of the stand. Among individual trees within a stand, the pattern of distribution was affected by the dominance of the tree in the stand. Generally speaking, distribution ratio into stem was lower and distribution ratio into the branches was higher in dominant trees. Fig. 16 shows an example of *Pinus densiflora* stand. In many cases distribution ratio into the stem was higher and the distribution ratio into the branches was lower in suppressed trees than medium trees, but there were some instances in which distribution ratio into the stem is lower in suppressed trees too (Fig. 17). On this subject, further studies are necessary.

In some cases, fairly wide variations in the pattern of distribution were recognized among trees of the same dominance. This may have some implications to the tree classification in thinning and selection of plus trees. We found two old trees of similar size of *Cryptomeria* in the same stand having quite different quantity of branches, in a natural forest. One of them had 721 kg of green leaves and 2740 kg of branches, and the other had 806 kg of green leaves and 785 kg of branches, though length of the crowns was not much different. In these trees distribution into stem and branch could be different. We are growing the graftings of them and preparing to propagate them to see if the difference is genetically controlled. If so, it may be possible to increase the distribution to the stemwood of produced matter and also timber yield by means of selection on this line. TODA¹⁵⁾ recently suggested the possibility of increasing timber yield by selecting narrow-crowned trees. It may be possible to increase the timber

yield by controlling the distribution of produced matter into parts of trees, despite the photosynthetic limitation of production¹⁶⁾.

In closing, I would like to emphasize again the necessity of the study of dry matter production in forest ecosystems as the basis of silviculture, though we are still on the first step of the study and there are many things to be done on this line.

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