

Some Discussions on the Leaf Biomass of Forest Stands and Trees.

Yoshiya TADAKI*

Since forestry has the purpose of yielding the stem wood of trees which is made from the organic substance produced by the foliage, it is naturally important for foresters to study the foliage of forests. But, it seems that foresters have regarded the foliage not so highly as the stems; therefore, in the study of forestry we find the available reports on leaf biomass of forest stands and the production efficiency of foliage scarce, contrary to our hopes and expectations. The course of the study on the metabolism of forests, on the other hand, has increased the necessity for more study concerning the foliage.

In this paper the available data on the foliage of forests investigated by various authors are taken up and some discussions are made. The discussed data include those worked out by the Joint Research Group of Four Universities, represented by Dr. T. SHIDEI, of which the author was a member, and by the Laboratory of Silviculture of Kyushu Branch, of which the author is a member. Acknowledgments are expressed to the staffs of these groups for the free use of their data.

The author would here point out that some parts of this paper have been reported by TADAKI and SHIDEI⁷⁰⁾, and by TADAKI⁶²⁾.

1. Leaf biomass in forests

Since the production of organic matter in higher plants depends mainly upon the photosynthesis by the foliage, a close relation of plant growth to the leaf biomass is undoubtedly significant. The photosynthesis being in need of the light which originates in the sun, the annual solar radiation along a certain terrestrial latitude has a constant value, and plant species growable on it are largely determined by the factors of temperature and other environmental characteristics. Therefore, the leaf biomass—strictly speaking, the chlorophyll amount—per unit ground area in a certain plant community could be expected to have a maximum value when the community is well covered with its foliage. Consequently, the leaf biomass per unit ground area in well closed forest stands may remain relatively constant for the same species.

MOLLER⁸⁴⁾ noted that the leaf biomass in *Fagus sylvatica* stands was comparatively constant regardless of the site, the age, the height and the degree of thinning, and also in *Picea abies* stands. Plantations of 13-year-old *Pinus densiflora* having various stand densities investigated by SATO *et al.*⁴⁹⁾ had the leaf biomass of 12 to 13 tons per hectare on a green weight basis. TADAKI *et al.*⁶⁷⁾ surveyed 10-year-old stands of *Betula platyphylla* v. *japonica* in different densities and estimated their leaf biomass to be 1.2 tons per hectare for oven dry weight and 3.5 in LAI—leaf area index—which indicates the ratio of leaf surface area (one side surface) to the ground surface.

Table 1 shows the various data on the leaf biomass in forests. It is notable that they seem to be somewhat similar not only for the same species but also for the related species, for instance, *Larix* spp., *Pinus* spp., and further for the same plant formation such as deciduous, evergreen,

* Laboratory of Silviculture, Kyushu Branch, Dr. Agri.

Table 1. Leaf biomass in forests.

Plant community	Location	Green weight t/ha	Oven dry weight t/ha	Leaf area index (ha/ha)	Investigator
<i>Fagus sylvatica</i>	Germany ?		3.3		EVERMEYER*
<i>Fagus sylvatica</i>	Denmark		2.1~2.7	4.3~5.5	MOLLER <i>et al.</i> (34, 35)
<i>Fagus sylvatica</i>	Denmark		3.1	5.4	BOYSEN JENSEN*
<i>Fagus sylvatica</i>	Switzerland	7.9	3.2	6.2~7.9	BURGER (10, 15)
<i>Fagus crenata</i>	Japan		2.81		OHMASA & MORI (41)
<i>Fagus crenata</i>	Japan		2.9~3.0		YAMADA & MARUYAMA (79)
<i>Fagus crenata</i>	Japan		6.7	5.2	IKUSHIMA (22)
<i>Nothofagus truncata</i>	Newzealand		2.7		MILLER***
<i>Quercus robur</i>	Denmark		1.7~2.0	2.6~3.1	MOLLER (34)
<i>Quercus robur</i>	Switzerland	14.3	5.3		BURGER (13)
<i>Quercus borealis</i>	U. S. A.		3.5		OVINGTON (44)
<i>Quercus</i>	U. S. S. R.		2.1~3.8		SONN***
<i>Quercus serrata</i>	Japan		2.33		OHMASA & MORI (41)
<i>Quercus mongolica</i> v. <i>grosseserrata</i>	Japan		0.93		OHMASA & MORI (41)
<i>Quercus mongolica</i> v. <i>grosseserrata</i>	Japan	7.3	2.5	4.4	TADAKI & TANIGUCHI (66)
<i>Quercus acutissima</i>	Japan		1.9~4.5		OHMASA & MORI (41)
<i>Fraxinus excelsior</i>	Denmark		2.7	5.4	BOYSEN JENSEN (6)
<i>Fraxinus mandshurica</i>	Japan	9.9	2.2	4.3	TADAKI & SHIRAI (66)
<i>Betula</i>	Scandinavia		1.3		MORK**
<i>Betula</i>	Scandinavia		1.5		NORDFORS**
<i>Betula</i>	Scandinavia		1.6		KUNDSEN & MAURITZ-HANSSON**
<i>Betula</i>	Germany ?	4.9			HARTIG*
<i>Betula verrucosa</i>	England		0.7~2.5	1.7~6.5	OVINGTON & MADGWICK (45)
<i>Betula verrucosa</i>	U. S. S. R.		2.8~3.8		SMIRNOVA & GORODENTSSEVA***
<i>Betula verrucosa</i>	Sweden		2.7		TAMM***
<i>Betula maximowiczii</i>	Japan		1.8~2.6		SATOO***
<i>Betula platyphylla</i> v. <i>japonica</i>	Japan	4.0	1.2	3.5	TADAKI <i>et al.</i> (67)
<i>Betula ermani</i>	Japan	10.6	2.4	5.2	KIRA <i>et al.</i> (unpubl.)
<i>Sapium sebiferum</i>	Japan		1.1~2.2	2.1~6.9	KIRA <i>et al.</i> (27)
<i>Populus davidiana</i>	Japan	5	2	2.2	SATOO <i>et al.</i> (50)
<i>Populus sieboldii</i>	Japan		1.3		OHMASA & MORI (41)
<i>Populus grandidentata</i>	Canada	3.52	1.55		BRAY & DUDKIEWICZ (7)
<i>Populus tremuloides</i>	U. S. A.	9.61	3.69	6.3	BRAY & DUDKIEWICZ (7)
<i>Zelkova serrata</i>	Japan	7	3	4	SATOO <i>et al.</i> (52)
<i>Zelkova serrata</i>	Japan		1.2~1.8		OHMASA & MORI (41)
<i>Ulmus parvifolia</i>	Japan	11	3	7	TADAKI & SHIDEI (66)
<i>Alnus</i> spp.	Japan		1.2~4.7		TSUTSUMI (76)
<i>Alnus sieboldiana</i>	Japan	7.5	4.3	5.9	SHIDEI <i>et al.</i> (66)
<i>Alnus hirsuta</i>	Japan	9.0	2.6	4.6	TADAKI & OGINO (66)

Table 1. (Continued)

Plant community	Location	Green weight t/ha	Oven dry weight t/ha	Leaf area index (ha/ha)	Investigator
<i>Alnus hirsuta</i> v. <i>sibirica</i>	Japan		2~4	3~5	SHIDEI <i>et al.</i> (66)
<i>Salix gracilistyla</i>	Japan	10.7	3.5		SHIDEI <i>et al.</i> (66)
<i>Salix vulpina</i>	Japan	5.6	2.3		SHIDEI <i>et al.</i> (66)
<i>Ligustrum tschonoskii</i>	Japan	10.2	2.5		SHIDEI <i>et al.</i> (66)
<i>Spiraea salicifolia</i>	Japan	4.3	0.7	3.9	TADAKI & OGINO (66)
<i>Robinia pseudoacacia</i>	Japan		2.5~4.0	5~7	TSUTSUMI <i>et al.</i> (66)
<i>Dipterocarp</i> savanna forest	Thailand		4.9	4.3	OGAWA <i>et al.</i> (40)
Mixed savanna forest	Thailand		4.9	4.2	OGAWA <i>et al.</i> (40)
<i>Machilus-Shiia</i>	Japan		10.1~13.1	7.4~9.6	KITAZAWA <i>et al.</i> (29)
<i>Distylium racemosum</i>	Japan		11.4	8.8	KITAZAWA <i>et al.</i> (29)
<i>Castanopsis-Machilus</i>	Japan		9.7		NOMURA & SATO (39)
<i>Castanopsis cuspidata</i>	Japan	27.3	11.4	12.5	TADAKI <i>et al.</i> (69)
<i>Castanopsis cuspidata</i>	Japan		6.8~9.6	6.0~8.3	KAN <i>et al.</i> (24)
<i>Castanopsis cuspidata</i>	Japan		7.4	8.0	TADAKI (62)
<i>Cinnamomum camphora</i>	Japan		4.1		SATOO***
<i>Camellia-Machilus</i>	Japan		12.6	6.3	MIYATA & SHIOMI (33)
<i>Acacia mollissima</i>	Japan	20~23	6.9~8.1		TADAKI <i>et al.</i> (71)
<i>Acacia mollissima</i>	Japan		9.9	9.7	TADAKI (63)
Tropical rain forest	Thailand		7.8	12.9	KIRA <i>et al.</i> (28)
Evergreen gallery forest	Thailand		19.5	16.6	OGAWA <i>et al.</i> (40)
Temperate evergreen forest	Thailand		14.5	12.6	OGAWA <i>et al.</i> (40)
Tropical evergreen forest	Congo		6.5		GREENLAND & KOWAL***
<i>Larix decidua</i>	Switzerland	5~7	1.8~2.6	5~7	BURGER (12)
<i>Larix decidua</i>	Denmark		2		MOLLER (34)
<i>Larix leptolepis</i>	Japan		3.3		SHIBAMOTO (54)
<i>Larix leptolepis</i>	Japan		2.03		OHMASA & MORI (41)
<i>Larix leptolepis</i>	Japan		2.8~4.5		SHIDEI <i>et al.</i> (58)
<i>Larix leptolepis</i>	Japan		3.69		SHIDEI <i>et al.</i> (58)
<i>Pinus sylvestris</i>	Switzerland	12~13	5	6.6~7.3	BURGER (11)
<i>Pinus sylvestris</i>	Scandinavia		4.9		AMILON**
<i>Pinus sylvestris</i>	Scandinavia		5		TIREN**
<i>Pinus sylvestris</i>	England		5.1~10.5	5.3~10.8	OVINGTON (43)
<i>Pinus sylvestris</i>	Scotland		4.7		WRIGHT & WILL***
<i>Pinus nigra</i>	Scotland		5.6		WRIGHT & WILL***
<i>Pinus densiflora</i>	Japan	12~13	5.3~5.4		SATOO <i>et al.</i> (49)
<i>Pinus densiflora</i>	Japan	12			MARUYAMA & SATO (32)
<i>Pinus densiflora</i>	Japan		5.5~9.7		KAWANABE <i>et al.</i> (25)
<i>Pinus densiflora</i>	Japan		4.0~7.0		HATIYA <i>et al.</i> (20)
<i>Pinus thunbergii</i>	Japan	20	8		KABAYA <i>et al.</i> (23)

Table 1. (Continued)

Plant community	Location	Green weight t/ha	Oven dry weight t/ha	Leaf area index (ha/ha)	Investigator
<i>Pinus longifolia</i>	W. Pakistan		2.8		KAWANABE <i>et al.</i> (25)
<i>Pinus excelsa</i>	W. Pakistan		4.5~4.7		KAWANABE <i>et al.</i> (25)
<i>Pinus strobus</i>	Switzerland	16~20		14~17	BURGER (8)
<i>Pinus strobus</i>	Japan	18~20	7.4~10.1		SENDA & SATOO (53)
<i>Pinus banksiana</i>	U. S. A.		4.9		HANSEN*
<i>Pinus banksiana</i>	U. S. A.		6		ADAMS*
<i>Pinus pumila</i>	Japan		21.67		SHIDEI (55)
<i>Picea abies</i>	Denmark		12	13.1	MOLLER (34)
<i>Picea abies</i>	Switzerland	33~34	15~20	17~28	BURGER (11)
<i>Picea abies</i>	U. S. S. R.		9.6~11.1		SONN***
<i>Picea abies</i>	Japan		16.9~24.6		SATOO***
<i>Picea abies</i>	Sweden		9.1~10.8		TAMM & CARBONNIER***
<i>Picea glehnii</i>	Japan	35	7.35		SHIDEI <i>et al.</i> (57)
<i>Picea mariana</i>	Canada		8.56	9.8	WEETMAN & HARLAND (78)
<i>Pseudotsuga douglasii</i>	Switzerland	27~44		18.4~27.1	BURGER (9)
<i>Pseudotsuga taxifolia</i>	U. S. A.		8.0~12.0		HEILMAN***
<i>Abies alba</i>	Switzerland	29		17	BURGER (16)
<i>Abies sachalinensis</i>	Japan	55	19.1		SHIDEI <i>et al.</i> (57)
<i>Abies mariesii</i> — <i>A. veitchii</i>	Japan		8.6~12.1		OSHIMA <i>et al.</i> (42)
<i>Abies veitchii</i>	Japan		7.6~14.4		ASADA & AKAI (2)
<i>Chamaecyparis obtusa</i>	Japan	23~24	9.5~10.0		SATOO & SENDA (51)
<i>Chamaecyparis obtusa</i>	Japan			11.04	FUJII (19)
<i>Chamaecyparis obtusa</i>	Japan	25			TSUTSUMI <i>et al.</i> (70)
<i>Cryptomeria japonica</i>	Japan	44~46	17~18		TSUTSUMI <i>et al.</i> (70)
<i>Cryptomeria japonica</i> (Yabukuguri cultivar)	Japan	38.3~52.7	16.5~22.7	9.4~13.0	TADAKI <i>et al.</i> (73)
<i>Cryptomeria japonica</i> (Aka cultivar)	Japan	40.3~59.6	17.3~25.6	10.0~14.7	TADAKI <i>et al.</i> (73)
<i>Cryptomeria japonica</i>	Japan	43.3~54.5	16.7~21.8	10.7~13.5	TADAKI <i>et al.</i> (72, 73)
<i>Cryptomeria japonica</i>	Japan		26.5	17.2	TADAKI & KAWASAKI (74)

Remarks:

1. This table is mainly referred to TADAKI and SHIDEI⁽⁷⁰⁾ and TADAKI⁽⁶¹⁾.
2. Key to References. *SATOO⁽⁴⁶⁾; **MOLLER⁽³⁴⁾; ***OVINGTON⁽⁴⁴⁾.
3. Leaf area index is presented on one side basis for broad leaved species and on whole side basis for needle leaved species.

Table 2. Reasonable range of leaf biomass in forests.

	Green weight t/ha	Oven dry weight t/ha	Leaf area index (ha/ha)
Deciduous broad leaved forest	6~8	2~3	4~6
Evergreen broad leaved forest	20~25	7~11	7~12
Deciduous coniferous forest	6~8	2~3	5~7
<i>Pinus</i> forest	12~15	5~6	7~12
Evergreen coniferous forest	30~35	9~15	15~20
<i>Cryptomeria</i> forest	45~55*	17~23*	12~15*

* green parts.

broad leaved or needle leaved forest. The leaf biomass in the forest from cool to warm temperate zones can be summarized as in Table 2 for every plant formation. In a formation, the leaf biomass per unit ground area for the so-called shade tree forest tends to be a little more than that for the sun tree one.

The leaf biomass in the deciduous broad leaved forest having the range between two and three tons per hectare on the oven dry weight basis is the minimum unit of the leaf biomass in a closed stand, and this may be called *the basic amount of foliage*. As TSUTSUMI⁷⁶⁾ reported, annual leaf falls in various evergreen forests amount to from 1.5 to 3.5 tons per hectare except for several laurel forests. This value is about as much as the basic amount of foliage. When the leaf biomass per stand has remained constant, the amount of annual leaf fall in an evergreen forest must be equal to that of the annual leaf regeneration. In other words, in a closed stand the basic amount of foliage, from two to three tons per hectare, gives the amount of foliage renewed annually regardless of the leaf biomass per stand in each plant formation.

The proportional relation is found between the amount of foliage in a forest and the life span of its leaves, the gradient of which is given by the basic amount of foliage; for instance, the leaf biomass of a *Pinus* stand, the life span of which is about two years on an average, is twice as much as the basic amount of foliage, and that of *Picea* or *Abies* stands, the life span being six or seven years, are six or seven times larger than the basic amount of foliage.

The case of the leaf weight for *Cryptomeria japonica* stand is an exception, because all green parts including scaly leaves and twigs of this species have been tentatively noted as foliage owing to the indistinctness between foliage and twigs.

The fact that the leaf biomass per unit ground area remains constant in closed forests of the same species seems to result from the limited intensity of light, although other needed factors for photosynthesis, i. e. water, temperature, etc. differ widely. We could say that light is the limiting factor of increasing foliage. MONSI and SAEKI³⁶⁾ have suggested the existence of an optimum leaf biomass in a plant community which realizes its maximum net organic matter production, since respiration loss by lower living foliage which cannot but receive less light than at the compensation point becomes relatively larger below an over-crowded leaf mass. The constant leaf biomass is arranged by the phenomenon that lower living leaves are withered and shed from the lack of light resulting from the influence of living leaf biomass above.

As the organic matter production is comparatively proportional to the leaf biomass for the same species, where site conditions are enough to make a stand close, the entire growth of a closed forest should be constant however rich the site may be. For instance, if a well closed

forest is given more water, its growth is never expected to increase with the amount of given water. Accordingly, artificial improvements of the site condition such as fertilization should make the growth of a closed stand increase less than that of an unclosed one.

But, in the case of a poorer site condition such as extreme shortage of water even if the light factor is fully sufficient, a forest cannot hold enough foliage as its growth is closely connected with water, in other words, the deficiency of water prevents the forest from closing its canopy. The desert is an example in this case, and there forestry management is non-existent.

2. Changes in leaf biomass

Microscopically considered, however, the periodical change of leaf biomass in a forest seems to have a considerable range. Especially in a deciduous forest its canopy closing and leaf falling are repeated every year. According to observations by TADAKI and SHIDEI⁶⁶⁾ in a dense stand of three-year-old *Ulmus parvifolia* its foliage increased toward a maximum of 14 in LAI during 50 days after the leaf emergence, followed by a gradual decline, then became almost constant as shown in Fig 1. The decline of leaf biomass was caused by successive falling of shaded leaves in lower layers owing to over-crowding.

In Fig. 2, the relations between the leaf biomass and the age of stand are shown. A rapid increase of leaf biomass toward a maximum is followed by a gradual decline in the same way as the monthly change of *Ulmus* previously mentioned. The canopy closure may be completed in a few years before the time of the maximum leaf biomass. The stands of *Abies* in the picture have been surveyed by OSHIMA *et al.*⁴²⁾ at Mt. Shimagare, where all *Abies* forests aged about 100 years perish naturally and the next generations develop. The leaf biomass of these *Abies* forests

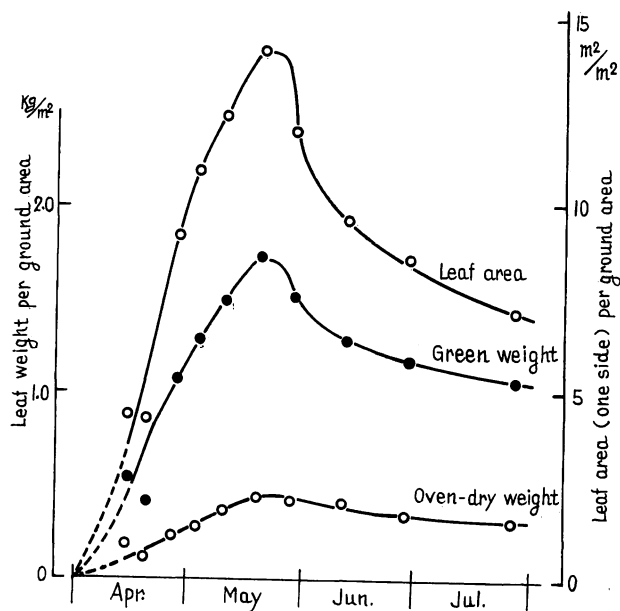


Fig. 1 Seasonal change of leaf biomass in a three-year-old *Ulmus parvifolia* stand (TADAKI and SHIDEI⁶⁶⁾).

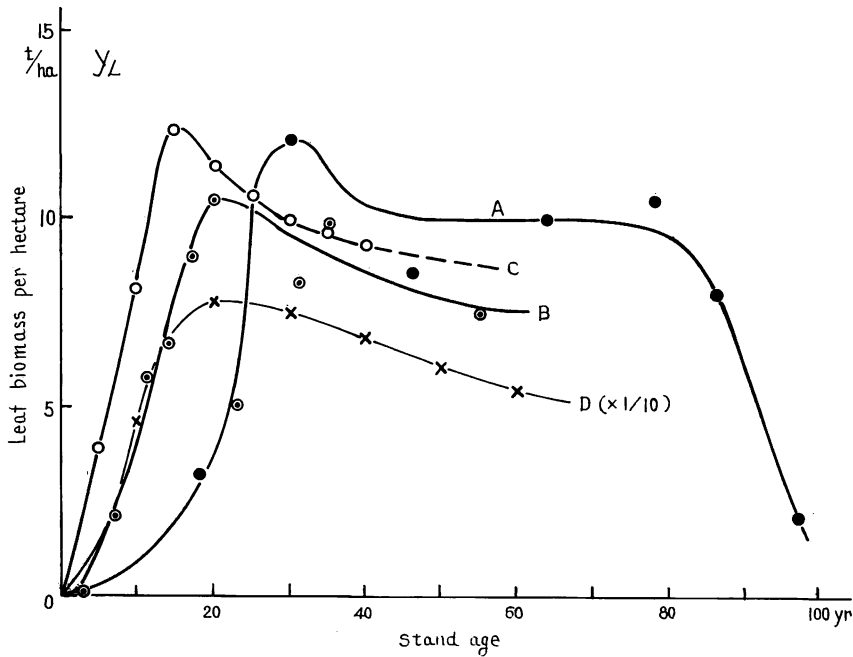


Fig. 2 Yearly changes of leaf biomass in forests.

- A: *Abies veitchii*—*A. mariesii* forest, in oven dry weight (OSHIMA *et al.*⁴²⁾)
 B: *Pinus sylvestris* forest, in oven dry weight (OVINGTON⁴³⁾)
 C: *Pinus densiflora* forest, in green weight (MARUYAMA and SATO³²⁾)
 D: *Cryptomeria japonica* forest, in $1/10 \times$ green weight (YURUKI³¹⁾)

decreases remarkably in stands over 80 years of age. The curve for *Pinus densiflora* estimated by MARUYAMA and SATO³²⁾ is noteworthy in the point of reasonable relation between the leaf biomass becoming maximum at about 15 years, and the current annual increment in the stem volume yield table attaining its maximum at about 20 years.

3. Vertical distribution of leaf biomass in forests

Foliage as the organ, and light as the energy, are the essential factors in the photosynthetic activity. A part of the incident light upon a canopy is reflected and used for the photosynthesis, and the rest passes downwards through the leaf mass. Consequently, the light intensity within a canopy decreases with descending leaf layers. MONSI and SAEKI³⁶⁾ have applied the following equation to the light intensity in the canopy which has been called the formula of Beer-Lambert,

$$I = I_0 e^{-KF} \dots \dots \dots (1)$$

where I expresses the light intensity under the leaf area index F , I_0 the incident light intensity, and K the extinction coefficient. The value of K is the specific constant determined by the size, shape, arrangement, inclination and transmissibility of the leaves. The extinction coefficients in various tree communities shown by Table 3 seem to be somewhat smaller than in grass and herb plants.

Since the ability of photosynthesis in lower living leaves cannot be regarded as that in upper

Table 3. Relative light intensity under canopy and extinction coefficient (K , K') in forests. K : calculated after Eq. (2), K' : oven dry leaf weight basis in place of leaf area index.

Plant community	Relative light intensity %	K (ha/ha)	K' (ha/t)	Source
<i>Betula platyphylla</i> v. <i>japonica</i>	5.4	0.83	2.43	TADAKI <i>et al.</i> (67)
<i>Betula ermani</i>	14.9	0.37	0.88	KIRA <i>et al.</i> (unpubl.)
<i>Fraxinus mandshurica</i>	3.3	0.79	1.55	TADAKI & SHIRAI (61)
<i>Quercus mongolica</i> v. <i>grosseserrata</i>	2.6	0.83	1.44	TADAKI & TANIGUCHI (61)
<i>Alnus hirsuta</i>	9.8	0.50	0.89	TADAKI & OGINO (61)
<i>Spiraea salicifolia</i>	6.0	0.72	4.02	TADAKI & OGINO (61)
<i>Ulmus parvifolia</i>	2.9	0.50	1.18	TADAKI & SHIDEI (66)
<i>Populus davidiana</i>	10.0	1.05	1.15	SATOO <i>et al.</i> (50)
<i>Machilus-Shiia</i>	2.5	0.38~0.50	0.28~0.37	KITAZAWA <i>et al.</i> (29)
<i>Distylium racemosum</i>	2.5	0.42	0.32	KITAZAWA <i>et al.</i> (29)
<i>Castanopsis cuspidata</i>	0.7	0.40	0.44	TADAKI <i>et al.</i> (69)
<i>Castanopsis cuspidata</i>	3.7	0.41	0.44	TADAKI (62)
<i>Acacia mollissima</i>	4.0		0.46	TADAKI <i>et al.</i> (71)
<i>Acacia mollissima</i>	3.1	0.35	0.34	TADAKI (63)
<i>Pinus densiflora</i>	2.1		0.40	TADAKI & SHIDEI (68)
<i>Picea glehnii</i>	1.2		0.49	SHIDEI <i>et al.</i> (57)
<i>Cryptomeria japonica</i>	0.6		0.26	TADAKI <i>et al.</i> (72)
<i>Cryptomeria japonica</i>	1.1	0.26	0.17	TADAKI & KAWASAKI (74)
Grass communities		÷ 0.5		MONSI & SAEKI (36)
Herbaceous communities		0.7~1.2		MONSI & SAEKI (36)

living ones, leaves can demonstrate their full abilities on the condition that they live in upper layers. Therefore, it is important to study the relation of the vertical distribution of leaf biomass to the light intensity, and also to the vertical distribution of non-photosynthetic parts, mainly stems, branches and roots, which have been produced by foliage. MONSI and SAEKI³⁶⁾ have introduced the stratified clip technique and presented the *productive structure diagram* in herbaceous plant communities.

Some vertical distributions of foliage for forests are shown in Fig. 3, in which the dotted curves express the variations of relative light intensities inside the canopies estimated by $100 \times I/I_0$ after Eq. (1). Two types of the vertical distribution of foliage have been recognized, herb-type and grass-type³⁶⁾. In the former the leaves appear mainly in relatively upper strata, and in the latter in relatively lower strata. In the case of forests, a pure and even-aged stand tends to be the herb-type and a many-aged stand the grass-type. Furthermore, a deciduous broad leaved stand is liable to be the herb-type and an evergreen needle leaved stand the grass type²⁷⁾ shown as examples by *Betula* and *Picea* respectively in Fig. 3. But in a needle leaved forest displaying the grass-type, admitting that it is even-aged, the grass-type distribution may progress to the herb-type one because of the vertical length of the canopy becoming relatively shorter than tree height by shedding of branches with the development of growth stage. Besides

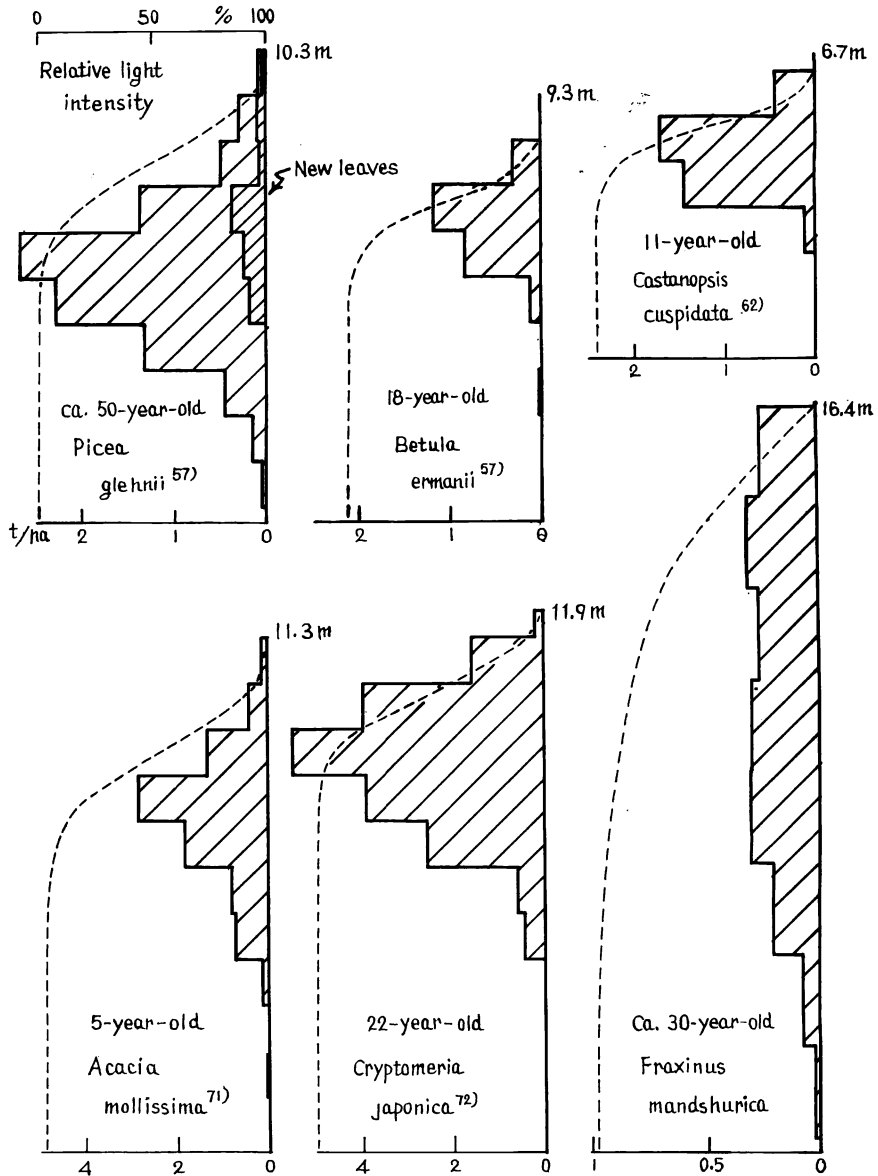


Fig. 3 Vertical distributions of leaf biomass in forests (oven dry weight).

these two types, another type in which the leaves distributed relatively constant from the top to the bottom of a stand has been found in the stands of *Larix leptolepis*⁶⁸⁾, *Fraxinus mandshurica* (in Fig. 3, TADAKI and SHIRAI, unpublished) and *Ulmus parvifolia* in the earlier stage of leaf emergence⁶⁶⁾.

4. Leaf biomass in a tree

The amount of foliage per tree is determined by a tree's size and increases with the growth of the tree. KITTREDGE⁸⁰⁾ has presented the relation between the amount of foliage of a tree (w_L)

and its DBH (D) as the following equation;

$$\log w_L = b \log D - a \quad (a, b: \text{constants}) \dots\dots\dots (2)$$

which has been utilized for the estimation of the leaf biomass of a stand from several sample trees. This is no more than the allometric relation which was proposed by HUXLEY as the relation between the amounts of two different organs in animals of the same species.

The value of the allometric constant b was noted by KITTREDGE⁸¹⁾ to range from 1.15 to 3.3 in several species and also compiled by HOZUMI⁸²⁾ to be from 1.85 to 2.13 for broad leaved trees, *Pinus*, *Cryptomeria* and *Chamaecyparis*, and from 2.35 to 2.62 for coniferus trees such as *Abies* and *Picea*.

When the constant b values two, the amount of foliage is proportional to D^2 or to the cross sectional area at the breast height. The relation of w_L to basal area (S); $w_L = KS$ (K : constant), given by YAMAOKA⁸⁰⁾ is the same as Eq. (2) when the constant b values two.

Many variations of Eq. (2) have been presented, such as D^2H (D : DBH, H : height)⁸⁷⁾, the diameter of crown⁸¹⁾, and the diameter at the branch base⁸³⁾ being employed in place of D . Eq. (2), however, may be more useful than others because of the easiness of DBH measuring.

The constants a and b in Eq. (2) seem to be similar for the individuals of the same plant life form in the same forest stand respectively, for instance, KITAZAWA *et al.*²⁹⁾ and KIMURA²⁶⁾ in laurel forests, SHIDEI *et al.*⁸⁷⁾ in *Picea* and *Abies* forests.

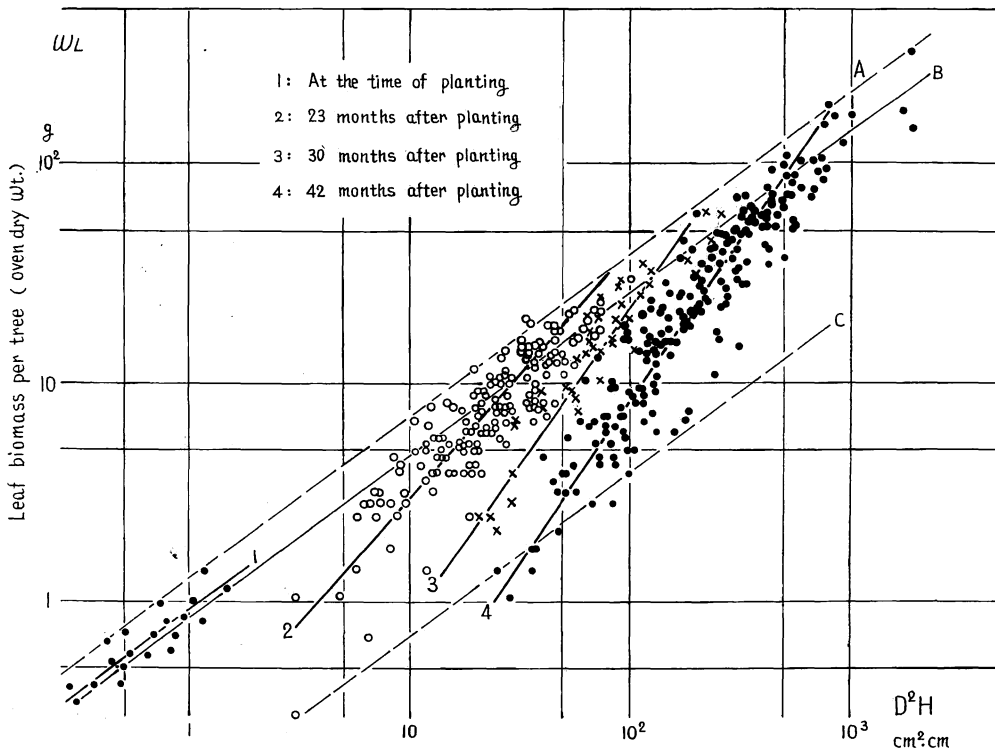


Fig. 4 Periodical change on the allometric relation between leaf biomass and D^2H per tree in a small stand of *Pinus densiflora* (TADAKI and SHIDEI⁶⁸⁾)
—on log-log axes.

But some disturbing fluctuations are liable to creep in here, because the constants a and b are not equal in all stands of the same species. That the constants in Eq. (2) vary with the growth stage, the competition and the site condition has been reported by TADAKI and SHIDEI⁶⁸⁾, ANDO *et al.*¹⁾ and SATO⁴⁷⁾⁴⁸⁾. Also TADAKI⁶¹⁾ previously made a discussion on this point with the following Figs. 4, 6 and 8.

In Fig. 4⁶⁸⁾, the periodical change of the allometric relations between D^2H and the leaf oven dry weight for a young stand of *Pinus densiflora* is shown, where D and H denote the diameter at stem base and the height per tree respectively. The stand was planted with 10 cm × 10 cm spacing of one-year-old seedlings; afterwards trees were sampled from the stand five times during four years and measured for leaf weights, diameters, and heights. The picture in which D^2H is used in place of D in Eq. (2) shows the variation of the leaf weight to D^2H , the regression line removing rightwards progressively with the time or the growth stage. Three lines are tentatively settled independently of the growth stage; line-A is settled for the upper limit of the leaf weight dealing with D^2H , line-B for the relatively dominant individuals consisting in the upper canopy of the stand, and line-C for the lower limit of the leaf weight which is required by an individual to keep itself up. Line-A, -B and -C are given the same gradients tentatively and the vertical intersection of line-C seems to be about 1/10 of that of line-A. These must be

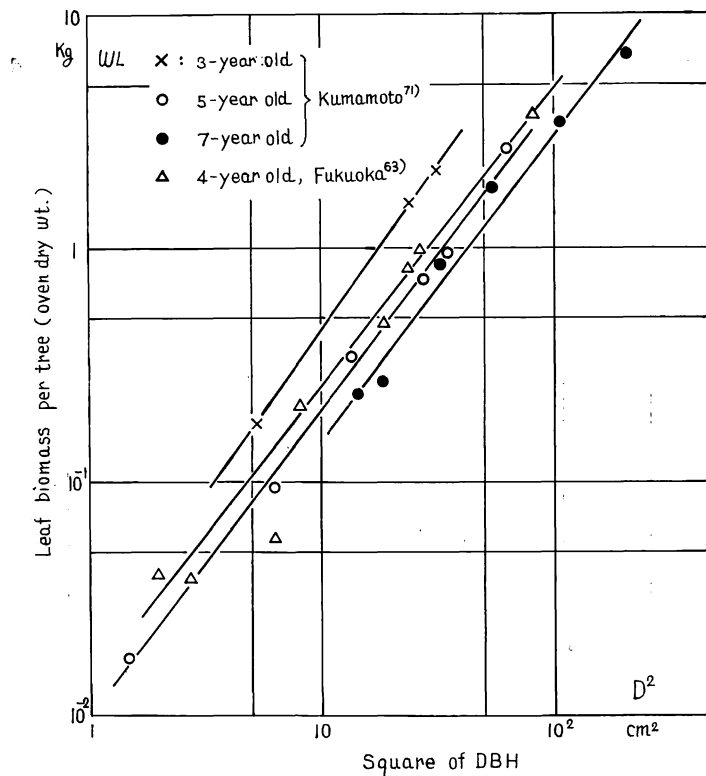


Fig. 5 Allometric relations of leaf biomass to square of DBH per tree in different aged *Acacia mollissima* stands in Kyushu (TADAKI *et al.*⁷¹⁾, TADAKI⁶⁸⁾) —on log-log axes, Three-, five- and seven-year-old stands are all near neighbors with similar site conditions.

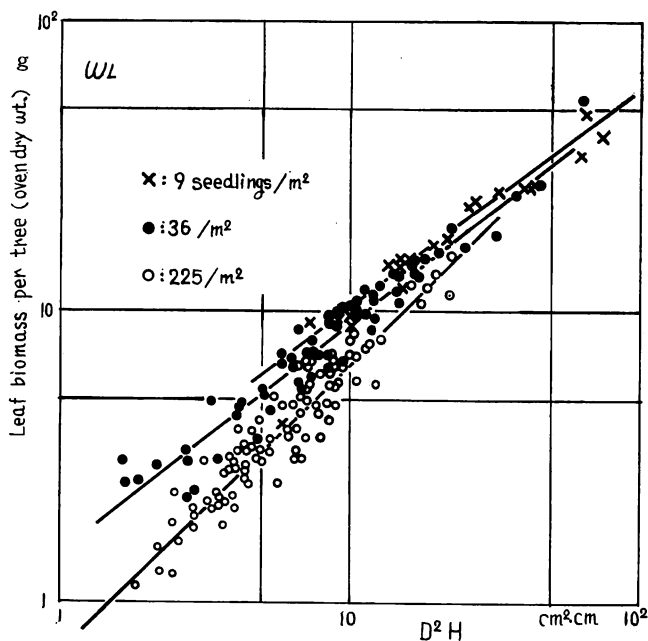


Fig. 6 Allometries of leaf biomass to D^2H per tree in different spaced seedlings of *Cryptomeria japonica*—on log-log axes.

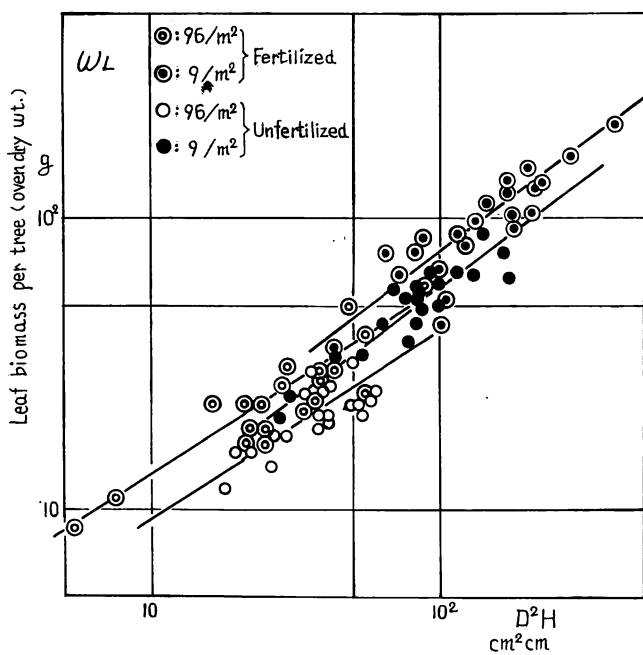


Fig. 7 The allometric relations between leaf biomass and D^2H per tree for cuttings of *Cryptomeria japonica* in different spacings and soil conditions (TADAKI *et al.*⁷⁶⁾)—on log-log axes.

further examined.

The change of the relation of the leaf oven dry weight of *Acacia mollissima*⁷¹⁾⁶³⁾ to D^2 (square of DBH) is also indicated in Fig. 5, three of these regressions dealing with the plantations situated near to each other and on the similar site. The relation tends to move to the right hand of the picture with the age of plantation.

In Fig. 6 the relations between the leaf oven dry weight and D^2H (D : diameter at stem base) with the different transplanting densities are shown. Yearling *Cryptomeria japonica* seedlings had been transplanted in different densities with the range between 9 and 225 individuals per square meter of the ground area and their increments were investigated after one year. The picture indicates the relations as to the three densities of 9, 36 and 225 seedlings per square meter, showing the different regressions independently. The gradient of the regression line increases and the ordinate intersection decreases with increasing density.

Further observations on the relations of the leaf oven dry weight to D^2H (D : diameter at stem base) are also shown in Fig. 7 which is drawn using a part of the following experi-

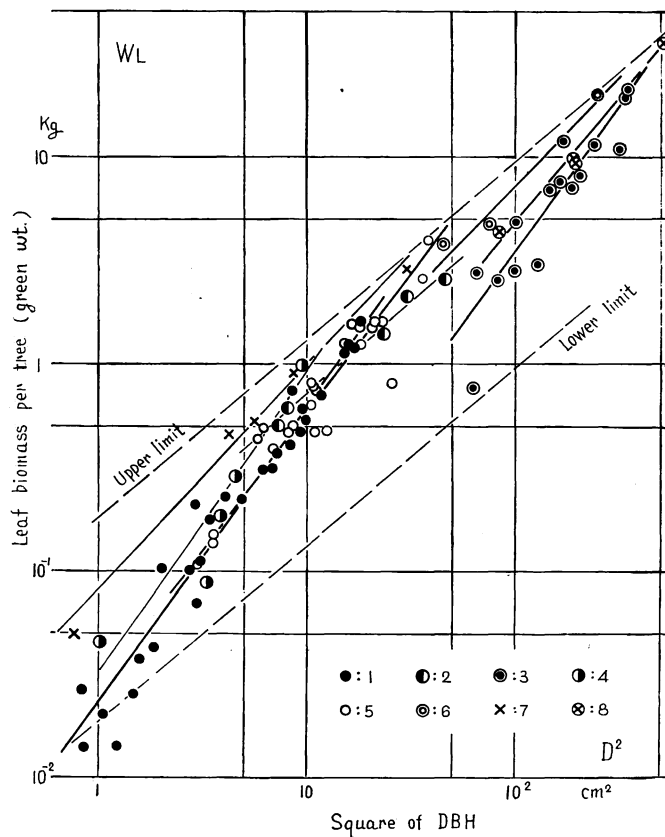


Fig. 8 Allometric relations between leaf biomass and DBH per tree in *Betula* stands of Hokkaido—on log-log axes. 1: *Betula platyphylla* v. *japonica* 10-year-old stand (TADAKI *et al.*⁶⁷⁾), 2: ditto ca. 20-year-old, 3: ditto 45-year-old, 4: ditto ca. 10-year-old, 5: *B. ermani* 18-year-old, 6: ditto ca. 40-year-old, 7: *B. maximowiczii* seven-year-old, 8: ditto 43-year-old.

ment data⁷⁵⁾: cuttings of *Cryptomeria japonica* were cultivated on fertilized and unfertilized beds in different spacings of from 9 to 96 cuttings per square meter of the ground area for one year. It can be recognized that the regressions differ with the density and fertilizing.

Since the allometric relation varies with the growth stage, competition, site condition, etc. as previously stated, the relation in the mature stand should be peculiar to the stand. TADAKI⁶¹⁾ studying the allometrics of the leaf green weight in three species of *Betula* to the square of DBH in Fig. 8, found the segregation of the regression to be more obvious among forest stands than among species, and conjectured the upper and lower limits of the leaf weight to DBH. Also, a similar situation of the relations between the leaf oven dry weight and square of DBH for *Cryptomeria japonica* is shown in Fig. 9.

Therefore, SATO⁴⁷⁾ has stated that the regression obtained for a particular stand can not be safely used for other stands of the same species, especially if they are of different nature, and TADAKI⁶¹⁾ has also noted that the segregation of the allometric relation may be more remarkable in the foliage than in other organs and in light demanding trees than in shade tolerant ones. KITTREDGE's formula —Eq. (2)— is applicable to individuals forming an upper canopy and to the upper- and lower-limit of leaf biomass to DBH. SHINOZAKI *et al.*⁶⁰⁾ has presented the direct proportionality between the leaf biomass and the cross-sectional area of the stem at the height just below the lowest living branch in place of DBH.

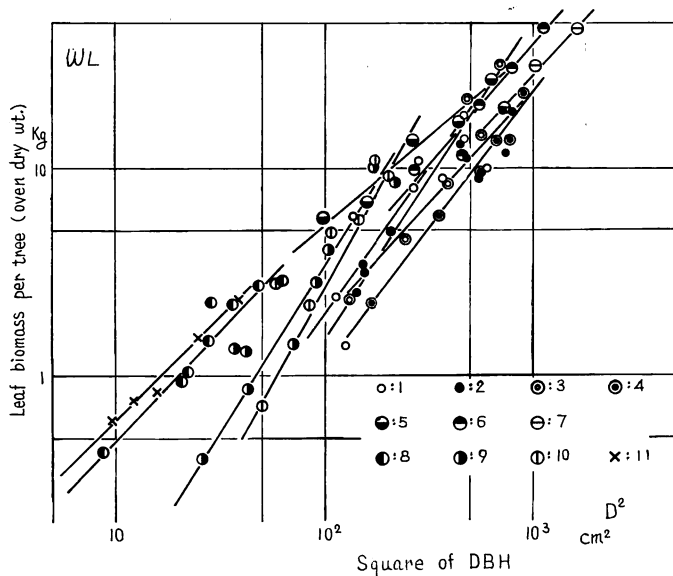


Fig. 9 Allometries of leaf biomass to square of DBH per tree in *Cryptomeria japonica* stands of Kyushu—on log-log axes. 1: Yabukuguri-cultivar thin 34-year-old stand, 2: ditto dense 34-year-old, 3: seed origin 27-year-old, 4: Aosugi-cultivar 27-year-old, 5: Aka-cultivar 24-year-old, 6: ditto 34-year-old, 7: ditto 49-year-old, 8: seed origin 11-year-old, 9: ditto 22-year-old, 10: ditto 31-year-old, 11: grafted elite five-year-old (1, 2, 5~7: TADAKI *et al.*⁷³⁾, 8~10: TADAKI *et al.*⁷³⁾, 11: TADAKI and KAWASAKI⁷⁴⁾).

5. Leaf efficiency

In general, the growth of a plant is determined by both the leaf biomass and the assimilation rate. The relation among the relative growth rate (RGR), the net assimilation rate (NAR) and the leaf area ratio (LAR) has been presented and the discussion on it has been developed by English investigators:

$$\text{RGR} = \text{NAR} \times \text{LAR} \quad \dots\dots\dots (3)$$

$$r = \frac{1}{A} \frac{dw}{dt} \times \frac{A}{w} \quad \dots\dots\dots (3')$$

where r represents the growth rate per unit time (RGR) of a plant having the weight w and the leaf area A , and t denotes the time.

NAR has been reported to be relatively constant for the same species and to have the range between 0.12 and 0.72 grams dry matter per 100 square centimeters leaf area per week among higher plants³⁷⁾. BLACKMAN and BLACK⁴⁾⁵⁾ found increasing NAR with increasing light intensity and with decreasing planting density, and WATSON⁷⁷⁾ noted proportional decreasing of NAR to increasing leaf area index.

NAR for one-year-old *Populus japono-gigas* has a range from 0.2 to 0.6 grams per 100 square centimeters per 10 days with a maximum in summer (NEGISHI *et al.*³⁸⁾). TADAKI and SHIDEI⁶⁶⁾ observed that NAR decreased with increasing leaf biomass after the leaf emergence in three-year-old

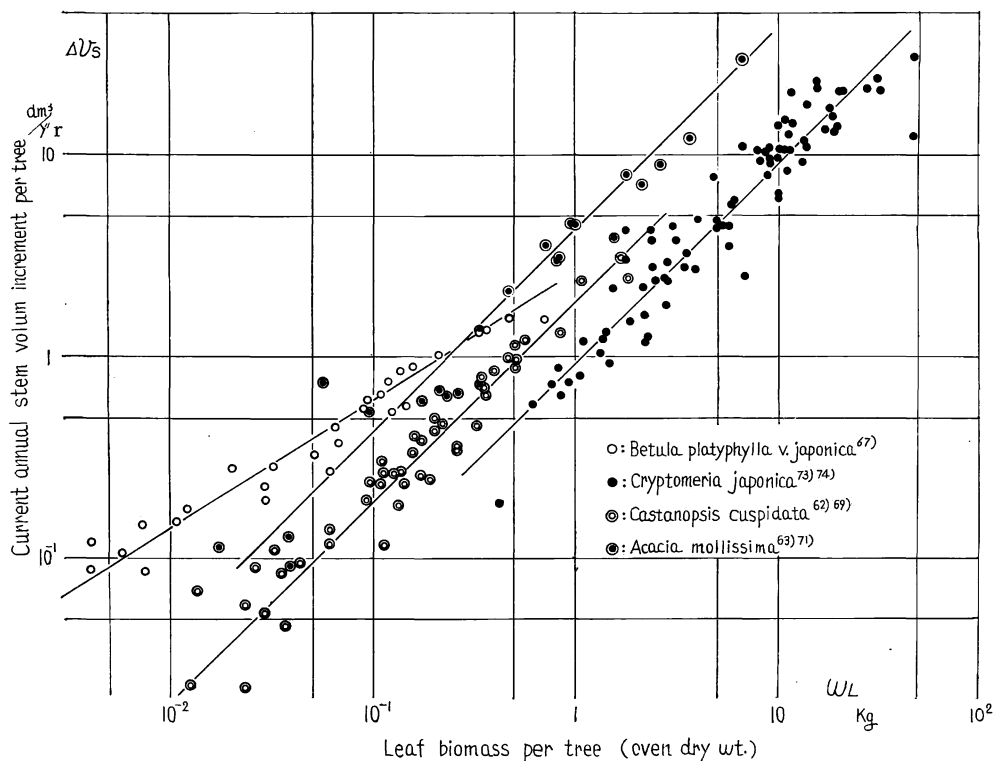


Fig. 10 Relation between annual stem volume increment and leaf biomass per tree—on log-log axes.

Table 4. Annual stem volume increment per unit leaf weight—leaf efficiency—in tree species.

Tree species	Stem increment per green leaf weight dm ³ /kg/year	Stem increment per oven dry leaf weight dm ³ /kg/year	Source
<i>Fagus sylvatica</i>	1.25		BURGER (10, 15)
<i>Fagus sylvatica</i>		4.4	MOLLER (34)
<i>Quercus robur</i>	1.2		BURGER (13)
<i>Fraxinus excelsior</i>		3.2	MOLLER (34)
<i>Fraxinus mandshurica</i>	0.33	1.47	TADAKI & SHIRAI (unpubl.)
<i>Fraxinus griffithii</i>	1.0	2.7	TADAKI & TAKEMOTO (unpubl.)
<i>Zelkova serrata</i>	0.9~1.2	2.3~3.2	SATOO <i>et al.</i> (52)
<i>Betula</i> sp.		3.8	KUNDSSEN & MAURITZ-HANSSON*
<i>Betula platyphylla</i> v. <i>japonica</i>	2.0	6.6	TADAKI <i>et al.</i> (67)
<i>Populus davidiana</i>	2.48		SATOO <i>et al.</i> (50)
<i>Castanopsis cuspidata</i>	0.7	1.65	TADAKI <i>et al.</i> (69)
<i>Quercus glauca</i>	0.5	1.12	TADAKI <i>et al.</i> (69)
<i>Acacia mollissima</i>		3.7	TADAKI <i>et al.</i> (71)
<i>Larix leptolepis</i>	0.65	2.1	SHIDEI <i>et al.</i> (58)
<i>Larix decidua</i>	1.5		BURGER (12)
<i>Larix decidua</i>		5.5	MOLLER (34)
<i>Pinus strobus</i>	0.9~1.0		SENDA & SATOO (53)
<i>Pinus sylvestris</i>	1.0		BURGER (11, 14)
<i>Pinus sylvestris</i>		2.2	AMILON*
<i>Pinus densiflora</i>	1.2		SATOO <i>et al.</i> (49)
<i>Picea abies</i>	0.5~0.6		BURGER (11, 17, 18)
<i>Picea abies</i>		1.4	MOLLER (34)
<i>Picea glehnii</i>	0.4	1.3	SHIDEI <i>et al.</i> (57)
<i>Picea mariana</i>		0.5~0.7	WEETMAN & HARLAND (78)
<i>Abies alba</i>	0.6		BURGER (16)
<i>Abies sachalinensis</i>	0.5	1.3	SHIDEI <i>et al.</i> (57)
<i>Pseudotsuga douglasii</i>	0.7		BURGER (9)
<i>Chamaecyparis obtusa</i>	0.5		SATOO <i>et al.</i> (51)
<i>Cryptomeria japonica</i>	0.34	1.03	TADAKI & SHIDEI (64)
<i>Cryptomeria japonica</i>	0.2~0.5	0.5~1.1	TADAKI <i>et al.</i> (73)
<i>Cryptomeria japonica</i>	0.3~0.4	0.7~1.0	TADAKI <i>et al.</i> (72)

* : after MOLLER³⁴⁾

Ulmus parvifolia and HATIYA *et al.*²⁰⁾ found decreasing NAR with higher stand density in mature stands of *Pinus densiflora*.

In forestry, the stem increment caused by the assimilation in leaves or the stem growth per unit leaf biomass is in itself an important subject. Besides, the growth measurement of stems is so much easier than that of branches and roots that various investigations are practicable.

The relations between the oven dry weight of the foliage present (w_L) and the stem volume increment in the recent one year (Δv_s) per tree in some tree species are indicated in Fig. 10.

Although the observed values belonging to different stands are scattered in a wide zone along the regression line, the specific trend can be recognized as

$$\log \Delta v_s = b \log w_L + a \quad (a, b: \text{constant}) \quad \dots\dots\dots(4)$$

and the gradient b of each line on the double logarithmic axes nearly equals one except the regression for *Betula*. When the gradient values one, the current annual stem growth increases in simple proportion to the weight of foliage present, and the ordinate intersection a gives the current annual stem growth per unit leaf weight. That the gradient for *Betula* is smaller than one shows the rate of current annual stem growth to the leaf weight decreasing with larger amount of foliage in a tree. This may be caused by the fact that the broad leaved species, especially *Betula*, has thicker branches and make a flatter canopy than the needle leaved one, so that the lower living leaves are relatively less able to catch the sunlight.

SATOO *et al.*⁴⁹⁾⁵²⁾ have introduced the leaf efficiency which expresses the annual increment in stem volume per unit amount of foliage and classified the relations between the leaf efficiency and the leaf biomass per tree into three groups; the stem increment being proportional to the leaf biomass, the peak leaf efficiency having an optimum leaf biomass, and the efficiency declining with larger leaf biomass. Although these situations have been collected and discussed by SATOO *et al.*⁵²⁾, the efficiency is effected from various conditions such as site, stand density, or thinning, so that we cannot give a definite description on the tendency of the leaf efficiency. However, the rough values of the stem increment per unit leaf weight in several tree species are shown in Table 4, which is mainly made up of the figures arranged by SATOO⁴⁶⁾ and MOLLER⁸⁴⁾.

The leaf efficiency for broad leaved species seems to be larger than for needle leaved ones, and for deciduous trees and sun trees larger than for evergreen ones and shade ones respectively. BOYSEN JENSEN⁶⁾ has reported that the sun leaves in sun trees have much larger production capacities than the most distinguished sun leaves in shade trees in the full daylight. The leaf efficiencies in needle shade trees such as *Picea* and *Abies* are smaller than a half of those in deciduous sun trees. But, since the leaf biomass per stand in the former is several times larger than in the latter, it would seem that *Picea* and *Abies* exceed deciduous sun trees in the stem increment per stand.

The case of *Acacia mollissima* is noteworthy, because the leaf efficiency in this species is much greater than in other evergreen broad leaved trees in spite of the leaf biomass per stand of *Acacia* being common among the evergreen broad leaved forests⁶⁸⁾⁷¹⁾ (cf. Table 1).

6. Vertical distributions of leaf biomass and of stem increment

The productive structure diagram introduced by MONSI and SAEKI⁹⁶⁾ has developed the studies on the vertical distributions of foliage and of other non-photosynthetic organs within a plant community. The vertical distribution of foliage as related to the light absorption has been discussed by several plant ecologists. SHINOZAKI *et al.*⁵⁹⁾ developed their *pipe model theory* in which the relation between the amount of non-photosynthetic organs at a certain height in a community and that of foliage above that height was made clear. TADAKI and SHIDEI⁶⁵⁾⁵⁶⁾ have also made investigations on the vertical distributions of foliage and of stem increment and proposed the *production structure diagram with stem growth*. Here some descriptions and applications concerning this are given.

Since MONSI and SAEKI's productive structure diagram has been developed in herbaceous plant communities whose non-photosynthetic organs are mainly produced by present foliage, for an aged woodland their diagram cannot give the accurate interrelation of the foliage present to

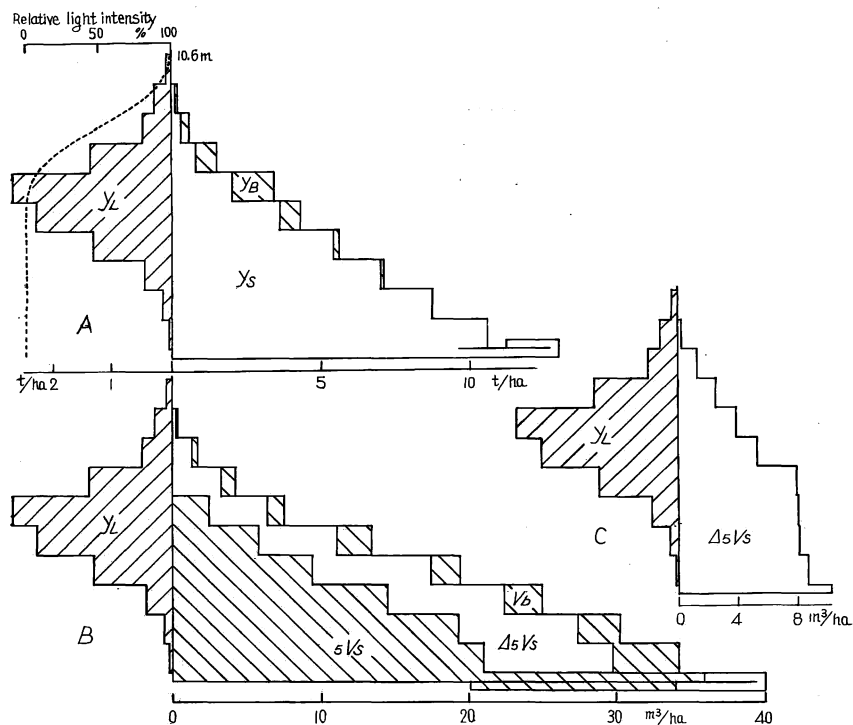


Fig. 11 Production structure diagrams in ca. 50-year-old *Picea glehnii* stand, A: MONSI and SAEKI's diagram showing the vertical distributions of oven dry weight in leaves (y_L), in stems (y_S) and in branches (y_B) per hectare (SHIDEI *et al.*⁵⁷⁾), B: vertical distributions of y_L , of stem volume five years ago (${}_5V_S$), of stem volume increment in recent five years ($\Delta{}_5V_S$) and of stem bark volume (V_B), C: relation of vertical distributions of y_L and $\Delta{}_5V_S$.

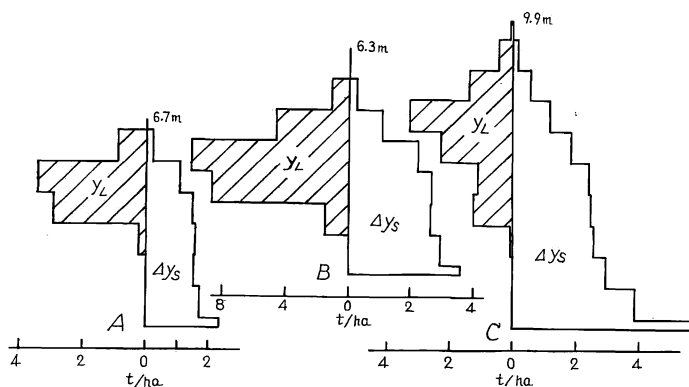


Fig. 12 Production structure diagrams with stem growth showing the vertical distributions of leaf weight (y_L) and of current annual increment of stems (Δy_S) per hectare in oven dry weight basis.

A: *Castanopsis cuspidata* 11-year-old stand (TADAKI⁶²⁾)

B: *Cryptomeria japonica* five-year-old stand (TADAKI and KAWASAKI⁷⁴⁾)

C: *Acacia mollissima* four-year-old stand (TADAKI⁶³⁾).

its products, because of the non-photosynthetic organs of forests including the products by the previous foliage. Then, the vertical distribution of non-photosynthetic organs in the diagram is replaced by that of stem wood growth which occupies the greater part in the growth of non-photosynthetic organs in a tree community and can easily be estimated.

As an example, Fig. 11 is presented ; picture-A is MONSI and SAEKI's diagram, B shows the vertical distributions of the stem volume five years ago, of the stem volume increment in the recent five years and of the stem bark, and C of the stem growth only. The stem volume and its growth in each stratum are calculated from individual stem diameters at the upper and lower ends of the stratum. Further attempts are made in Fig. 12 in which the stem growth in the recent one year is presented on an oven dry weight basis.

In the relation between the vertical distributions of stem growth and of foliage, there is a fairly obvious difference between the strata having larger leaf mass and having larger stem growth. The stem growth in each stratum becomes greater down within the canopy, and remains relatively constant below the canopy although it seems to increase gradually with descending strata.

This situation is more obvious in single trees as shown in Fig. 13. In the diagram, the vertical changes of stem diameter growth being also presented, the stem diameter growth seems to be greater inside the crown, and its peak growth is realized at the height just below the

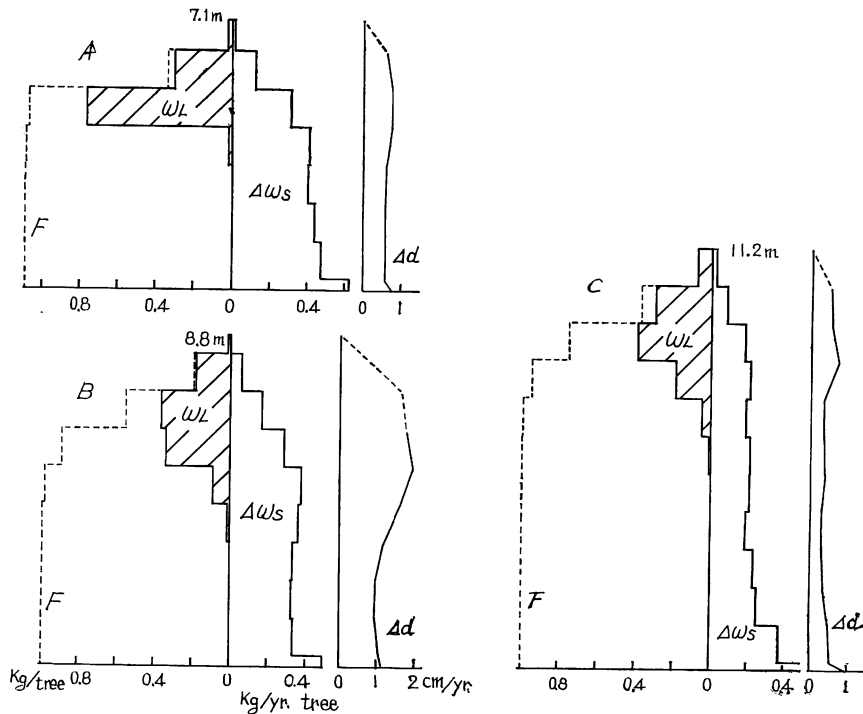


Fig. 13 Production structure diagram with stem growth per single tree showing the vertical distributions of leaf oven dry weight (w_L), of stem oven dry weight increment (Δw_s), of accumulated leaf amount (F) and of stem diameter growth (Δd) per tree, A: *Castanopsis cuspidata* 11-year-old tree, B: *Acacia mollissima* four-year-old, C: *Cryptomeria japonica* 24-year-old.

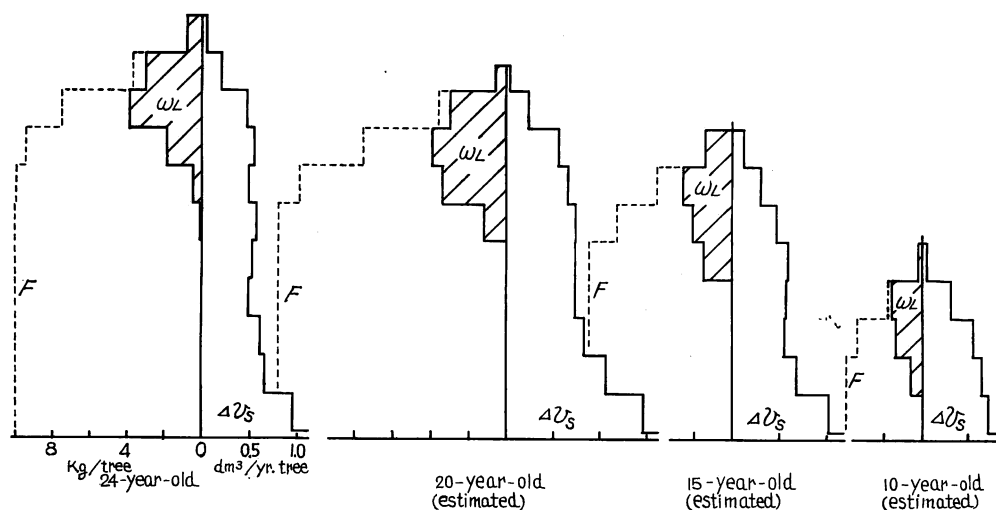


Fig. 14 Estimation of vertical distribution of leaf biomass in the past per single tree (The same tree as C in Fig. 13). From the relation of leaf amount (w_L) to current annual stem volume growth (Δv_s) present—at the age of 24 years—and Δv_s at the age of 20, 15 and 10 years, w_L at the age of 20, 15 and 10 years are decided. The vertical changes of the accumulated leaf amount (F) at each age are estimated by the vertical distribution of Δv_s at that age. The vertical distributions of leaf amount (w_L) are converted from F .

stratum having a maximum leaf amount. The dotted lines (F) express the accumulated leaf amount which denotes the total sum of leaf biomass from the uppermost part of a tree successively, in other words, the total leaf amount above a certain height.

The stem growth in a certain stratum may be thought to be proportional to the accumulated leaf amount from the similarity between their distribution types. In any case, it seems that the amount of stem growth in a stratum is determined by leaf biomass existing above it. This is supported by the following observation; when all leaves above a certain height are removed, the leafless part of the stem cannot grow, and withers in spite of holding enough leaves in the lower layers. On the other hand, a considerable constancy of the stem growth among the strata below the canopy provides an approach to illustrate the fact that the pruning or removing of lower living leaves does not make a stem taper.

When the relation of the stem growth to the accumulated leaf amount in a stratum is accessible, a rough estimation of the previous distribution of foliage may be possible by reading annual rings in a stem, but on this point further studies are required. An attempt concerning this is shown in Fig. 14 made up with the following method: the current annual stem growth at a certain age in the past is measured separately for strata by reading annual rings within the stem; from the total stem increment the leaf biomass at that age is decided by the present ratio of stem increment to leaf biomass, the accumulated leaf amount in each stratum at that time can be estimated as being proportional to the distribution of stem increment and it is converted into the vertical distribution of foliage.

Summary

Research on the foliage plays a key role in the course of studies on the metabolism of plant

communities. The leaf biomass of a forest or individual tree, and the productivity of foliage were discussed in this paper.

In general, the leaf biomass per unit ground area in a closed forest seems to be somewhat similar among the species, among the related species and also among the same plant formation, e. g. deciduous broad leaved, evergreen broad leaved forest, etc. (Table 1 and 2). But the periodical change of the leaf biomass in a forest is observed (Fig. 1 and 2).

The vertical distributions of foliage in forests are divided into three types (Fig. 3); leaves appearing mainly in upper strata, those in relatively lower ones and those distributing relatively constant along stems. Some observations on the relative light intensity under the canopy and the light extinction coefficient of foliage in forests are shown in Table 3.

KITTREDGE's formula: $w_L = aD^b$ (w_L : leaf biomass per tree, D : DBH, a and b : constants) is useful for estimating the leaf biomass of other trees. But the constants a and b vary with the growth stage (Fig. 4 and 5), growing density (Fig. 6) and site condition (Fig. 7) so that the constants naturally differ among mature forests of different conditions (Fig. 8 and 9).

The stem growth of a tree is approximately determined by its leaf biomass (Fig. 10). Although the leaf efficiency.....stem growth per unit leaf biomass.....is effected by various conditions, its rough value is given (Table 4).

The production structure diagram with stem growth which shows the relations between the vertical distributions of foliage and of stem growth is presented (Fig. 11 and 12). This is effective in ascertaining the relation of the products by the foliage to the leaf biomass. The stem growth in the strata below the canopy is relatively constant, and the vertical distribution of stem growth is similar to that of the accumulated leaf amount which shows the total leaf biomass above a certain height. This situation is more obvious in single trees (Fig. 13). Furthermore, Fig. 14 shows an attempt estimating the vertical distribution of foliage in the past using the relation between the stem growth and the accumulated leaf amount.

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*: in Japanese.

**: in Japanese with English summary.

林分および単木の葉量に関する若干の検討

只 木 良 也⁽¹⁾

摘 要

葉の同化作用によって生産された有機物の蓄積である幹を収穫目的とする林業にあって、林分あるいは単木の保有する葉量について研究することは大切なことだが、いわゆる林学の研究では、幹そのものは詳細に研究されてはいるものの、葉自体を取り扱った報告は案外すくないようだ。最近、植物群落の有機物生産を知るための研究が進んできたが、植物群落の物質生産機構解析の上でも、葉量と生産の問題をはあくし検討することがまず第1の手がかりになる。

この報告では、林分や単木の葉量や、その有機物とくに幹の生産について若干検討してみた。

1. 林分の葉量：一般に閉鎖した林分は、樹種によってほぼ一定の葉量をもつ。そして、その一定量は、地位、林齢、樹高、間伐度などの影響をうけないといわれている。Table 1 には、いろいろな林分の葉量が示してあるが、同樹種の林分だけでなく、近縁種同志間、さらには同一植物群系内（たとえば落葉広葉樹林、常緑広葉樹林など）でもあまり大きな差はないようだ。植物群系ごとの葉量の概数は Table 2 のとおりだ。落葉広葉樹林の葉量（乾重で 2~3 t/ha）は、閉鎖林分の葉量としては最小単位で、これを基本葉量という名で呼ぼう。一方、常緑樹林でも、その年間落葉量は基本葉量にほぼ等しい。林分葉量が一定だとすると、年間の落葉量と新葉量は等しいはずだから、基本葉量に樹種ごとの葉の寿命をかけ合わせると林分の葉量となる。

林分の葉量が一定となるのは、その樹種の群落として生育可能な地域での投下光線量がほぼ定まっており、この光に対して最大葉量が決まっているからだ。つまり閉鎖林では光が制限因子になっているのだ。したがって、閉鎖林では他の成長要素、たとえば水とか土壌養分とかが増しても、光量に規制されてしまって林分の生産はそんなに増さないだろう。逆に光は十分あっても、成長要素が極端にすくなければ、林分は閉鎖できない。砂漠がその例だが、もはや林業地としては問題外だ。

2. 林分葉量の変化：林分の葉量は常に一定というわけではない。月ごとにも年ごとにも変化している。Fig. 1 のアキニレ稚樹林では、春の開葉完了直後に葉量最大期が認められ、また Fig. 2 のいろいろな樹種の林分でも林冠閉鎖直後に一時的に葉量が多くなる。この時期は収穫表の幹材積連年成長最大期に近いようだ。

3. 林分葉量の垂直分布：林冠に投下された光は一部は反射され、一部は同化生産に利用されるため葉に吸収され、残りは下層へと透過される。林冠層内のある高さでの照度 I は、その高さより上にある葉面積合計を F 、林冠への投下光線の照度を I_0 とするとき

$$I = I_0 e^{-KF} \dots \dots \dots (1)$$

であらわせる。 K は樹種に固有な吸光係数だ。いろいろな樹種についての K の値を Table 3 に集めた。Fig. 3 にはいくつかの林分の葉量の垂直分布を示した。一般に常緑針葉樹林や択伐林では葉が下層まで存在するイネ科草本型、広葉樹林や一斉林では葉が群落の上部に集中する広葉草本型になるが、この

(1) 九州支場造林研究室・農学博士

他に葉が、比較的均等に上下に分布する型があるようだ。

4. 単木の葉量：KITTREDGE が提出した単木の葉量 (w_L) と胸高直径 (D) との関係式

$$\log w_L = b \log D - a \quad (a, b \text{ は係数}) \dots\dots\dots (2)$$

は、すくない資料から多くの個体の葉量を推定するのに便利で、いろいろ変型も行なわれているが、同じ樹種でも林分が違くと係数 a, b の値が変わるのが欠点だ。

たとえば、同一林分から (Fig. 4), あるいは土地条件が似た隣接林分から (Fig. 5) 得られた資料でも、生育段階ごとに係数 a, b に差を生ずる。また、生育密度差があったり (Fig. 6), 生育密度に加えて土地条件が変わったり (Fig. 7) すると、やはり違った関係になる。したがって、生育密度、土地条件、生育段階のそれぞれ違う林分ごとに関係が異なるのは当然だ (Fig. 8, Fig. 9)。つまり、ある林分で求めた KITTREDGE 式を他の林分にあてはめることは危険だ。ただし、上層木のみ、葉量の上限または下限をあらわすには使用できる。

5. 葉の能率：葉量とともに、葉の同化能率は樹木の成長を考える上に重要な因子だ。ここでは、葉の幹生産能率を主として取り上げた。単木の幹の年間成長量は、その個体が保有している葉量によってほぼ決まる (Fig. 10)。葉の幹材生産能率は、土地条件や立木密度などによって影響をうけるが、いろいろな樹種での概数をみると (Table 4), 広葉樹は針葉樹より、落葉樹は常緑樹より、また陽樹は陰樹より能率が高い。つまり、一般に林分葉量がすくない樹種ほど能率が良いようだ。ただし、モリシマアカシアのように、林分葉量は一般の常緑広葉樹なみでありながら、葉の能率のよい樹種もある。

6. 葉量と幹材成長の垂直分布：いわゆる生産構造図では、葉と非同化部の現存量が対比されるが、多年生植物である樹木では葉の現存量に対して最近の非同化組織の成長量を示すのが、葉による同化生産物の配分を知る上では有効だろう。そこで、成長量が推定しやすく、また非同化組織の大部分を占める幹についてのみ、成長量と葉の垂直分布を図にしてみた (Fig. 11, 12)。幹の成長量は、林冠層内では下層ほど大きいのが、林冠層より下ではあまり変わらない。こうした傾向は単木についての図 (Fig. 13) でさらに明白だ。上層よりの積算葉量と幹成長量の垂直分布はよく似ていることから、ある高さにおける幹材の成長は、その高さより上にある全葉量で決まるといえるようだ。したがって、現在の葉量と幹成長量の関係を知り、年輪を読んで何年か前の幹材成長の垂直分布を求めれば、その年のその個体（あるいは林分）の葉の量の垂直分布を推測できるだろう。Fig. 14 にその試みを示してみた。