

森林の生産構造に関する研究(XVII)

林冠内での葉の比面積の垂直的变化

誌名	日本林學會誌 = Journal of the Japanese Forestry Society
ISSN	0021485X
著者名	只木,良也
発行元	日本林學會
巻/号	52巻9号
巻号補足	
掲載ページ	p. 263-268
発行年月	1970年9月

農林水産省 農林水産技術会議事務局筑波産学連携支援センター
Tsukuba Business-Academia Cooperation Support Center, Agriculture, Forestry and Fisheries Research Council
Secretariat



 論文

 Studies on the production structure of forest (XVII)
 Vertical change of specific leaf area in forest canopy*

Yoshiya TADAKI**

森林の生産構造に関する研究 (XVII)

林冠内での葉の比面積の垂直的变化*

只木良也**

Summary: Canopies of six forest stands (Table 1) were investigated by the stratified clip method and the specific leaf area in each stratum was decided. As the specific leaf area becomes larger as the leaf layer descends, the vertical distribution of leaf area comes to be somewhat more swelling in the lower leaf layer than that of leaf weight (Fig. 1). The relation between the leaf area index F and the specific leaf area f under F could be approximated by (Figs. 2, 3, Table 2)

$$f = aF^b + c \quad (1)$$

$$\text{or} \quad \log f = dF + \log c' \quad (2)$$

Combining Eq. (2) with Eq. (3) of the BEER-LAMBERT's formula, we have

$$\log f = -k \log (I/I_0) + \log c' \quad (5)$$

where I/I_0 denotes the relative light intensity (Fig. 4, Table 3).

The constants c and c' ought to be the same as they represent the f -value in the uppermost leaf layer or in the full daylight. The fitness of the three formulae, Eq. (5) and other worker's Eqs. (6) and (8) representing $f \sim I/I_0$ relation, was examined against each other (Table 4).

要 旨: 6 林分 (Table 1) の林冠層をいくつかの層に分け、それぞれの層での葉の比面積 (面積/乾重, specific leaf area) を求めた。比面積は下層ほど大きくなるので、葉面積の垂直分布は葉重量のそれより若干下層がふくらんだ形となる (Fig. 1)。比面積 (f) とそれより上に存在する葉面積指数 (F) の関係は

$$f = aF^b + c \quad (1)$$

$$\text{あるいは} \quad \log f = dF + \log c' \quad (2)$$

で近似できる (Fig. 2, 3, Table 2)。(2) 式と BEER-LAMBERT 式 ((3) 式) を組み合わせると

$$\log f = -k \log (I/I_0) + \log c' \quad (5)$$

となり、比面積と相対照度 (I/I_0) の関係が得られる (Fig. 4, Table 3)。ここで、係数 c , c' は、本質的に同一のもので、 $F=0$ あるいは $I/I_0=1$ (100%) のときの f の値、すなわち、林冠最上層あるいは陽光量満度のときの比面積を示す。(5) 式および f と I/I_0 の関係を表わす他の 2 つの式 ((6), (8) 式) の適合度に関して若干の比較が行われた (Table 4)。

Introduction

Two methods have been developed for most studies on the primary production of forest communities. The one is to estimate the total canopy photosynthesis by integrating the light dependent photosynthetic rate of a single leaf along the light profile through a canopy. The other is based on the sum of biomass increment, loss due to death and respiration, and consumption due to animal

grazing.

To estimate the primary production and to discuss the production structure of plant community by the methods afore-mentioned, especially by the first one, several characters of leaf in a canopy such as specific leaf area, light transmissibility, photosynthetic and respiratory activities, etc. are the important factors. It is natural that those characters are not stable in all leaf layers, but variable along the canopy profile.

* Contributions from JIBP-PT No. 89. A part of this paper was read at the 15th Annual Meeting of Ecological Society of Japan, 1968

** 農林省林業試験場 Gov. For. Exp. Sta., Meguro, Tokyo

The vertical change of the specific leaf area in several forest canopies is discussed in this paper which, however, is far from perfect because of the insufficient number of exemplification.

Material and method

The data used in this study were taken from six forests as briefly explained as follows:

Castanopsis stand: About 16-year-old second growth forest composed of *Castanopsis cuspidata*, situated at about 80m above the sea level on a gentle slope of the Experimental Forest belonging to the Kyushu Branch of Government Forest Experiment Station, near Kumamoto City, Kyushu. The mean height of dominant trees was about 9m. The stand was fully closed, so the natural pruning had been taking place up to 3~4m above the ground on which few undergrowth vegetation could be found. Six sample trees with various tree sizes were felled in December of 1967 for the biomass estimation.

Abies stand: A 23-year-old plantation of *Abies veitchii* in the lower range of subalpine zone of Mt. Fuji, Yamanashi Prefecture. Flat area, 1,530m above the sea. About 8m in mean tree height. Since the canopy closure had been completed a few years before the survey, the leaf biomass was at the maximum, so the ground vegetation could not be found. The biomass and productivity of this forest surveyed in October of 1967 have been reported by TADAKI *et al.*¹⁾

Larix stand: A 39-year-old plantation of *Larix leptolepis* belonging to Koiwai Farm, near Morioka City, north-east part of Japan. Flat area on relatively deep black soil, about 360m above the sea. The mean height of *Larix* reached 19m and unbroken leaf layer of deciduous hardwood species such as *Morus bombycis*, *Stachyurus praecox*, *Prunus grayana*, etc. developed at 4~5m high. Ten sample trees of *Larix* were felled in September of 1966.

The biomass and productivity of this stand have been described in detail by SATOO *et al.*²⁾—Data code: JPTF '66 KOIWAI.

Fagus 'N' stand: A natural forest of *Fagus crenata* aged about 100, developed at about 680m above the sea on a steep slope down to a shallow valley in the Ashiu Experimental Forest of Kyoto University, about 40km north of Kyoto City. The main canopy or the over story of the forest was composed of *Fagus crenata* mixed with a few *Carpinus spp.*, *Acer spp.* and other deciduous hardwoods as tall as around 20m. The under story of several deciduous trees developed at 2~3m high. All trees in a quadrat of 10×10m² settled inside the sample area of 20×30m² were felled in August of 1966 for the biomass measurement.—Data code: JPTF '66 ASHIU.

Fagus 'P' stand: A plantation of *Fagus crenata* aged 50 or more years, about 580m above the sea, growing on a gentle slope of river terrace of Shinano River, Niigata Prefecture. The mean height of dominant trees reached 20m. The biomass and productivity of this stand estimated from eight sample trees in September of 1968 have been reported by TADAKI *et al.*³⁾

Betula stand: Second growth of *Betula ermanii* aged about 30 in the subalpine zone of the national forest managed by Nagano Regional Forest Office, central Japan. About 1,800m above the sea, NW gentle slope. The over story, 10~11m high, was composed of *Betula* and the dense under story of conifers such as *Tsuga diversifolia* and *Abies veitchii* was found about 3~4m above the ground. Eleven sample trees of *Betula* were felled in August of 1969.

When the sample trees in each stand were investigated by the method of stratified clip technique⁴⁾, a small amount of leaves was sampled from every one or two meters thick canopy stratum for the leaf area determination.

The leaf area of sampled broad leaves, *Castanopsis*,

Table 1. Outline of the forests studied

Stand	Age yr	Mean tree height m	do. (domi- nants) m	Mean DBH cm	No. of trees no./ha	Basal area m ² /ha	Biomass* in				Leaf area** ha/ha	Relative light intensity***
							stem t/ha	branch t/ha	root t/ha	leaf t/ha		
<i>Castanopsis</i> evergreen broad-leaf	ca. 16	8.9		9.1	4,125	28.4	63.1	17.3	20.7	9.5	8.7	0.029
<i>Abies</i> evergreen conifer	23	8.5		13.1	2,076	29.3	45.0	17.0	25.9	21.3	12.8	0.019
<i>Larix</i> deciduous conifer	39	19.4		21.1	1,155	36.0	145.4	15.5	34.8	3.6	4.1	0.271
<i>Fagus</i> 'N' deciduous broad-leaf	ca. 100	12.8	18.8	18.7	800	31.4	136.1	58.4	(30.4)	2.1	3.9	0.029
<i>Fagus</i> 'P' deciduous broad-leaf	50	13.9	19.9	11.6	2,829	39.9	202.2	39.5	49.9	4.9	7.8	0.023
<i>Betula</i> deciduous broad-leaf	ca. 30	8.5	10.9	5.5	6,800	19.7	50.5	14.3	18.8	2.6	4.2	0.102

* presenting in oven dry unit.

** one side area of leaves

*** at the height just below the canopy

Fagus and *Betula*, was directly measured by the dot-grid or dot counting method. The needle leaves of *Larix* were separated into verticillate leaves attached to short branches and dispersed leaves attached to long branches, and their forms were photographically enlarged to enable to employ the planimeter. Also, the needles of *Abies* were divided into current needles and aged ones, and their leaf area was determined by the dot-grid method applied to the photographically enlarged leaf forms.

After the determination of area, leaf samples were oven dried to obtain the specific leaf area or the rate of leaf area per unit dry weight of leaf, the value of which representing each stratum was decided as the weighted mean value calculated from the data of 2~5 sample trees. On the other hand, the biomass in each of all stands was estimated as shown in Table 1 by the method of allometry or by the method based on the assumption that the rate in biomass of the sum of sample trees to that on the whole sample plot area was proportional to the respective basal areas.

Results and discussion

Vertical distribution of leaf biomass and specific leaf area

As the biomass in each forest was investigated according to the stratified clip technique, the vertical distribution of leaf area could be estimated from that of leaf weight combined with that of specific leaf area as illustrated in Fig. 1.

In all stands, the specific leaf area was the smallest at the top layer of the canopy and became larger with descending leaf layers. The relation of specific leaf area to the height of leaf layer seems, more or less, to be in inverse proportion, so the vertical distribution of leaf area comes to be somewhat more swelling in the lower layer in comparison with that of leaf weight.

Certain characteristic trends are apparent in the profile of specific leaf area. Their values ranged from 134 to 326 cm² per g dry weight in *Fagus* 'N' stand, 98 to 489 in *Fagus* 'P', 116 to 234 (to 290 inside the leaf layer of undergrowth) in *Betula*, 100 to 157 (to 183 inside the under story) in verticillate

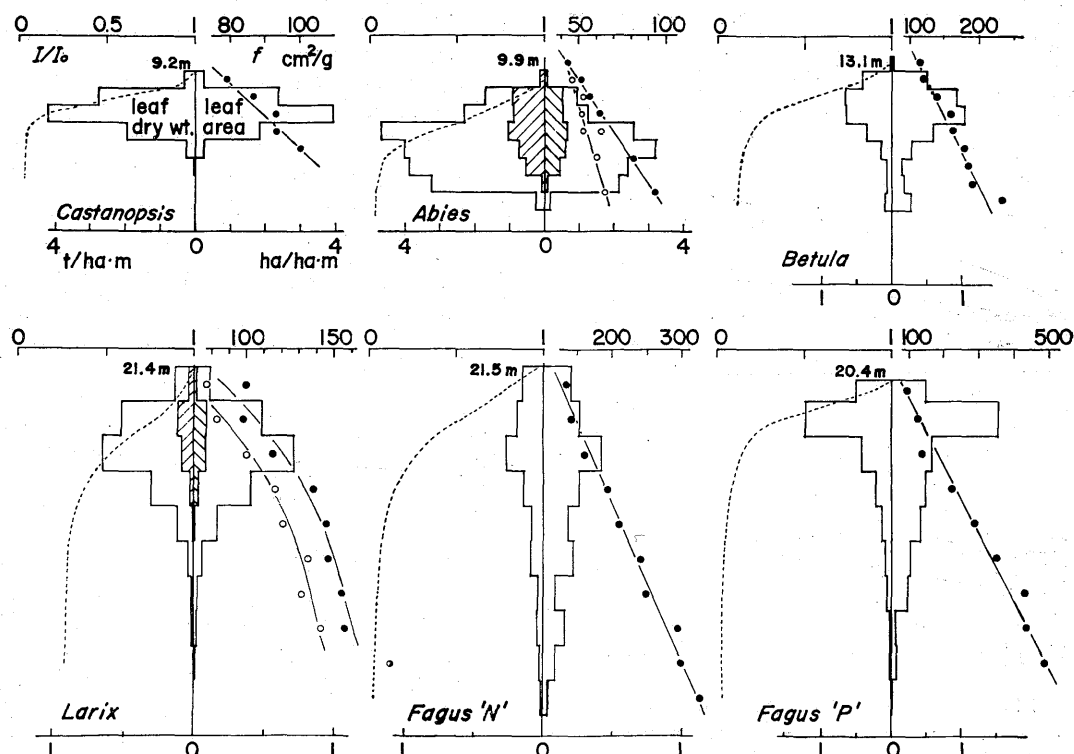


Fig. 1. Vertical distribution of leaf dry weight and leaf area of stand, with vertical variation of specific leaf area (f , solid line) and relative light intensity (I/I_0 , dotted line) along the canopy profile

Abies—closed circle (hatched area): current needle, open circle: aged needle,
Larix—closed circle (hatched area): verticillate leaf, open circle: dispersed leaf.

leaf and 78 to 143 in dispersed leaf of *Larix*, 44 to 94 in current needle and 47 to 65 in aged needle of *Abies*, and 79 to 101 in *Castanopsis*.

In any stratum, the specific leaf area of verticillate leaf in *Larix* is larger in its rate than that of dispersed one, and also that of current needle in *Abies* larger than of aged one.

As far as these observations indicate, the vertical variation in specific leaf area seems to be more obvious in deciduous species than in evergreen ones. For instance, the rate in the lowest leaf layer of *Fagus* 'P' stand is about five times larger than in the uppermost layer of the same stand, while the corresponding value in *Castanopsis* stand is only 1.3 times.

Relation between specific leaf area and leaf area index

As the figure of specific leaf area used here represents the rate for the stratum with one or two meters depth, let us assume that the figure indicates the rate in the leaf occurring at the center horizon of that stratum. So the leaf area index which affects a leaf representing the specific leaf area in a certain stratum must be given as the sum of total leaf area in upper strata and a half of leaf area in that stratum. Thus, the relation of specific leaf area in a certain horizon (f , cm² per g dry

weight) to leaf area index above that horizon (F) is illustrated in Fig. 2.

The observed correlation shown in Fig. 2 is fairly well fitted by the formula,

$$f = aF^b + c \quad (1)$$

where a , b and c are constants which can be approximated by the figures as shown in Table 2.

Table 2. Values of constants in Eq. (1); $f = aF^b + c$ and Eq. (2); $\log f = dF + \log c'$.

Stand	a cm ² /g	b	c cm ² /g	d	c' cm ² /g
<i>Castanopsis</i>	5.0	0.75	78	0.010	81
<i>Abies</i> current	10.4	0.58	49	0.024	51
aged	3.9	0.58	48	0.011	49
verticillate	6.8	1.26	98	0.053	94
<i>Larix</i> dispersed	6.8	1.26	78	0.063	76
<i>Fagus</i> 'N'	12.5	2.00	134	0.107	112
<i>Fagus</i> 'P'	3.2	2.24	102	0.093	85
<i>Betula</i>	16.4	1.25	116	0.057	117

The increasing rate of f -value in the deciduous species such as *Fagus*, *Betula* and *Larix* is accelerated while that in evergreen ones such as *Castanopsis* and *Abies* decelerated by increasing of F as far as this observation indicates. Namely, the constant b of Eq. (1) in the former species is larger while that in the latter smaller than 1.0.

The $f \sim F$ relation can also be approximated by

$$\log f = dF + \log c' \quad (2)$$

which expresses the proportional relation of $\log f$ to F as illustrated in Fig. 3, where d and c' are constants whose values are determined as also shown in Table 2. The d -value, representing the inclination of the regression line in $\log f \sim F$ relation, is from three to five times, sometimes ten times,

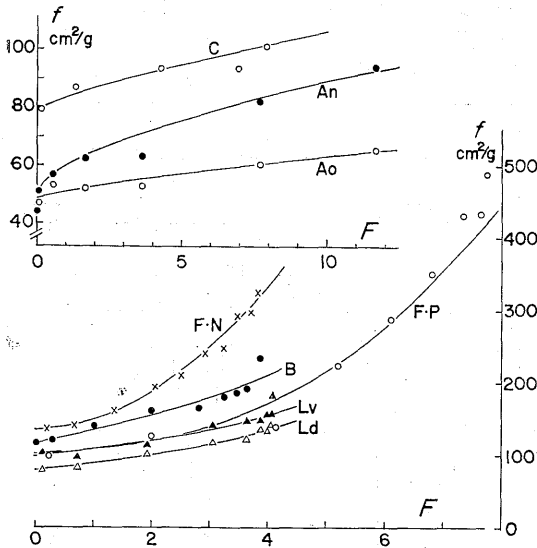


Fig. 2. Specific leaf area (f) under leaf area index F , the relation of which is approximated by Eq. (1).

Notations: C: *Castanopsis cuspidata*, An and Ao: current needle and aged needle of *Abies veitchii*, Lv and Ld: verticillate leaf and dispersed leaf of *Larix leptolepis*, FN: natural forest of *Fagus crenata*, FP: plantation of *Fagus crenata*, B: *Betula ermanii*.

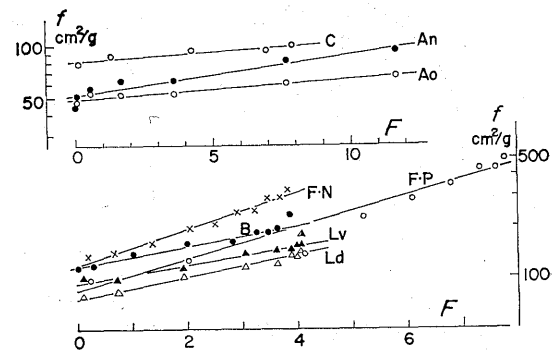


Fig. 3. Specific leaf area (f , logarithmic scale) under leaf area index F , the relation of which is approximated by Eq. (2). Notations are indicated in the explanation of Fig. 2.

larger in deciduous species than in evergreen ones. This trend may indicate that the specific leaf area of deciduous species is more liable to be affected by the amount of leaves occurring above.

Relation between specific leaf area and relative light intensity

Based on the fact that the specific leaf area at a certain horizon is affected by the leaf area extending above that horizon, we can easily suppose a close relation between the specific leaf area and the relative light intensity (I/I_0) at a certain horizontal layer.

Already, we know the BEER-LAMBERT's formula is applicable to the attenuation of light through a plant canopy,⁴⁾

$$I/I_0 = \exp(-KF) = e^{-KF} \quad (3)$$

in which I_0 and I denote the illumination on a horizontal surface respectively above the canopy and at a certain height inside the canopy under the leaf area index F , and K is the light extinction coefficient specific to the canopy concerned.

Combining Eq. (3) with Eq. (2), we can get

$$\log f = -\frac{d}{K \log e} \log (I/I_0) + \log c' \quad (4)$$

Assuming the value of K is the same in all leaves of the canopy concerned, replacing $d/K \log e$ with constant k , we have

$$\log f = -k \log (I/I_0) + \log c' \quad (5)$$

The correlation of $\log f$ to $\log (I/I_0)$ represented by Eq. (5) in each stand is illustrated in Fig. 4 and the values of K and k are shown in Table 3, in which the attenuation of relative light intensity through the canopy was calculated by Eq. (3) based on the relative light intensity at the height just below the canopy and the vertical distribution of leaf area, providing the light extinction coefficient was unchangeable in all leaves of the canopy.

ARAKI^{5,6)} has found the variation of the specific leaf area in seedlings of *Abies veitchii* and *Larix leptolepis* under the artificially controlled light conditions, and adopted the formula of BLACKMAN and RUTTER⁷⁾ to the relation as

$$f = -k' \log (RLI) + c'' \quad (6)$$

in which RLI denotes the relative light intensity expressed by per cent, and k' and c'' are constants. He determined the values of k' and c'' as 57.4 and 247.9 in current needles of *Abies v.*, while 139.7 and 362.5 in *Larix l.* respectively, when the dimension of f is cm^2 per g dry weight. Also he described that the $f \sim \log (RLI)$ regression of Eq. (6) in the case of *Larix* was realized on 1.0 per cent level with 29.68 of the variance ratio in statistical meaning.

However, our formula of Eq. (5) is also realized

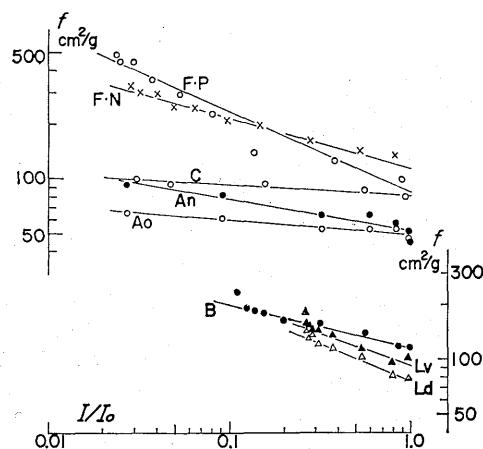


Fig. 4. The relation between specific leaf area (f , log-scale) and relative light intensity (I/I_0 , log-scale), which is expressed by Eq. (5).

Notations are indicated in the explanation of Fig. 2.

Table 3. Values of light extinction coefficient K and constant k in Eq. (5); $\log f = -k \log (I/I_0) + \log c'$, where $k = d/K \log e$.

Stand	K	k
<i>Castanopsis</i>	0.41	0.057
<i>Abies</i> (current)	0.31	0.180
aged		0.080
<i>Larix</i> (verticillate)	0.32	0.384
dispersed		0.450
<i>Fagus</i> 'N'	0.92	0.267
<i>Fagus</i> 'P'	0.48	0.444
<i>Betula</i>	0.57	0.231

by his same data on 1.0 per cent level with 30.88 variance ratio, so we cannot make a discrimination between Eqs. (5) and (6) so far as this case concerns.

But, if Eq. (6) is combined with Eq. (3), we have

$$f = k'' F + c'' - 2k' \quad (7)$$

where $k'' = k' K \log e$,

which indicates the proportional relation between f and F . Nevertheless, we cannot find out this $f \sim F$ simple relation among the examples illustrated in Fig. 2, although it is not impossible to apply this to the examples in aged needle of *Abies* and some of others. The light extinction coefficient K being, indeed, given as the average value in the whole canopy of the stand here, it needs to notice that K may change according to F or may be given as a function of F . This problem will be checked by further studies.

On the other hand, KIRITA and HOZUMI⁸⁾ have approximated the relation of f to I/I_0 in an evergreen broad leaved forest as

$$f = \frac{A}{I/I_0} + B, \quad (8)$$

in which A and B are constants, and found the value of A varied with season, while, that of B was relatively stable.

The fitness of three linear correlations, expressed by Eq. (5) on $\log f \sim \log(I/I_0)$, Eq. (6) on $f \sim \log(I/I_0)$ and Eq. (8) on $f \sim 1/(I/I_0)$, was examined to compare the differences among their correlation coefficients as shown in Table 4, which were calculated on all cases of examples aforementioned. The table shows that the correlations are fairly well fitted by every formula in all cases, especially in the correlations indicated by Eqs. (5) and (6) with a slight advantage for Eq. (5).

Table 4. Correlation coefficients in three cases adopted by Eqs. (5), (6) and (8)

Stand	$\log f \sim \log(I/I_0)$ Eq. (5)	$f \sim \log(I/I_0)$ Eq. (6)	$f \sim 1/(I/I_0)$ Eq. (8)
<i>Castanopsis</i>	-0.949	-0.933	0.861
current	-0.942	-0.974	0.872
<i>Abies</i>			
aged	-0.923	-0.958	0.885
verticillate	-0.983	-0.983	0.991
<i>Larix</i>			
dispersed	-0.977	-0.981	0.986
<i>Fagus</i> 'N'	-0.990	-0.966	0.982
<i>Fagus</i> 'P'	-0.991	-0.944	0.992
<i>Betula</i>	-0.999	-0.990	0.969

Meaning of constants c and c'

There are no differences in the sense of constants both c in Eq. (1) and c' in Eqs. (2) or (5), whose values in a stand ought to be the same with each other, because they indicate the f -values when $F=0$ or $I/I_0=1$. Namely, they represent the specific leaf area in the uppermost leaf layer or in the full daylight.

In the case of Eq. (6), since the relative light intensity is given by the figure in per cent, the f -value in the full daylight, $RLI=100$ per cent, can be indicated as $(c'-2k')$. Also the corresponding value in the case of Eq. (8) is $(A+B)$ when $I/I_0=1$.

The author is indebted to the members of the JIBP-PT Research Groupes on Primary Productivity of Natural Forests, represented by Prof. Dr. T. KIRA of the Osaka City University, and of Artificially Managed Forests, represented by Prof. Dr. T. SATOO of the Tokyo University, for the joint field work and the free use of the data.

Literature cited

- 1) TADAKI, Y., HATIYA, K., TOCHIAKI, K., MIYAUCHI, H. and MATSUDA, U.: Studies on the production structure of forest (XVI). Primary productivity of *Abies veitchii* forests in the subalpine zone of Mt. Fuji. Bull. Gov. For. Exp. Sta., Tokyo 229: 1~22, 1970
- 2) SATOO, T. et al.: Primary production in a plantation of Japanese larch, *Larix leptolepis*, a summarized report of JPTF-66 KOIWAI. J. Jap. For. Soc. 52: 154~158, 1970
- 3) TADAKI, Y., HATIYA, K. and TOCHIAKI, K.: Studies on the production structure of forest (XV). Primary productivity of *Fagus crenata* in plantation. J. Jap. For. Soc. 51: 331~339, 1969—in Japanese with English summary
- 4) MONSI, M. und SAEKI, T.: Über den Lichtfaktor in den Pflanzen-gesellschaften und seine Bedeutung für die Stoffproduktion. Jap. J. Bot. 14: 22~52, 1953
- 5) ARAKI, M.: Shading effect on the specific leaf area of *Abies veitchii*. Rec. 78th Meeting Jap. For. Soc.: 102~104, 1967—in Japanese
- 6) ARAKI, M.: Shading effect on the specific leaf area of *Larix leptolepis* GORD. J. Jap. For. Soc. 50: 185~186, 1968—in Japanese
- 7) BLACKMAN, G.E. and RUTTER, A.J.: Physiological and ecological studies in the analysis of plant environment (III). The interaction between light intensity and mineral nutrient supply in leaf development and in the net assimilation rate of the Bluebell. Ann. Bot. N. S. 11: 1~26, 1948
- 8) KIRITA, H. and HOZUMI, K.: Estimation of photosynthetic rate of the broadleaved evergreen forest—some specific values of leaf layer. Ann. Rep. 'Studies on the biological production of warm-temperate evergreen forest', JIBP-PT.; 16~35, 1969—in Japanese

(Received May 9, 1970)