論　　文

Distribution Structure of Foliage and the Light Interception in a Young *Cryptomeria japonica* Stand

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HASHIMOTO, Ryoji: **Distribution structure of foliage and the light interception in a young *Cryptomeria japonica* stand J. Jpn. For. Soc. 74: 466~474, 1992** Canopy profiles of crown-occupation area, foliage area, and light interception are modelled on the basis of crown measurement data for a young *Cryptomeria japonica* stand. The crown-occupation area reaches maximum just above base of the canopy and the distribution curve is remarkably skewed downward. The distribution density of foliage area rises to the peak below the middle of the canopy and shows a distribution curve skewed downward, whereas that of light interception reaches maximum near the middle of the canopy and depicts almost a symmetrical distribution curve with depth. Dividing the canopy into two parts by defining the boundary as the position where the distribution density of foliage area is maximum, the ratios of foliage area between the upper and lower canopies are 51: 49 but those of light interception 73: 17. On the other hand the ratios of foliage area among the upper- (height > 15 m), middle- (13 < height ≤ 15 m), and lower-story trees (height ≤ 13 m) are 35: 53: 12, and those of light interception 48: 47: 5. It is noteworthy that the light interception by the tree individuals with heights above the stand average occupies more than 80% of the whole light interception by the canopy. The variation in light interception of the individual trees is due to the additive effects of the crown foliage area and the light interception per unit foliage area, where the former increases in proportion to the square of stem diameter at the crown base and the latter in proportion to the fourth power of tree height.

橋本良二：若いスギ林における葉群の分布構造と受光状態　日林誌 74:466~474, 1992
若いスギ林の林冠における樹冠占有面積，葉群面積および葉群受光量の垂直分布について
モデル化した。樹冠占有面積が最大になる位置は林冠底のわずか上方にあり，その分布曲
線は著しく下方に偏る。葉群面積の分布密度は林冠中央部の下方でピークに達し分布曲線
も下方に偏るが，葉群受光量の分布密度は林冠中央部付近で最大に達し正規分布型の曲線
を示す。葉群の分布密度が最大になる位置を境にして林冠を上下に二分すると，上部林冠
と下部林冠のそれぞれが占める比率は葉群面積で 51：49, 葉群受光量で 73：17 である。他
方，上層木（樹高 >15 m），中層木（13<樹高 ≤ 15 m），下層木（樹高 ≤ 13 m）が占める
比率は葉群面積で 35：53：12 であるのに対し，葉群受光量では 48：47：5 であり，平均樹
高を越える個体の受光量が全個体の受光量の約 80% を占める。個体の受光量の変動には，
樹冠の葉群面積と単位葉群面積当りの平均受光量が相乗的に働いており，前者は樹冠底に
おける幹の直径の 2 乗に後者は樹高の 4 乗に比例して増大する。

I. Introduction

Organic matter production carried out in forest communities is based on photosynthetic activity of the foliage building up the canopies. In the structural attributes of forest stands the spatial distribution of foliage is one of the most important elements because it determines the light regime in the canopies.

MONSI and SAEKI (1953) devised the "stratified clip method" to represent the vertical distribution of above-ground photosynthetic and non-photosynthetic organs, and by incorporating the light extinction profile into it proposed a so-called "production structure diagram." There have been a great number of studies dealing with the vertical distribution of foliage in forest canopies. Some workers have shown that the WEIBULL function can fit many of the foliage distribution patterns (SCHREUDER and SWANK, 1974 ; HAGIHARA

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and HOZUMI, 1986; VOSE, 1988). Furthermore, HASHIMOTO (1991) recently describes that the canopy profile of foliage mass is successfully modelled with the allometric function.

Forest canopy is regarded as an aggregation of individual tree-crowns with geometrical forms (KAJIHARA, 1977; SATOO and IMOTO, 1979). The crown-occupation area at a depth from top of the canopy changes vertically (HASHIMOTO, 1986), where the between-crowns gaps would facilitate the downward penetration of solar beams incident on the canopy. Hence the canopy profile of crown-occupation area is indispensable to examine the light environment in the canopy.

The photosynthetic production of a forest canopy can be estimated under the principle of combining the photosynthetic response of leaves to light intensity with the light profile in the canopy (HOZUMI and KIRITA, 1970; OKER-BLOM and KELLOMÄKI, 1981), but the calculation procedure is not so simple. It is light (here, photosynthetically active radiation) interception by the foliage that is easily obtained and surely informative on productivity of the forest canopy (WHITEHEAD, 1986; GRACE et al., 1987). The canopy profile of light interception by the foliage would determine the vertical distribution of newly produced foliage, hence provide useful information on the canopy development or its upward movement.

The light interception by the whole canopy is understood as the sum of the light interception by each canopy-layer with a certain depth. On the other hand it can be seen as the sum of the light interception by crowns of the individual trees. In even-aged stands of coniferous species a number of types of thinning are made in accordance with the production plans of timber (ANDOU et al., 1968). It would be of practical importance to understand the productive situation of forest stand on the basis of light interception of the individual trees.

Using measurement data of tree crowns in a young sugi (*Cryptomeria japonica* D. DON) stand, this paper firstly deals with the modelling of distribution structure of the canopy foliage, and then analyzes the light interception by the foliage-layers of the canopy and further that by foliage of the individual crowns to know functional aspects of the stand.

II. Materials and Methods

1. Site and stand characteristics

The sample plot was located on gently sloping ground in a 22-year-old plantation (in 1987) of sugi at the Iwate University Forest at Takizawa, 500 km north of Tokyo. The initial planting density was 3,000 trees ha^{-1}, and the canopy of the stand closed about 15 years after planting. Suppressed trees and those damaged by snow were removed after canopy closure.

Size of the sample plot was 2,000 m^2 (ca. 40×50 m), and diameter at breast height, height, and clear length were measured for each tree in the plot: the averages were 15.2 cm, 13.8 m, 7.3 m, respectively. The intensities of illumination relative to those above the stand canopy were measured at 200 spots on the stand floor on cloudy days (Minolta T-1H). The mean relative illuminance on the stand floor was 5.8% (Fig. 1).

2. Crown measurements

Tree individuals in the plot were divided into three height classes: upper-story trees (UST) with heights > 15 m, middle-story trees (MST) with heights between 13 and 15 m, and lower-story trees (LST) with heights ≤13 m. Crown measurements were made on 5, 8, and 7 sample trees which were randomly selected from the UST, MST, and LST height classes, respectively. After felling, each crown was divided into vertical layers each 1 m in depth. Each crown-layer was set up vertically on the ground to record the position of base of each primary branch and to measure horizontal and vertical distances to the tip of each branch. Each branch was cut parallel to the stem surface, and the branch length and the fresh weight of leaves were determined. All com-
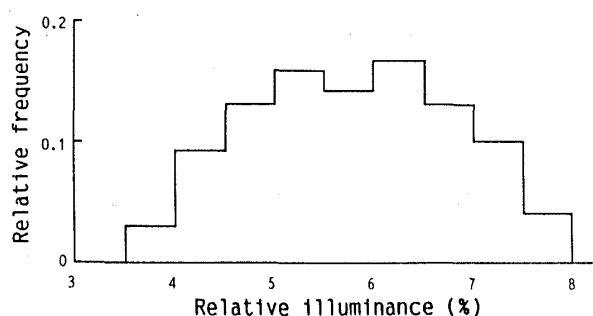

Fig. 1. Histogram with relative illuminance measured on the stand floor

ponents growing from the primary branch were treated as leaves because they were usually covered with a large number of green needles. Leaf samples from every crown-layer were oven-dried to constant weight in a forced-air dryer at 80°C. Cumulative foliage dry weight from the crown apex to each primary branch was calculated and converted into foliage area multiplying by a certain coefficient, mean projected area of needles per unit dry weight (4.46 m² kg⁻¹) (HASHIMOTO and SUZAKI, 1979).

3. Analysis of light interception

Let f_z (m² tree⁻¹, $0 \leq z \leq z_b$) represent cumulative foliage area at depth z from crown apex of a tree. Similarly, let F_z (m² m⁻², $0 \leq Z \leq Z_b$) represent cumulative foliage area at depth Z from top of a canopy. Here, z_b is the crown depth and Z_b the canopy depth. The derived function of the first order of f_z (f_z') or F_z (F_z') shows the vertical change in distribution density of foliage area.

Light beams incident on a forest stand are intercepted first by the canopy and then· by trunks of the individual trees under the canopy. The relative illuminance on the stand floor (R_{flr}) is therefore written as follows :

$$R_{flr} = R_{Z_b} \varepsilon, \tag{1}$$

where R_{Z_b} is relative illuminance at base of the canopy and ε is light transmittance of the trunks under the canopy. ε is computed from the three-dimensional arrangement of the trunks using a physical model of light interception under a standard overcast sky. In this study the value of ε was determined from the following equation (HASHIMOTO, 1985):

$$\varepsilon = e^{-0.282S + 0.0531S^2}, \tag{2}$$

where S is the total surface area of trunks under the canopy and is computed using the relative curve of stem form (KAJIHARA, 1973). In Eq. (1), as R_{flr} is directly measured, R_{Z_b} is determined by calculating R_{flr}/ε.

In well closed forest stands the LAMBERT and BEER's law is generally applied to the canopy profile of light environment (KIRA *et al.*, 1969). The relative illuminance at depth Z from top of the canopy (R_Z) is written as

$$R_Z = e^{-KF_z}, \tag{3}$$

where K is light extinction coefficient of the canopy and obtained by substituting R_{Z_b} and F_{Z_b} for R_Z and F_Z respectively.

In the plant canopy the vertical decrease of the relative illuminance agrees approximately with that of the relative value for the photon flux density of photosynthetically active radiation (PAR) (ŌTANI, in private communication). Therefore, the cumulative light interception (PAR) at depth Z from top of the canopy (E_Z) is equivalent to $1 - R_Z$, and the derived function of E_Z for Z gives the vertical change in distribution density of light interception by the foliage :

$$E_Z' = (1 - R_Z)'$$
$$= K e^{-KF_z} F_Z'. \tag{4}$$

The light interception by a canopy-layer at depth Z is understood as the light interception by crown-layers of the individual trees at the same depth, where the light interception by the crown-layer of each tree could be considered to be proportional to the corresponding foliage area. So the light interception of the whole crown of a tree (e*) can be written as

$$e^* = \int_t^{t+z_b} E_Z' \frac{f_z'}{10000 F_Z'} dZ$$
$$= \int K e^{-KF_z} \frac{f_z'}{10000} dZ. \tag{5}$$

Here, e* is expressed as ratio to the light interception on the horizontal plane of 1 ha above the canopy. And t represents the vertical distance between top of the canopy and the crown apex : $z = Z - t$.

III. Results

1. Crown form and crown profile of foliage area

The crown radius (r_z) and cumulative foliage area (f_z) at depth z from the crown apex were approximated by the allometric equation (RUARK *et al.*, 1987) (Fig. 2 (A), (B)):

$$r_z, f_z = az^b e^{cz}, \qquad (6)$$

where a, b, and c are parameters of the allometric equation: a, $b > 0$ and $c < 0$. The Parameter a concerns the scale of r_z or f_z and b the shape of the allometric curve. The Parameter c provides the value of z at which the allometric curve takes maximum. Values of the parameters varied with the tree size, where the relationship between the parameter value and the crown length were statistically significant (Fig. 3, Table 1). Each parameter of r_z and f_z resembles each other in the tree size dependency. The Parameter a decreased with an increase in crown length, but the Parameter b and c increased.

The distribution density of foliage area in the crown (f_z') increased from the crown apex downward with a maximum around the middle of the crown, and t % en declined toward the crown base (Fig. 2 (C)). The decrease of f_z' in the lower part of the crown is due to the withering and shedding of leaves caused by the low light intensities. Accordingly, the crown can be divided into two parts: the upper crown exposed to sufficient sunlight and the lower crown under poor light condition.

Heights to bases of the upper and lower crowns raised with an increase in tree height, where the increase in the former was more pronounced (Fig. 4 (A)). The taller trees had the deeper crowns. Lengths of the upper crown appeared to be short compared with those of the lower crown for the lower-story trees. Ratios of length, volume, and foliage area of the upper crown to those of the whole crown were in the range of 0.45~0.55, 0.25~0.35, and 0.45~0.50 respectively (Fig. 4 (B)). The ratios for length and volume definitely increased with tree height, but the variation with tree size was unclear for foliage area. The relationships between these ratios and tree height were well approximated by the power function.

2. Canopy structure and light interception

The cumulative volume of crowns (V_Z) and cumulative foliage area (F_Z) at depth Z from top of the stand canopy can be computed, on the basis of the height and clear length and the values of Parameters a, b, and c of r_z and f_z for each stand tree (HASHIMOTO, 1991).

The change of V_Z by the infinitesimal change of $Z(V_Z')$ shows the crown-occupation area at depth Z from top of the canopy. V_Z' increased from top of the canopy downward and showed maximum 1.5 to 2.5 m above base of the canopy (Fig. 5 (A)). V_Z' exceeded the stand area, $V_Z' > 1 \text{ m}^2 \text{ m}^{-2}$, at the part about 8 to 10 m above ground. F_Z increased with depth in the upper part of the canopy, but the
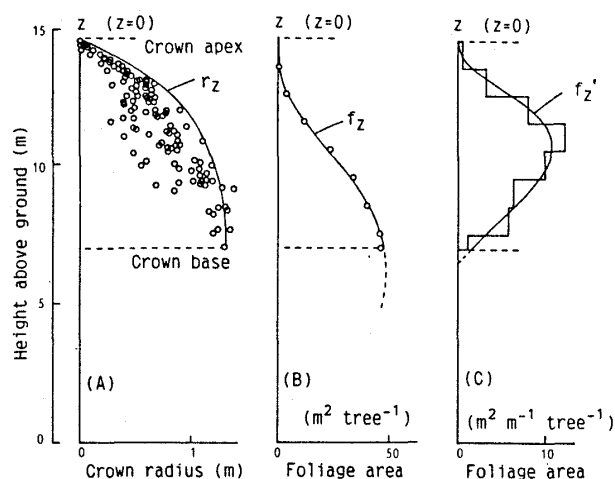

Fig. 2. Crown form (A) and vertical changes in cumulative foliage area (B) and distribution density of foliage area (C) for a sample tree (DBH=14.15 cm; h=14.54 m; crown length=7.5 m)

A freehand curve for the crown form was formulated by Eq. (6).
$r_z = 0.610z^{0.753}e^{-0.100z}$.
$f_z = 0.808z^{3.64}e^{-0.435z}$.

Table 1. Relationship equations between parameter values of r_z and f_z and crown length

Parameter	r_z					f_z				
	g_0	g_1	g_2	R^2		g_0	g_1	g_2	R^2	
ln a	0.811	−0.227	0.00639	0.90 ($p<0.01$)	(I)	1.58	−0.162	−0.0116	0.58 ($p<0.01$)	(I)
b	0.427	0.0228	0.00343	0.53 ($p<0.05$)	(I)	4.40	−1.74	−12.5	0.54 ($p<0.05$)	(II)
c	−0.122	0.366	−1.84	0.54 ($p<0.05$)	(II)	−0.691	−0.00536	0.00415	0.43 ($p<0.10$)	(I)

R^2 is the coefficient of determination. g_0, g_1, and g_2 represent constant and coefficients of the regression equations ((I), (II)).
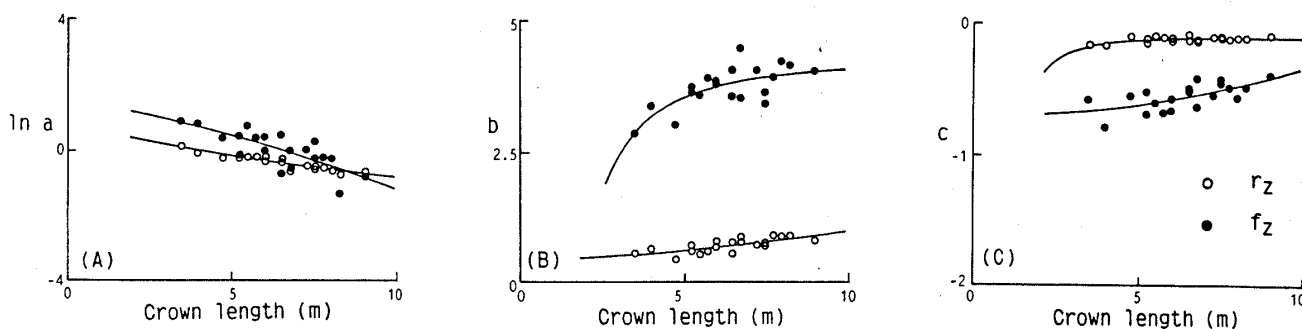(I): $y = g_0 + g_1 x + g_2 x^2$; (II): $y = g_0 + g_1(1/x) + g_2(1/x)^2$.

Fig. 3. Relationship between parameter values of r_z and f_z and crown length for the sample trees
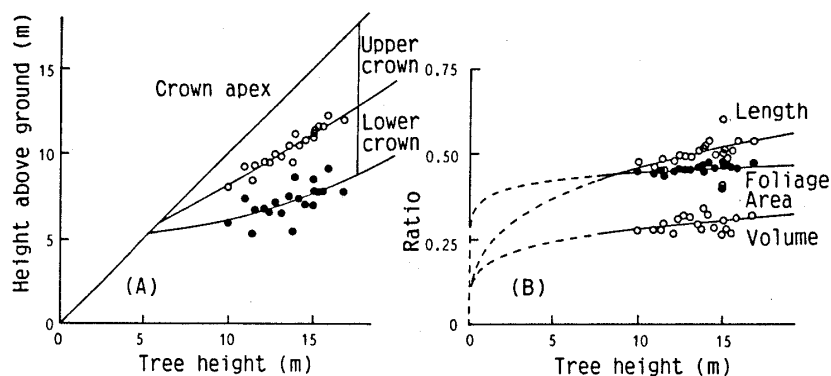Constants and coefficients of the regression equations are listed in Table 1.

Fig. 4. Individual variations in heights to bases of the upper and lower crowns (A) and ratios of length, volume, and foliage area of the upper crown to those of the whole crown (B)

The regression curves are drawn : by a curve of second degree for (A) and . a power function for (B).

increase was less in the lower part of the canopy (Fig. 5 (B)) indicating that the vertical change is biphasic. F_z was also formulated by the allometric equation :

$$F_z = aZ^b e^{cZ}.$$ (7)

F_z' which shows the distribution density of foliage area in the canopy increased with depth reaching maximum below the middle of the canopy. The distribution density of light interception in the canopy (E_z') showed maximum near the middle of the canopy and then declined rapidly with depth. Values of E_z' were extremely low near base of the canopy.

The distribution curves of crown-occupation area (V_z'), foliage area (F_z'), and light interception (E_z') differed from one another in shape. The distribution curves for V_z' and F_z' were skewed, with a larger proportion below the middle of the canopy than above it, whereas almost symmetrical with depth for E_z'. The positions at which V_z', F_z', and E_z' rise to the peak were 8.5, 10.5, and 12.1 m above ground, respectively.

3. Light distribution among tree height classes

The light interception by the whole foliage of a tree individual increased proportionally to the seventh power of the tree height (Fig. 6). The coefficient of determination (R^2) value for the regression equation was 0.91 and highly significant.

Compared with the histogram of height for the stand trees, the distribution of foliage area among the height classes was skewed, with a larger proportion above the mean height (13.8 m) than below it (Fig. 7). This tendency was more pronounced for the distribution of light interception. Mode of those distribution curves was 13~14, 14~15, and 15~16 m, respectively. The distribution ratios among the three height classes,
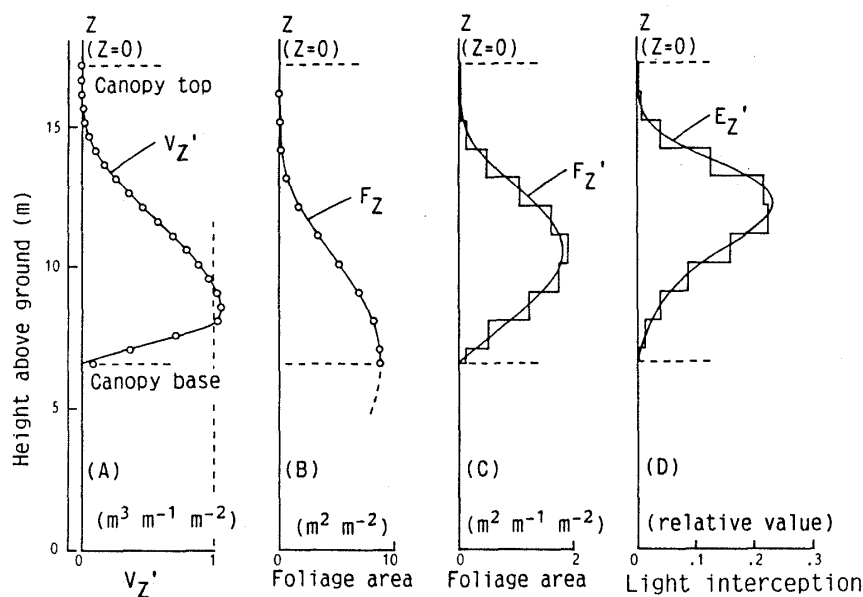
Fig. 5. Canopy profile of crown-occupation area (A), foliage area ((B), (C)),
and light interception (D)

$F_z = 5.57 \times 10^{-4} Z^{7.16} e^{-0.682Z}$.

$E_{z}' = 0.286\ e^{-0.286 F_z} F_{z}'$.

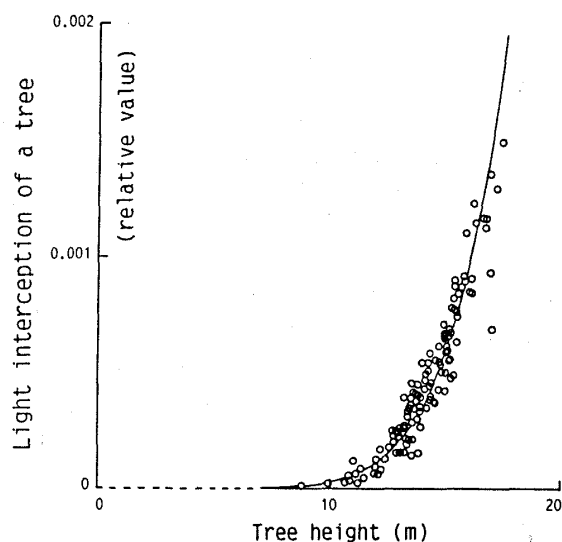
Fig. 6. Light interception of a tree individual (e*)
as a function of height (h)

The computation of e* was made for the 132 trees standing
at the central part (20×30 m) of the sample plot.
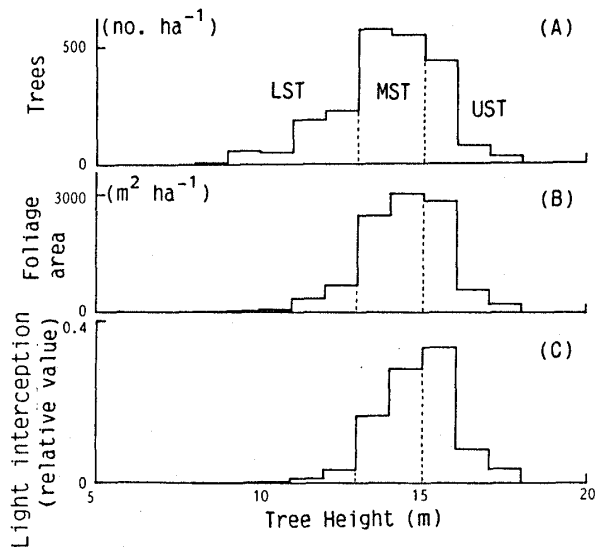$e^* = 2.30 \times 10^{-12} h^{7.15}$ ($R^2 = 0.91$).

Fig. 7. Histogram with height for the stand trees
(A) and within-canopy distributions of
foliage area (B) and light interception
(C) among height classes

UST, MST, and LST represent the upper-, middle-, and
lower-story trees, respectively.

the upper-story (height>15 m), middle-story (13<height≦15 m), and lower-story trees (height≦13 m),
were 24 : 51 : 25 for the number of trees, 35 : 53 : 12 for the foliage area, and 48 : 47 : 5 (%) for the light
interception, respectively.

IV. Discussion

The crown form in closed stands of sugi is often divided into two parts morphologically different, the
upper one with a conical or paraboloidal shape and the lower one with a cylindrical shape (KAJIHARA, 1975).

However, the whole crown form is regarded as a simple geometrical body and well approximated by the allometric equation (Fig. 2 (A)). The crown form is characterized with the Parameter b of the allometric equation : it takes a conical shape at $b=1$ and paraboloidal shape at $b=0.5$. The values of b are in the range of 0.5 to 1 and the taller trees (with deeper crown length) have the smaller values (Fig. 3 (B)). It follows, therefore, that the crown form changes from paraboloidal to conical shape with an increase in tree height.

The smaller values of the crown-occupation area at the upper part of the canopy (Vz') (Fig. 5 (A)) suggest that the incident light beams would easily penetrate downward through the between-crowns gaps. On the other hand the larger values of Vz' at the lower part of the canopy would enable that part to intercept light beams more effectively. Such canopy profile of crown-occupation area is considered to provide more uniform distribution of light over the whole foliage (KUROIWA, 1970 ; OKER-BLOM and KELLOMÄKI, 1983). Thus, the vertical structure of crown-occupation is one of the key factors which affect photosynthetic productivity of the canopy (FARMER, 1976 ; LOOMIS et al., 1976 ; KELLOMÄKI et al., 1986). The modelling on crown form proposed here could be a great help, when analyzing such canopy structure.

The upper part of the canopy is considered to involve actively growing shoots of the individual trees and rarely shed the leaves and branches because of the relatively favorable light condition, where the distribution density of foliage area increases with depth. However, the lower remaining part is under the low intensity light condition which restrains the shoot growths and further causes the leaves and branches to wither and die. This would provide the vertical decrease in distribution density of foliage area (Fig. 5 (C) ; KINERSON et al., 1974 ; WHITEHEAD, 1978 ; BEADLE et al., 1982). By defining the boundary as the position where the distribution density of foliage area is maximum, the canopy could be therefore divided into two parts : the upper canopy on a "constructive stage" and the lower canopy on a "destructive stage."

Provided that the vertical decrease in light intensity in the canopy is extremely slow, the vertical changes in light interception in the canopy would almost accord with that in foliage area. But actually, in spite that the vertical distribution of foliage area is definitely skewed downward, the light interception shows almost a symmetrical distribution with depth (Fig. 5 (C), (D)), because the incident light is rapidly attenuated with depth. In the canopy it is considered that new foliage is produced according to the vertical distribution of light interception. The difference of the distribution curve of light interception from that of foliage area, therefore, implies that the stand canopy is moving upward accompanied by the foliage loss in the lower canopy. In spite of almost the same distribution ratio of foliage area between the upper and lower canopies the light interception in the former exceeds more than 80% of the whole light interception. As is well known, the high pruning treatments for stand trees do not so largely reduce the production of stem wood (FUJIMORI, 1975 ; TAKEUCHI and HATIYA, 1977). This could be well explained by the above canopy profile of light interception.

The light interception by the whole foliage of a tree individual (e^*) is expressed as product of foliage area of the crown and light interception per unit foliage area. According to the pipe model theory (SHINOZAKI et al., 1964) the crown foliage mass is proportional to the square of stem diameter at the crown base (d_u) (Fig. 8). On the other hand the light interception per unit foliage area is, as shown in Fig. 9, proportional to the tree height (h) to the fourth power. The tree size dependency of e^* can be understood as

$$e^* \propto d_u^2 h^4. \tag{8}$$

Accordingly, the remarkable increase in e^* with tree size (Fig. 7) is due to both the increases in crown foliage area and light interception per unit the foliage area.

Since the light interception of individual trees is proportional to the seventh power of the corresponding tree height, the distribution of light interception by the canopy among the height classes skews with a larger proportion for the taller trees. The trees above the mean height (13.8 m) account for about 80% of the whole light interception in the stand canopy, even though these trees comprised no more than half of the total number of trees. Even if the stand was heavily thinned for the trees less than the mean height, the decreased ratio of light interception of the canopy would be limited to about 10% because the crowns of the remaining trees intercept more light than before the thinning. This suggests that the heavy lower-story thinning would not so largely reduce the stand growth.
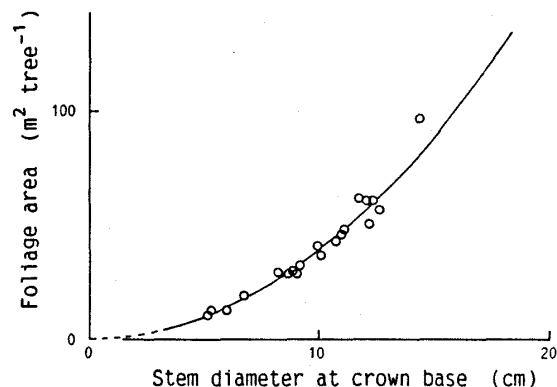
Fig. 8. Crown foliage area (f^*) as a function of the square of stem diameter at the crown base (d_u)

Data from the 20 sampled trees are plotted.
$f^* = 0.393 d_u^{2.00}$ ($R^2 = 0.98$).

With increasing light intensity the CO_2 uptake curve of leaves increases linearly at first but then more slowly to a maximum value; the photosynthetic response to light intensity is represented by a saturating curve (CAUSTON and DALE, 1990). From this physiological property of leaves, the linear relationship would not be seen between the photosynthetic production and light interception of individual trees. It seems that the photosynthetic production of individual trees (kg CO_2 tree^{-1} year^{-1}) is proportional to the stem diameter at the crown base to the power of 2.9 (about 3) in a young *Chamaecyparis obtusa* stand (HAGIHARA and HOZUMI, 1986). According to the present study the light interception of individual trees is proportional to the stem diameter at the crown base to the power of 3.8 (about 4). Since the difference between the two coniferous stands is not so large in respect of the CO_2 uptake curve of leaves to light intensity and the distribution pattern of foliage in the canopy (HAGIHARA and HOZUMI, 1977; HASHIMOTO and SUZAKI, 1979), it follows that the photosynthetic production of the individual trees varies with the corresponding light interception to the 3/4th power.
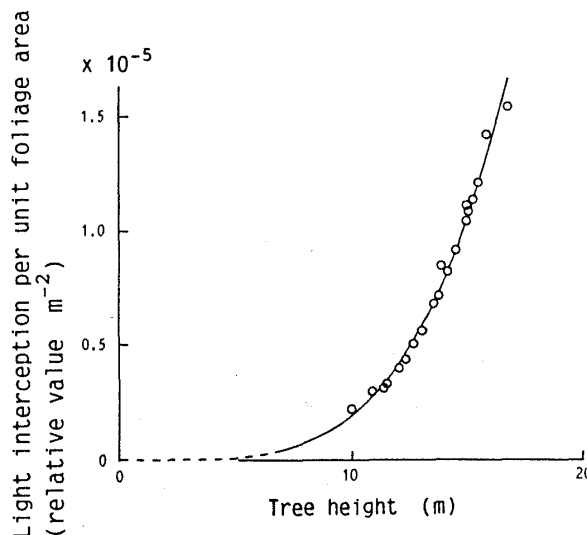

Fig. 9. Light interception per unit foliage area (e_{ave}) as a function of height (h)

Data from the 20 sample trees are plotted.
$e_{ave} = 1.59 \times 10^{-10} h^{4.10}$ ($R^2 = 0.99$).

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