

## Gross photosynthetic production of individual trees in a *Chamaecyparis obtusa* plantation

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### Abstract

Radiation regimes were measured for five sample trees in a 29-year-old *Chamaecyparis obtusa* (SIEB. *et* ZUCC.) ENDL. plantation. Relative radiation within and above a crown decreased exponentially with increasing cumulative leaf area density per unit crown projection area from the top of the crown downward. Middle-sized trees showed steep light attenuation as compared with large- or small-sized trees. Gross photosynthetic production on a whole tree basis was evaluated using a modified model of the Monsi-Saeki model. As the total leaf area of a tree approached a critical leaf area, the gross photosynthetic production dropped abruptly. The dependence of the gross photosynthetic production on the total leaf area was described by a generalized power function. There was no considerable difference in gross photosynthetic production per unit leaf area, or in mean photosynthetic activity at a whole tree level, among larger-sized trees accounting for 85% of the total number of trees. The gross photosynthetic production per unit leaf area decreased more drastically in the smallest-sized tree having foliage near the critical leaf area.

Key words : gross photosynthetic production, individual trees, *Chamaecyparis obtusa*.

### I. Introduction

Forests are composed of various-sized trees; each is subjected to the corresponding environmental conditions. As a result, forest trees are expected to have various amounts of functions, such as photosynthesis, respiration, and litter-fall, in accordance with their body size. In fact, studies on the size-dependence of the functions have made it clear that respiration (NINOMIYA and HOZUMI, 1981, 1983a; OGAWA *et al.*, 1985), litter-fall (MIYAURA and HOZUMI, 1985, 1988, 1989), and attached dead leaves and branches (TANGE *et al.*, 1987) of a whole tree (aerial parts) change with its body size according to a certain regularity.

As far as photosynthesis is concerned, it is difficult to measure whole tree photosynthesis owing to the methodological problems arising from the huge size inherent to trees (MATSUMOTO, 1985; HAGIHARA *et al.*, 1987). HAGIHARA and HOZUMI (1986) made an attempt to estimate the whole tree photosynthesis of *Chamaecyparis obtusa* on the basis of a

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canopy photosynthesis model. KAKUBARI (1987) conducted to calculate the whole tree photosynthesis of *Fagus crenata* on the basis of a computer simulation model.

This paper is an attempt to assess the photosynthetic production on a whole tree basis in a *Chamaecyparis obtusa* plantation. First, the radiation regime of five sample trees is clarified as related to the cumulative leaf area density per unit crown projection area. Second, the gross photosynthetic production of each sample tree is estimated on the basis of a modified form of the Monsi-Saeki model (MONSI and SAEKI, 1953; SAEKI, 1960). Finally, we discuss the photosynthetic production of forest trees in relation to their leaf area. This discussion may provide a better understanding of the relationship between the production and the size structure of trees in *Chamaecyparis obtusa* plantations.

## II. Material and Methods

### 1. Study site

This study was carried out on a 29-year-old *Chamaecyparis obtusa* plantation (as of 1985) of Nagoya University Forest at Inabu, Aichi Prefecture, in the central of Japan. This plantation was located at an elevation of 1000 m on a 35° slope with a north exposure. Tree density, mean tree height, mean stem diameter at breast height (1.3 m above ground), and leaf area index were 5835 trees ha<sup>-1</sup>, 9.8 m, 9.3 cm, and 7.0 ha ha<sup>-1</sup>, respectively.

### 2. Description of sample trees

Five sample trees were selected for representing size class distribution in August 1985. The general features of the sample trees were compiled in Table 1. The total leaf area of the sample trees was indirectly estimated by means of an allometric relationship between the leaf area  $u$  [m<sup>2</sup>] and the stem diameter at clear bole length  $D_b$  [cm] ( $u = 0.0763D_b^{2.54}$ ; number of observations=14; coefficient of determination=0.91). This relationship was formulated on the basis of data with respect to the fourteen sample trees which were provided for the stratified clip technique.

Table 1. General features of the sample trees.

Tree No.	1	2	3	4	5
Tree height $H$ [m]	10.5	9.7	8.5	7.0	4.6
Clear bole length [m]	4.9	5.0	5.1	4.0	2.3
Diameter at clear bole length $D_b$ [cm]	11.5	6.8	4.3	3.8	3.5
Diameter at breast height $dbh$ [cm]	13.4	9.7	6.6	6.1	4.1
Total leaf area $u$ [m <sup>2</sup> ]	36.3	9.7	3.0	2.1	1.8
Crown projection area $s$ [m <sup>2</sup> ]	6.0	4.3	1.8	1.5	1.2
Total leaf area per unit crown projection area $f^*(=u/s)$	6.1	2.3	1.7	1.4	1.5
$I_T/I_0$ [%]	90	85	69	15	1.7
Coefficient $k$ in Eq. (4) [m <sup>-2</sup> m <sup>2</sup> ]	0.66	1.69	1.70	1.42	0.53

Abbreviations:  $I_T$ , radiation intensity at the top of a tree;  $I_0$ , radiation intensity above the canopy.

### 3. Measurement of photosynthesis

One or two twigs bearing leaves were collected in the morning at 1.0 m intervals from 4.3 to 10.3 m height on the sample trees of Tree No. 1, 2, 3, 4, and at 0.5 m intervals from 2.3 to 4.3 m height on the sample tree of Tree No. 5. Immediately after sampling, the twigs were transferred to a laboratory of Nagoya University Forest.

The CO<sub>2</sub> exchange-rates of leaves were measured using an infrared gas analyzer (Shimadzu URA-2S). Leaves detached from the twigs were used for the photosynthetic measurement. An assimilation chamber was kept in a thermoregulated water bath with 1.0 cm deep water layer above the chamber surface. Air was stored in a plastic bag and let into the assimilation chamber at the rate of 0.5 liter min<sup>-1</sup>. The air temperature was kept at the mean monthly air temperature in July (19°C) using a thermoregulator (Toyo TE-106S). The radiation source consisted of two 500 W incandescent lamps of a flood type (National REF-LAMP). The photosynthetic photon-flux density was measured with a quantum sensor (LI-COR LI-190SB). The area of leaf samples was determined with an area meter (Hayashi AAC-100). The photosynthetic measurement was performed on 31 July to 6 August 1985.

Photosynthetic rates were corrected to normalized rates at CO<sub>2</sub> concentration of 330 ppm (TOTSUKA, 1966). The gross photosynthetic rate was assumed to be the sum of the net photosynthetic rate and the respiration rate in the dark.

### 4. Radiation measurement in the stand

The measurement of solar radiation was made using a pyranometer sensor (LI-COR LI-200SB) with an automatic recorder (LI-COR LI-550). The sensor was installed above the canopy surface. The measured solar irradiance was converted into the photosynthetic photon-flux density (MORI *et al.*, 1984).

As shown in Fig. 1, the radiation regime of the sample trees was measured with a chemical light-meter (HAGIHARA *et al.*, 1982) from 17 to 18 August 1985. The number of observations for each layer measurement ranged from 15 vials for the smallest-sized tree (Tree No. 5) to 30 vials for the largest-sized tree (Tree No. 1).

The same method was employed to obtain the radiation profile within the canopy from 18 to 19 August 1985. The observations for each layer measurement consisted of 50 vials. For each layer measurement, another 15 vials were placed in full sunlight above the canopy.

## III. Results

### 1. Gross photosynthetic rate - photosynthetic photon-flux density curve

As shown in Fig. 2, the regression curves of the gross photosynthetic rate  $p$  [mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>] on photosynthetic photon-flux density  $I$  [ $\mu$ E m<sup>-2</sup> s<sup>-1</sup>] incident on leaf surfaces was approximated fairly well by the formula,

$$p = b \cdot I / (1 + a \cdot I). \quad (1)$$

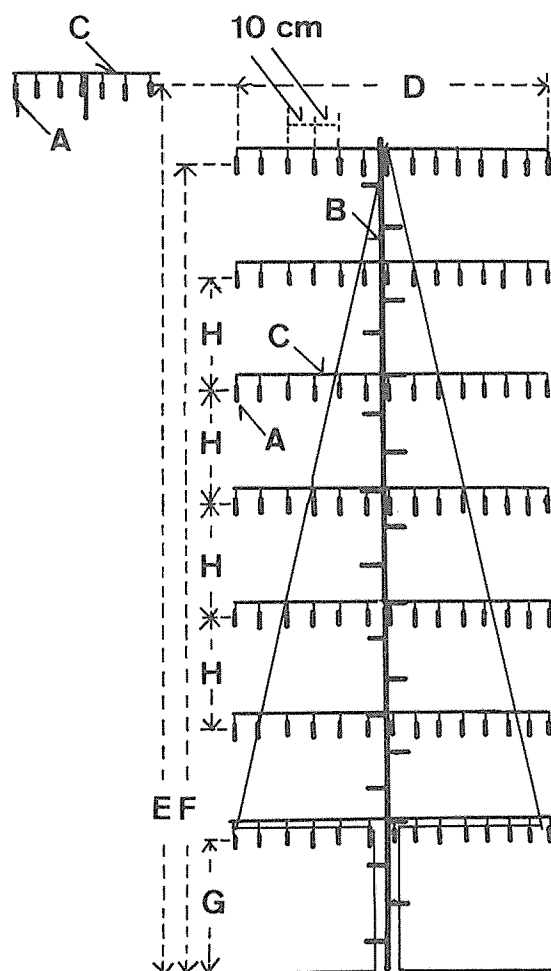


Fig. 1. Schematic representation of radiation measurement for individual sample trees. A, vial (Nichiden s-1); B, steel ladder; C, stainless bar ( $\phi=1.2$  cm); D, width of a crown; E, height of the canopy surface; F, tree height; G, clear bole length; H, interval between layers (1.0 m for Tree No. 1, 2, 3, 4 or 0.5 m for Tree No. 5). The vials contained 4 ml solution of anthracene dissolving in ethyl alcohol ( $30 \text{ mg l}^{-1}$ ).

Here,  $a$  and  $b$  are coefficients.

Figure 3 shows that the value of  $a$  in Eq. (1) was variable according to the relative value of radiation  $I''$ , to which leaves were exposed within crowns, to radiation above the canopy surface  $I_0$ . On the other hand, such a tendency was not so clear between the value of  $b$  and the value of  $I''/I_0$ .

HOZUMI and KIRITA (1970) found that the values of  $a$  and  $b$  in Eq. (1) decreased with increasing  $I''/I_0$  following the hyperbolic equations,

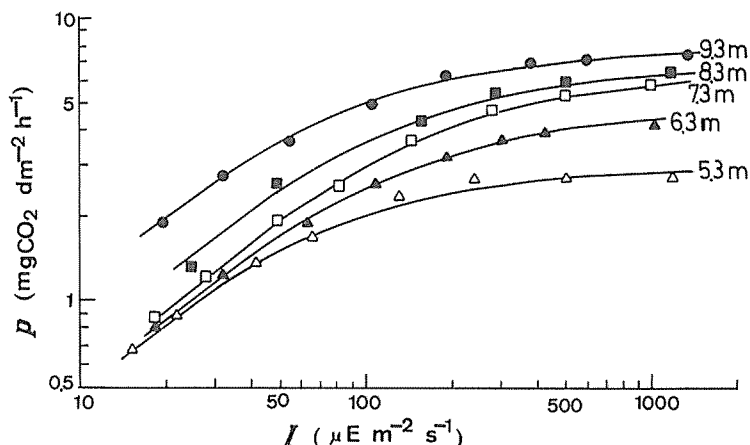


Fig. 2. Representative gross photosynthetic rate  $p$  - photosynthetic photon-flux density  $I$  curves in detached leaves belonging to different layers on Tree No. 2. The data are fitted to Eq. (1).

$$a = A/(I''/I_0) + B, \quad (2)$$

$$b = C/(I''/I_0) + D. \quad (3)$$

Here,  $A$ ,  $B$ ,  $C$ , and  $D$  are constants common to all the sample trees. Our results support Eqs. (2) and (3) on condition that the value of  $C$  is zero, or  $b = D$  in Eq. (3).

## 2. Radiation profile within crowns

To evaluate the photosynthetic production by sample trees on the basis of canopy photosynthetic model, the vertical distribution of leaf area of the sample trees must be known. We used the Weibull function to assess the vertical distribution of leaf area of the sample trees (HAGIHARA and HOZUMI, 1986). The parameters of the function, or shape and scale parameters, were estimated on the basis of the relationships between the parameters and the stem diameter at breast height in the study site (MORI and HAGIHARA, 1991).

As shown in Fig. 4, the relative radiation within  $I''$  and above a crown  $I_T$  decreased exponentially with increasing cumulative leaf area density per unit crown projection area  $f$  [ $\text{m}^2 \text{m}^{-2}$ ] from the top of the crown downward:

$$I''/I_T = \exp(-k \cdot f). \quad (4)$$

In Eq. (4), the coefficient  $k$  is an indicator describing a degree of light attenuation within a crown.

Figure 5 illustrates that the coefficient  $k$  had the highest value in middle-sized trees. This shows that the radiation incident on crown surfaces decreases abruptly with increasing cumulative leaf area density per unit crown projection area in middle-sized trees as compared with in large- or small-sized trees. The value of  $k$  may be considered

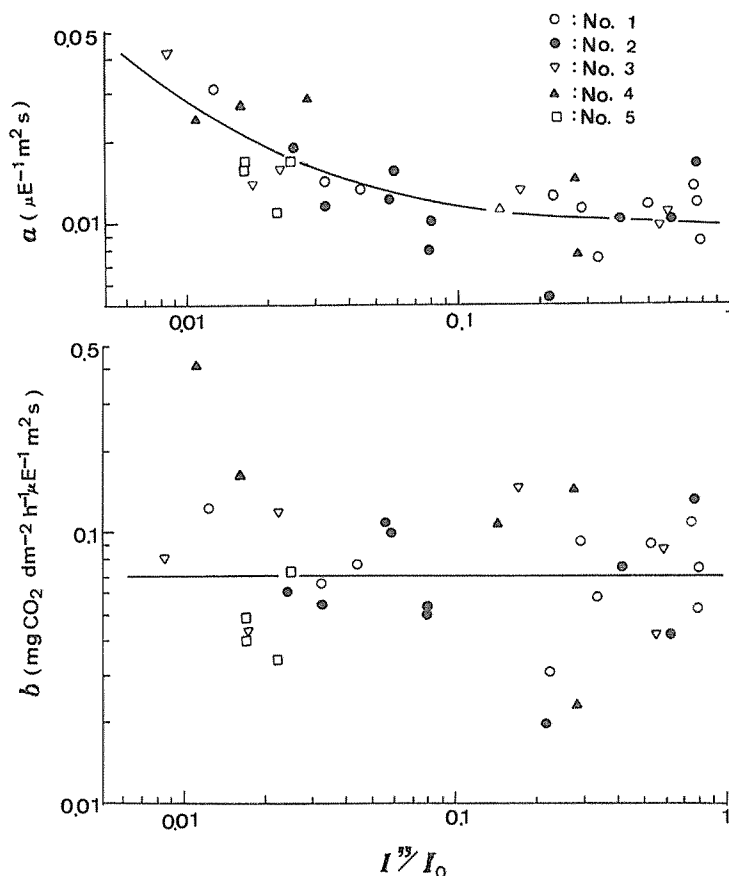


Fig. 3. Relationship between the coefficients  $a$  and  $b$  in Eq. (1) and the relative value of radiation  $I'$ , to which leaves were exposed within crowns, to that above the canopy surface  $I_0$ . The data are fitted to Eq. (2):  $a=0.000192/(I'/I_0)+0.00972$ ; and to Eq. (3):  $b=0.0691 (C=0)$ .

to express the radiation regime of forest trees influenced not only by their own foliage, but also by the foliage of their surrounding trees. In this sense, the coefficient  $k$  differs from the light extinction coefficient  $K$  proposed by MONSI and SAEKI (1953).

### 3. Radiation profile within the canopy

As shown in Fig. 6, the radiation incident on the canopy decreased exponentially with increasing cumulative amount of leaf area  $F$  ( $\text{ha ha}^{-1}$ ) according to the equation (MONSI and SAEKI, 1953):

$$I'/I_0 = \exp(-K \cdot F). \quad (5)$$

Here,  $I'$  denotes mean radiation at a given height within the canopy. The value of the light extinction coefficient  $K$  was  $0.656 \text{ ha}^{-1} \text{ ha}$ . On the basis of Eq. (5), MONSI and SAEKI

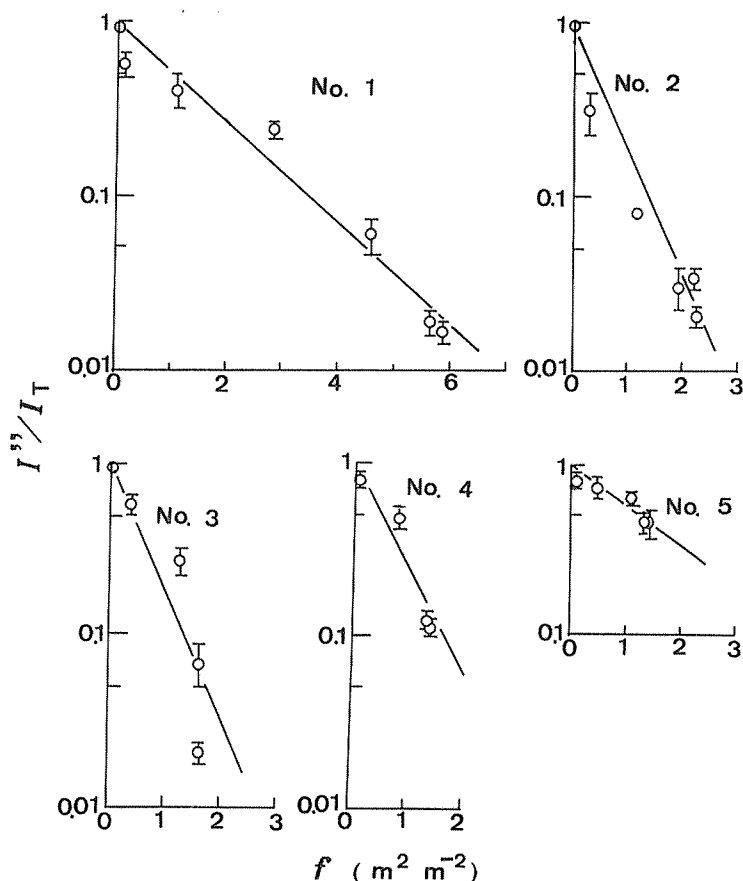


Fig. 4. Exponential attenuation of the radiation at a specific height  $I''$  on each sample tree relative to that above the crown surface  $I_T$  with increasing cumulative leaf area density per unit crown projection area  $f$ . Each data is expressed as the mean value with its 95%-confidence interval. The straight line is based on Eq. (4):  $I''/I_T = \exp(-k \cdot f)$ . The values of the coefficient  $k$  are given in Table 1.

(1953) suggested that the radiation incident on leaves at a given height within canopies is expressed in terms of the product of the coefficient  $K$  and the radiation on the horizontal plane at the height. On the analogy of this theoretical consideration, we postulate that the photosynthetic photon-flux density incident on leaves within crowns is given by

$$I = K \cdot I'', \quad (6)$$

where the light transmissibility of leaves (SAEKI, 1960) is neglected.

As illustrated in Fig. 7, the diurnal course of the radiation incident on the canopy, namely  $I_0$  in Eq. (5), was fitted to the following equation (KUROIWA, 1966),

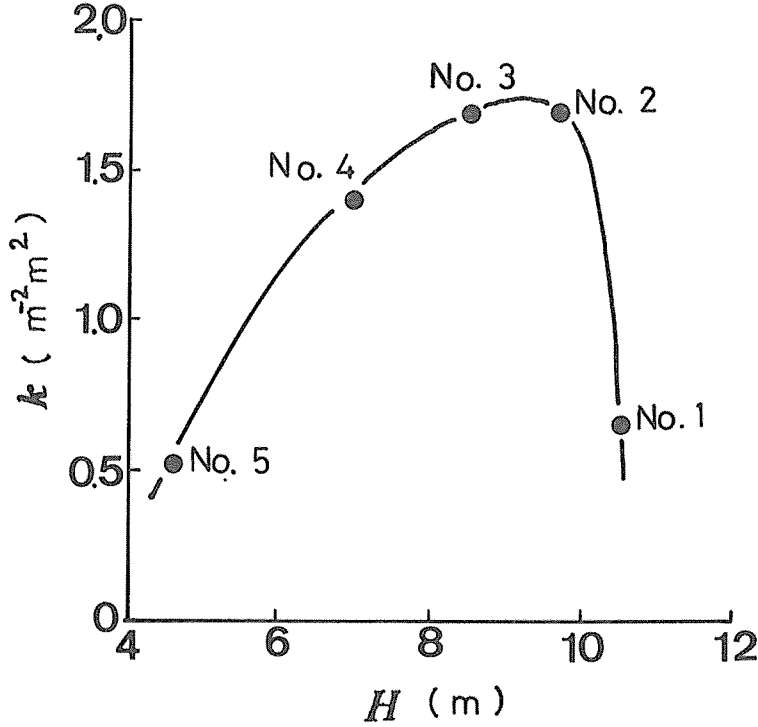


Fig. 5. Relationship of the coefficient  $k$  in Eq. (4) to tree height  $H$ . The curve is freehanded.

$$I_0 = I_M \sin^2(\pi \cdot t/d). \quad (7)$$

The symbols  $I_M$  [ $\mu\text{E m}^{-2} \text{s}^{-1}$ ],  $t$  [h], and  $d$  [h] denote the maximum value of radiation, time after sunrise, and day length, respectively.

#### 4. A mathematical model for estimating the daily gross photosynthetic rate of a whole forest tree

Assuming that Eqs. (2), (3), (4), (6), and (7) hold, we can regard  $p$  in Eq. (1) as a function of  $f$  and  $t$ . Thus, the formula for calculating the daily photosynthetic rate of a whole forest tree  $p_g$  can be given by integrating Eq. (1) from 0 to  $d$  with respect to  $t$  and from 0 to  $f^*$ , total leaf area per unit crown projection area, with respect to  $f$ . The result of the integral is as follows,

$$p_g = ((d \cdot s)/(k \cdot A)) (k \cdot C \cdot f^* + 2((A \cdot D - B \cdot C)/B)) \ln((1+M)/(1+N)) \\ + (C/L) \ln(((M+L)(N-L))/((M-L)(N+L))), \quad (8)$$

where  $s$  is the crown projection area, and

$$M = (1 + K \cdot I_M (A + B(I_T/I_0)))^{1/2}, \\ N = (1 + K \cdot I_M (A + B(I_T/I_0) \exp(-k \cdot f^*)))^{1/2},$$



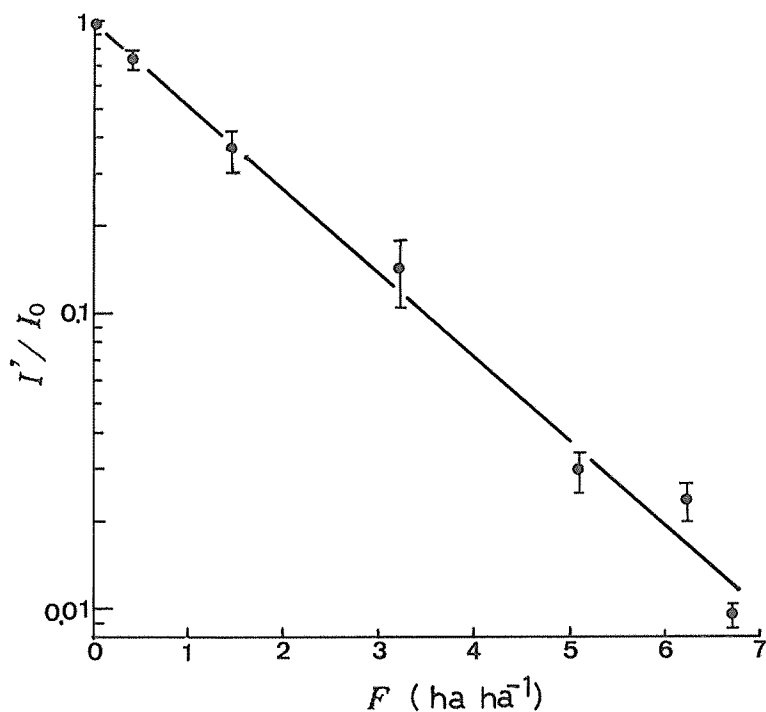


Fig. 6. Exponential attenuation of relative radiation  $I'/I_0$  with increasing cumulative leaf area density  $F$  in the whole plot. Data expressed as the mean value with its 95%-confidence interval are fitted to Eq. (5):  $I'/I_0 = \exp(-0.656F)$ .

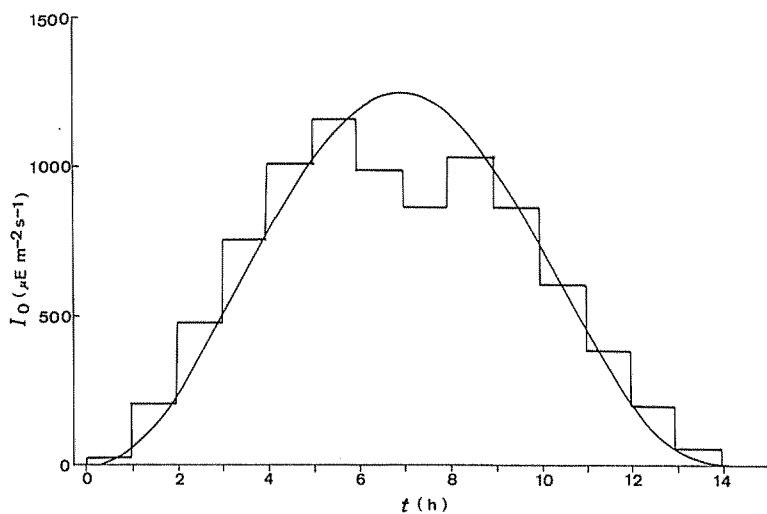


Fig. 7. Diurnal course of photosynthetic photon-flux density  $I_0$  incident on the canopy. Each histogram shows the mean value during the period of 31 July to 6 August 1985. The curve is based on Eq. (7):  $I_0 = 1240 \sin^2(\pi \cdot t / 13.85)$ .

and

$$L = (1 + K \cdot I_M \cdot A)^{1/2}.$$

The observed values of  $s$ ,  $f^*$ ,  $I_T/I_0$ , and  $k$  for each sample tree are summarized in Table 1 and are used for the calculation of  $p_g$  in Eq. (8).

#### IV. Discussion

On the basis of Eq. (8), we estimated the photosynthetic production of individual sample trees. Figure 8 shows the relationship between the photosynthetic production of individual sample trees and the corresponding leaf area. As the total leaf area approached the critical leaf area  $u_{min}$  which forest trees can retain, the gross photosynthetic rate decreased abruptly. The relationship was well approximated by the following generalized power function,

$$p_g = g \cdot (u - u_{min})^h, \quad (9)$$

where  $g$  and  $h$  are coefficients. The value of the exponent  $h$  was 0.74. Equation (9) is the same form that NINOMIYA and HOZUMI (1983a, b) suggested for describing the size-dependence of the respiration rate of forest trees in *C. obtusa* plantation. If  $u$  is sufficiently larger than  $u_{min}$ , Eq. (9) is reduced to the simple power function with the exponent of  $h$ .

Dividing both sides of Eq. (9) by  $u$  results in

$$p_g/u = g \cdot u^{-1} (u - u_{min})^h. \quad (10)$$

Here,  $p_g/u$  stands for the gross photosynthetic rate per unit leaf area, or mean photosynthetic efficiency at individual tree level. This relationship is illustrated in Fig. 9. Since the value of the exponent  $h$  was less than unity, the gross photosynthetic rate per unit leaf area has a maximum value of  $g \cdot u_{min}^{h-1} h^h (1-h)^{1-h}$  at  $u = u_{min}/(1-h)$  (NINOMIYA and HOZUMI, 1983b). The  $p_g/u$  of Tree No. 1 ( $dbh=13.4$  cm), however, was smaller than that of Tree No. 3 ( $dbh=6.6$  cm) by only 10%. The number of trees with  $dbh > 6.6$  cm accounted for about 85% of the total number of trees. It may be likely that there does not exist so clear difference among these larger-sized trees in terms of the mean photosynthetic efficiency.

On the other hand, the smallest-sized tree of Tree No. 5 with leaf area just above the critical one showed an extremely lower value of the photosynthetic efficiency. Smaller-sized trees tend to be suppressed by their surrounding trees, so that their radiation regime becomes extremely poor. In fact, the ratio of radiation on the crown of the smallest-sized tree (Tree No. 5) to that on the canopy was only 1.7% (Table 1). It may be due to high tolerance of *C. obtusa* able to survive in deep shade that such trees grown under low radiation conditions can manipulate their photosynthetic production in some

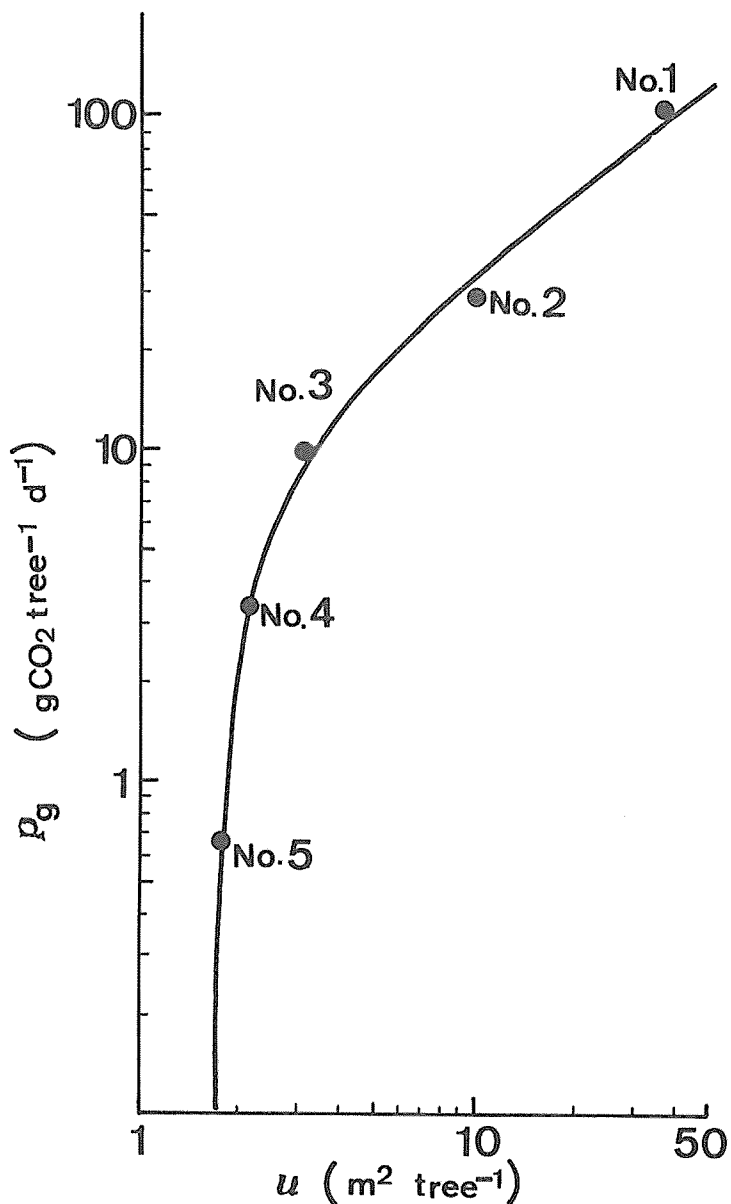


Fig. 8. Dependence of the gross photosynthetic rate of sample trees  $p_g$  to their leaf area  $u$ . The curve is based on Eq. (9) :  $p_g = 7.16(u - 1.73)^{0.74}$ .

degree. These smaller trees may be supposed to experience natural thinning in the near future, owing to the bankruptcy of CO<sub>2</sub> economy.

The structure of forests can be affected by the physiological characteristics of trees composing the forest stands. Therefore, we may be able to understand the relationship between the structure of forests and the function of trees in terms of the physiological characteristics of forest trees.

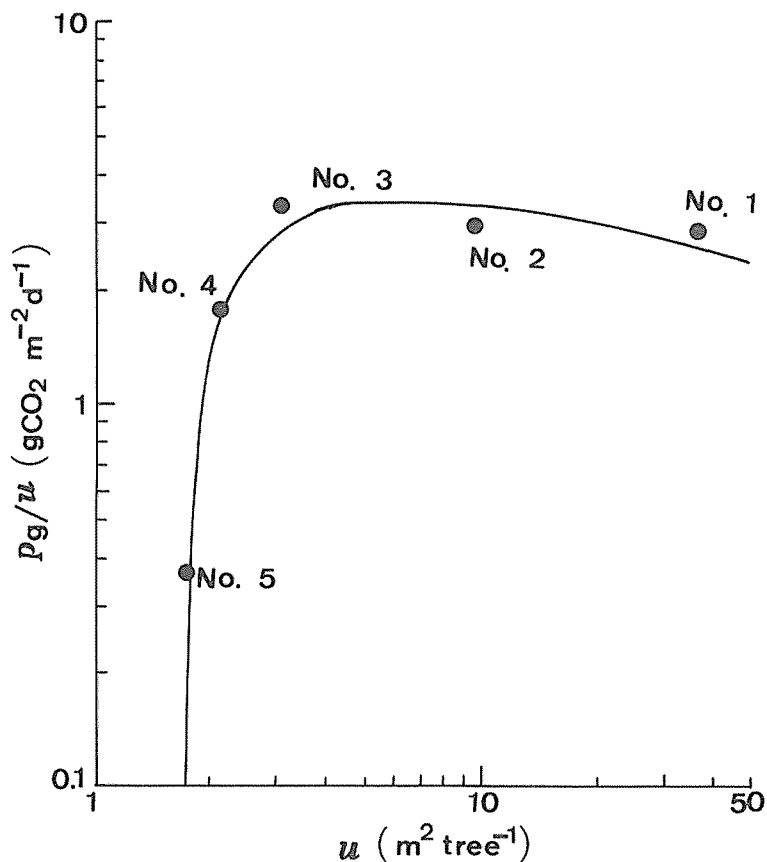


Fig. 9. Relationship between the gross photosynthetic rate per unit leaf area  $p_g/u$  and the leaf area  $u$  of individual sample trees. The curve corresponds to Eq. (10):  $p_g/u = 7.16u^{-1}(u - 1.73)^{0.74}$ .

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## ヒノキ人工林の林木個体の総光合成生産

森 茂太・萩原 秋男

29年生のヒノキ人工林で大小5個体の光環境を測定した。樹冠上部に対する樹冠内の相対光強度は、梢端部から下部へ向って積算した樹冠投影面積当たりの葉面積の増加に伴い指数関数的に減少した。大、小サイズの個体に比べ中サイズの個体では、光強度は急激に低下した。個体の総光合成速度を推定するのに門司・佐伯モデルの改変モデルを用いた。個体の葉面積が生存可能な最小個体の葉面積に近づくにつれて、個体の総光合成速度は急激に低下した。個体の総光合成速度の個体葉面積への依存性は拡張された巾乗式で近似された。葉面積当たりの総光合成速度、すなわち個体レベルでの平均光合成能率は、総個体数の85%を占める大きい方の個体間で大きな差は見られなかった。生存可能な最小個体の葉面積に近い小さな個体ほど、個体の葉面積当たりの総光合成速度は急激に低下した。