

論 文

Studies on the Response of Photosynthesis to Light Intensity in Leaves Attached at Various Positions in Tree Crowns of a *Cryptomeria japonica* Even-aged Stand—Effects of Shading and Leaf Aging*

Ryoji HASHIMOTO** & Tamio SUZAKI***

HASHIMOTO, Ryoji & SUZAKI, Tamio: **Studies on the response of photosynthesis to light intensity in leaves attached at various positions in tree crowns of a *Cryptomeria japonica* even-aged stand—Effects of shading and leaf aging** *J. Jap. For. Soc.* 61: 193~201, 1979 In this 17-year-old stand, the photosynthetic rate per unit of light intercepting area was measured and compared at various positions in the crown during a vigorous growing season. At light saturation, the rates were higher in the upper and the lower surface positions in the conical shaped part of the crown exposed to sunlight (13 to 18 mg CO₂ dm⁻²hr⁻¹), than in the upper and the lower positions in the cylindrical shaped shaded part (8 to 10 mg). At lower light intensities, a reverse relationship occurred. The seasonal changes in the photosynthetic rates measured at light saturation and at lower light intensities differed from each other. Also different seasonal changes were observed at different positions in the crown. The photosynthetic rate in shaded parts was relatively steady. In seedlings grown under artificial shading and in saplings grown in the open, the photosynthetic rates measured at light saturation and at lower light intensities increased with shading, whereas the rates at light saturation decreased with increased age of leaves (i.e. current year leaves and one-year-old leaves). In dense stands, older leaves in the crown generally grow under heavier shade conditions, and the differences in photosynthetic rates at various positions at light saturation may be due mainly to leaf aging, whereas those at lower light intensities are due to shading.

橋本良二・須崎民雄：スギ同齢林における樹冠各部の葉の光強度-光合成関係に関する研究—樹冠部光環境と葉齢の影響— 日林誌 61:193~201, 1979 17年生スギ林分における生長期の樹冠各部の葉の光強度-光合成関係を調べた。その際、葉が光をさえぎる有効表面積をベースにして光合成速度を表わした。また、スギ葉の光合成に及ぼす光環境と葉齢の影響を苗木と幼齢木で調べた。強光域の純光合成速度は、陽樹冠上部と下部表面で高く、13~18 mg CO₂ dm⁻²hr⁻¹の値を示し、陰樹冠上部と下部で低く、8~10 mgの値を示した。一方、弱光域の純光合成速度は、陰樹冠で高い値を示した。光合成速度の季節変化は、強光域と弱光域で異なり、また樹冠部位によっても異なるようだ。強光域と弱光域の純光合成速度は、葉が庇陰下で生育することで上昇し、強光域の光合成速度は、当年生から1年生にいたる葉齢の進行で低下した。スギの閉鎖林分では、概して、葉齢の進んだ葉ほど強い庇陰下で生育するから、樹冠部位による強光域の光合成速度のちがいは、主として葉齢の影響により、弱光域の光合成速度のちがいは、光環境の影響によると考えた。

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** Fac. of Agr., Iwate Univ., Morioka 020 岩手大学農学部

*** Fac. of Agr., Kyushu Univ., Fukuoka 812 九州大学農学部

I. Introduction

Studies on the response of photosynthesis to different light intensities in leaves attached at various positions in the crown are important in explaining forest tree growth from the viewpoint of dry matter balance. HOZUMI & KIRITA (1970) have investigated the photosynthesis-light intensity curves of leaves in the canopy of an evergreen broadleaved forest to estimate photosynthetic production. HAGIHARA & HOZUMI (1977) have done the same in a *Chamaecyparis obtusa* S. et Z. plantation. They showed that the parameters of photosynthesis-light intensity curves changed regularly with the diminishing of light from the top to the bottom of the canopy.

Information on photosynthesis in *Cryptomeria japonica* D. DON depends mainly on a study by NEGISI (1966), in which the effects of external factors such as light, temperature, and soil moisture on photosynthesis have been studied in one-year-old seedlings. However, we have little information on photosynthesis in *C. japonica*. In this paper, the response of photosynthesis in *C. japonica* to light intensities was studied at various positions in the crown of 17-year-old forest trees, in 2-year-old seedlings grown under different artificial shadings, and in 4-year-old saplings grown in the open.

II. Materials and Methods

Experiment 1: A 10m×20m plot was located in a 17-year-old *C. japonica* plantation in the Iwate University Experimental Forest at Takizawa, adjoining Morioka. The stand density, mean stem diameter at breast height, and mean tree height within the plot in November 1977 were about 2,700 trees ha⁻¹, 12.6 cm, and 11.3m, respectively. Branches bearing branchlets of leaves were detached from four different heights in the crown in order to measure the CO₂ gas exchange in branchlets of leaves attached at various positions, i.e. at the upper (SUN-1), the lower surface (SUN-2) and the lower inner (SUN-3) positions in the conical shaped portion of the crown exposed to direct sunlight; at the upper (SHADE-4) and the lower (SHADE-5) positions in the cylindrical shaped part of the shaded crown. Soon after detachment the cut ends of the branches were placed in a container of water, recut under the water, and taken to the laboratory. The samplings were made in May, August, and October corresponding with the early, the middle, and the late parts of the growing season, respectively. The branches were taken from at least five individual tree in each part of the growing season.

The sample branchlets of leaves, about 10 g in

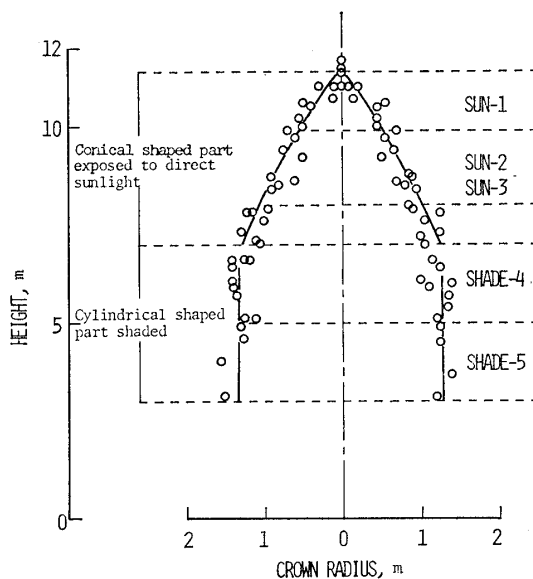


Fig. 1. Longitudinal section of crown of four standard trees

Open circles represent crown radii at various heights. SUN-1, SUN-2, SUN-3, SHADE-4 and SHADE-5 represent the position in the crown. See the explanation in the text.

fresh weight and 10 cm in length, were detached from branchlet tips for measuring the CO₂ gas exchange. In May, shoot growth had not yet begun, and all of the leaf samples were more than one year old. Then shoot growth occurred mainly in the upper and lower surface positions in the conical shaped part of the crowns exposed to sunlight. Therefore, in August and October the leaves of the samples detached from these two positions, SUN-1 and -2, were of the current year's growth only, whereas those from the other positions were older than one year.

The chamber shown in Fig. 2 was used in Experiment 1. The chamber was made of transparent acrylic board with the inside walls lined with black plastic film to decrease light reflection. The cut bases of branchlets with leaves were inserted in small vinyl tubes (V) filled with water. Air was circulated past the leaves and the copper sheets (C), (the latter which served as a radiator in the chamber) by a fan (F) set near an end wall. The fan was monitored with a revolution-indicator (Yokokawa type-2602) and set to rotate at a constant rate of 2,300 rpm keeping the wind velocity near the leaves at about 0.5 to 1m sec⁻¹. Leaf temperature was maintained at about 20°C by controlling the temperature of the water flowing in the copper pipe attached to the copper sheets. A thin thermocouple (T) was inserted into a leaf for measuring its temperature. The rate of air supply to the chamber was one liter per minute.

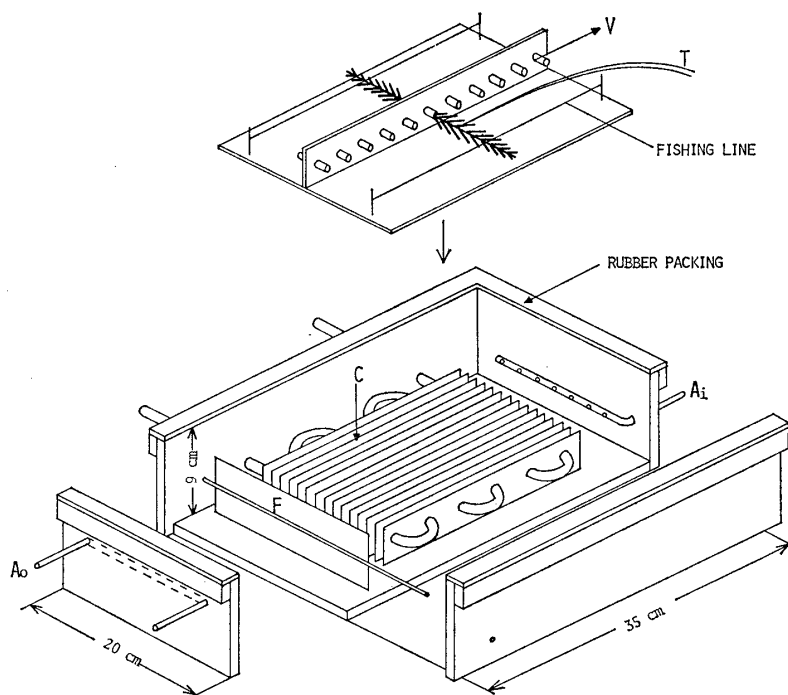


Fig. 2. Assimilation chamber used in Experiment 1

The lid of the chamber is not shown. See explanation of letters in the text.

The measurement of CO_2 gas exchange was carried out by an open system using an infrared gas analyzer (Horiba LIA-2 A). The rate of CO_2 exchange was determined by measuring the CO_2 concentration in fresh air entering through the inlet (A_1) and in the air passing past the sample leaves and discharging through the outlet (A_0). The photosynthetic rates obtained were corrected to normalized rates at CO_2 concentration of 300 ppm. Light was supplied by three electric discharge lamps (Toshiba Sun-Lamp 400 W, 250 W) and four incandescent flood-type lamps (Toshiba Photoreflector 300 W) placed above the chamber. A filter, made with a water layer 5 cm deep, was placed between the light source and the chamber to absorb heat radiation. Measurements were made at various light intensities. Light intensity was changed by inserting black Saran shading cloth screens between the light source and the chamber. Light intensity was measured with a selenium photometer (Toshiba model-5).

After the measurement of the CO_2 gas exchange the leaves were placed on a plate of unreflective frosted glass in order to take photographs of the adaxial sides of leaves exposed to light in the measurement. The area of leaves photographed was measured by a dot grid method. This area may be effective in intercepting light. The total surface area was measured also of some needles cut out singly and photographed after pressing their bases lightly with a pincette. Figure 3 shows points of

measurement and the formula used to estimate the total surface area of a needle. The sample then was kept for 24 hours at 105°C and measured for dry weight. The leaf surface area effective in intercepting light and the total surface area per unit of dry weight were calculated. Horizontal light intensities at different positions in the crowns of two standard trees were measured with two selenium photometers in September, 1977.

Experiment 2: Two-year-old *C. japonica* seedlings, cultivar Kumotoshi, were transplanted to pots containing a mixture of red soil, sand, and a compost of bark in November, 1973 and grown in a nursery at Kyushu University in Fukuoka. From

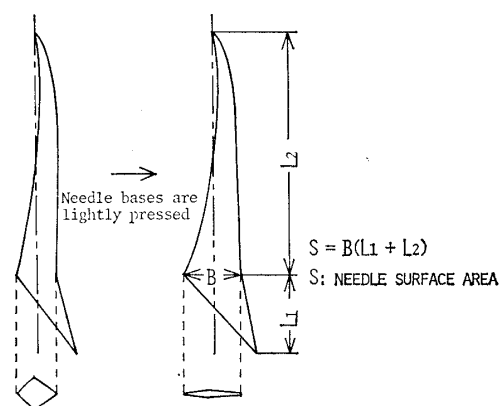


Fig. 3. Points of measurement and the formula used for estimating needle surface area

June, 1974 the seedlings were grown under artificial shading permitting 8, 22, and 45 percent relative light intensities, and a 100 percent light intensity was used as a control. The shading was provided by frames, 150 cm high and 80 cm square, covered with a different number of layers of black Saran shading cloth. The relative light intensities were measured at about noon on cloudy days with two selenium photometers placed horizontally. Five seedlings were selected for each degree of shading. Attention was given to the uniformity of crown size, foliage appearance, and height of the seedlings. All were well watered during the experimental period.

On a day in September, the potted seedlings were watered and placed in the laboratory for the measurement of the CO₂ gas exchange on the following morning. Sample branchlets of leaves, about 6 g in fresh weight and 7 cm in length, were detached from the seedlings and stood vertically in the assimilation chamber which was made of wood and acryl board. The cut bases of branchlets with leaves were inserted in small vinyl tubes filled with water. Light was supplied by four astral lamps, composed of nine incandescent lamps (25 V, 40 W), so that each leaf of the sample branchlets could be exposed to light as uniformly as possible. The leaf temperature was maintained at about 25 °C by controlling the temperature of the water enveloping the chamber. The system for measuring CO₂ gas exchange was the same as in Experiment 1 except for the use of a different gas analyzer (URAS). The light intensity was changed by varying the voltage supplied to the lamps, and it was measured with a selenium photometer.

After the measurement of the CO₂ gas exchange the total surface area of leaves was estimated by assuming that the shape of each needle was a triangular pyramid as described in detail in our previous paper (HASHIMOTO & SUZAKI, 1978). This method for measuring total surface area of leaves is different from that employed in Experiment 1. A comparison between these two methods actually was not made, but the difference in estimated values is not supposed to be appreciable. The height and dry weight of seedlings grown under four different shadings were determined.

Experiment 3: Four-year-old trees of *C. japonica*, cultivar Kumotoshi, two meters tall, were selected from a nursery at Kyushu University in Fukuoka. In August, 1975, branchlets of leaves were detached from the apexes of trees to measure CO₂ gas exchange and transpiration. The cut ends of the branchlets were placed in a container of water, recut under the water, and taken to the laboratory. Measurements of CO₂ gas exchange and transpiration

were made in the leaves of the current year's growth and in those one year old, at a leaf temperature of 30°C. The difference in photosynthetic rates between leaves of the two ages was examined with consideration of the difference in diffusive resistance to CO₂ transfer. This method for these measurements was described in our previous paper (HASHIMOTO & SUZAKI, 1978).

III. Results and Discussion

1. Differences in leaf area-weight relationships and in the response of photosynthesis to different light intensities in leaves attached at various positions in the crown

1) Leaf area-weight relationship

In *C. japonica*, the leaf consists of subulate needles in three dimensions. The leaf surface area effective in intercepting light is not equal to one half of the total surface area as in broadleaved trees. The ratio of light intercepting area to total area is not constant. Therefore, the determination of leaf area-weight relationship is important in comparing the photosynthetic rates in leaves attached to different positions in the crown.

The leaf area-weight relationship differed with position in the crown (Fig. 4). That in the lower surface position in the conical shaped part of the crown exposed to sunlight (SUN-2) was largest, and that in the upper position in the conical shaped part of the crown (SUN-1) came second. Next in order were the relationships in the lower and the upper positions in the cylindrical shaped part of the shaded crown (SHADE-4, -5) followed by the inner position in the conical shaped part (SUN-3). In *C. japonica* leaves, both the light intercepting area and the one half of the total area per unit of dry weight seem to be small when compared with the specific leaf area in evergreen broadleaved trees studied by KIRITA & HOZUMI (1969). In *C. japonica* seedlings, the specific leaf area was larger in the current year's leaves than in older leaves (TANIMOTO, 1975), and it increased with the shading under which seedlings were grown (KAWANABE & SHIDEI, 1968; TANIMOTO, 1975). Neither the light intercepting area nor the one half of the total area per unit of dry weight treated here is the same as the specific leaf area. But it is supposed that these two values may be affected similarly by leaf age and shading. As described in Part II above, the sample leaves in SUN-1 and -2 in August came only from the current year's growth. The larger area per unit of dry weight in these positions may be due to leaf age. Figure 5 shows an example of the light intensity at each position in the crown. The light intensity in SUN-1 was nearly equal to that of full daylight above the crown. On a cloudy

day, relative light intensities in SUN-2, SUN-3, SHADE-4 and SHADE-5 averaged 43, 20, 7 and 2 percents respectively. The differences in leaf area-weight relationship between SUN-1 and SUN-2 (sample leaves were from only the current year's growth) and between SUN-3 and SHADE-4,-5 (sample leaves were from only older growth) may be caused by the different shadings in the crown. In broadleaved trees, the ratio of light intercepting area to total area is 5 : 10, whereas in *C. japonica* the ratio is near 3 : 10. The ratio seems to differ with position in the crown (Fig. 4), being slightly lower in SUN-1 and -2 than in SHADE-4 and -5. Leaves in SHADE-4 and -5 appear relatively flat in shape which may result in a higher ratio.

The seasonal change in leaf area-weight relationship was not apparent in SHADE-4 and -5, whereas

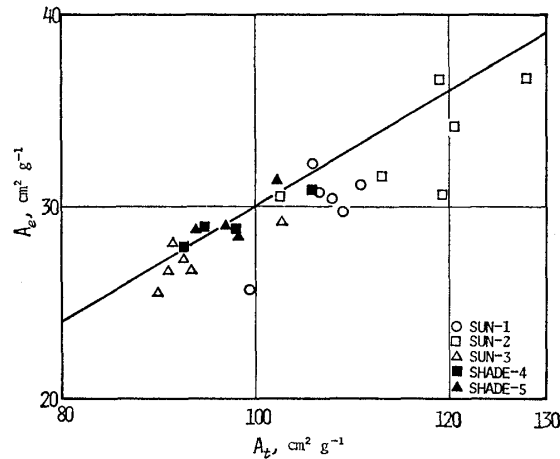


Fig. 4. Relationship between surface area effective in intercepting light per unit of dry weight (A_e , $\text{cm}^2 \text{g}^{-1}$) and total surface area per unit of dry weight (A_t , $\text{cm}^2 \text{g}^{-1}$) in leaves attached at different positions in the crown of *Cryptomeria japonica* in August. The straight line shows a ratio of intercepting area to the total area of 3:10.

it was apparent in SUN-1, -2, and -3 with an increase from May to August and a decrease from August to October (Table 1). The difference in leaf area-weight relationship in different positions of the crown was remarkable in May as compared with those in August and October. The ratio of light intercepting area to total area changed similarly with position in the crown with each

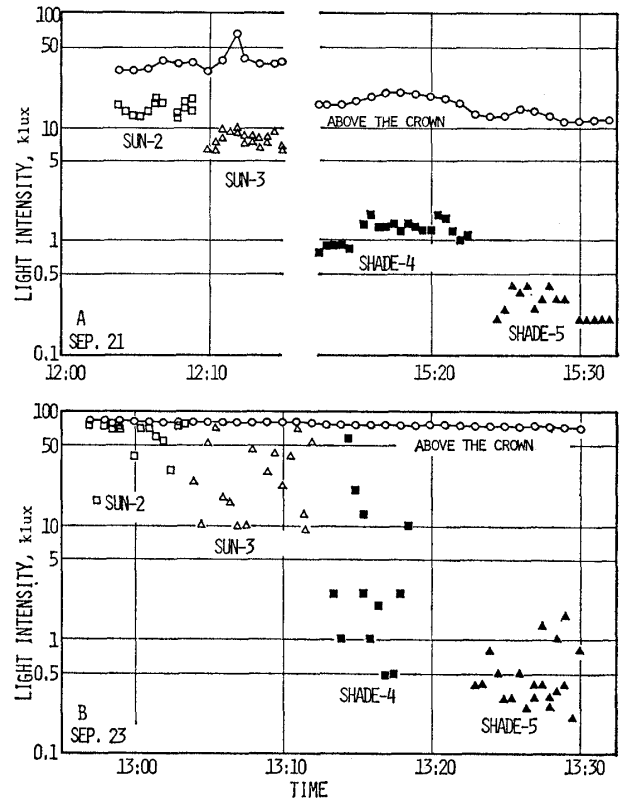


Fig. 5. Fluctuations in light intensity at each position in the crown on a cloudy day (A) and on a clear day (B). SUN-2, SUN-3, SHADE-4 and SHADE-5 are the same as in Fig. 1. On the clear day, the light intensity was measured on the south side of the crown.

Table 1. Average surface area effective in intercepting light per unit of dry weight (A_e , $\text{cm}^2 \text{g}^{-1}$), total surface area per unit of dry weight (A_t , $\text{cm}^2 \text{g}^{-1}$), and ratio of A_e to A_t , of leaves attached at different positions in the crown of *Cryptomeria japonica* in May, August, and October

		Positions in the crown				
		SUN-1	SUN-2	SUN-3	SHADE-4	SHADE-5
May	A_e	16.82	20.43	20.05	26.28	30.21
	A_t	67.86	75.59	67.89	88.37	90.98
	A_e/A_t	0.248	0.270	0.295	0.297	0.332
August	A_e	30.20	33.38	27.24	28.90	29.42
	A_t	106.63	117.03	93.60	97.94	98.34
	A_e/A_t	0.283	0.285	0.291	0.295	0.299
October	A_e	25.41	27.72	25.45	27.79	31.75
	A_t	91.39	98.22	90.48	96.34	102.60
	A_e/A_t	0.278	0.282	0.281	0.288	0.309

SUN-1, SUN-2, SUN-3, SHADE-4 and SHADE-5 are the same as in Fig. 1.

season being higher in leaves grown under heavier shading. The increases in leaf area per unit of dry weight and the ratio of light intercepting area to total area with shading may be effective in photosynthetic production under lower light intensities.

2) Response of photosynthesis to light intensity

The photosynthetic rate per unit of surface area effective in intercepting light at light saturation was higher in SUN-1 and -2 and lower in SHADE-4 and -5; whereas at lower light intensities the reverse relationship occurred (Fig. 6). Only in August was the photosynthetic rate at light saturation lowest in SUN-3. The average rates of dark respiration per unit of total area and per unit of dry weight changed with position almost in accordance with the change in photosynthetic rate at light saturation in each season (Table 2). The photosynthetic rate at light saturation was probably higher in SHADE-4 than SHADE-5, but the rate at lower light intensities did not differ appreciably between them. On the other hand, the difference in the rate at light saturation between SUN-1 and -2 was not obvious, whereas the rate at lower light intensities probably was higher in SUN-2 than in SUN-1.

HOZUMI & KIRITA (1970) also reported that the gross photosynthetic rate differed at various positions in the forest canopy of evergreen broadleaved trees. The rate at light saturation decreased while the rate at lower light intensities increased with the shading under which the leaves were grown. The higher photosynthetic rates at lower light intensities and the lower respiration rate observed in leaves of the cylindrical shaped part of the crown may be effective in maintaining the balance between carbohydrate production by photosynthesis and its use by respiration.

The photosynthetic rates at light saturation in leaves of SUN-1 and -2 did not differ from May to August, whereas the rates in October were higher than in either May and August. The rates in SHADE-4 and -5 were relatively steady at 8 to 10 mg throughout the vigorous growing season. The higher rates in SUN-1 and -2 in October may be related to slow leaf maturation in *C. japonica*. Leaves of SHADE-4 and -5 showed higher photosynthetic rates at lower light intensities in May than in both August and October, whereas leaves of SUN-1 showed a lower rate in May. The seasonal changes in photosynthetic rates at light saturation and at lower light intensities seem to be different from each other, and differ with position in the crown too.

The changes in photosynthetic rate per unit of dry weight with position in the crown and season

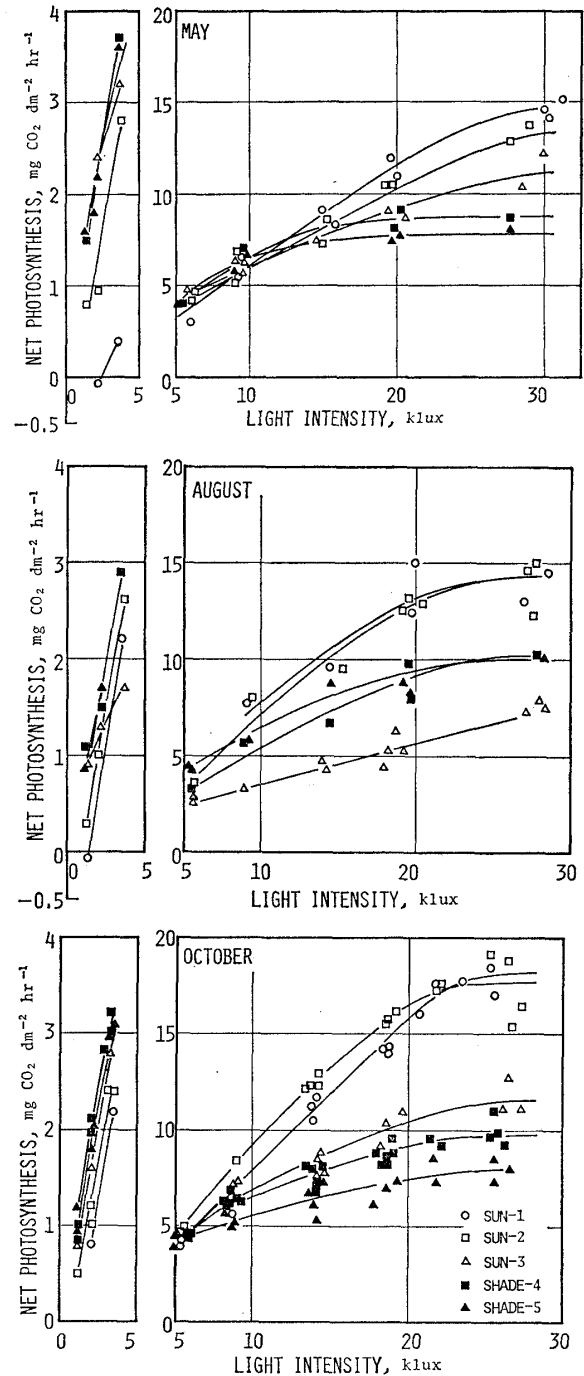


Fig. 6. Effect of light intensity on the net photosynthesis per unit of surface area effective in intercepting light in leaves attached at different positions in the crown of *Cryptomeria japonica* in May, August, and October

SUN-1, SUN-2, SUN-3, SHADE-4 and SHADE-5 are the same as in Fig. 1.

were different from changes in photosynthetic rate per unit of light intercepting area (Table 3). For instance, the change with position was not apparent in May, and the photosynthetic rates of SUN-1 and

Table 2. Average rate of dark respiration per unit of dry weight (R_w , mg CO₂ g⁻¹ hr⁻¹) and per unit of total surface area (R_t , mg CO₂ dm⁻² hr⁻¹) in leaves attached at different positions in the crown of *Cryptomeria japonica* in May, August, and October

		Positions in the crown				
		SUN-1	SUN-2	SUN-3	SHADE-4	SHADE-5
May	R_w	0.75	0.44	0.26	0.26	0.20
	R_t	1.11	0.58	0.38	0.29	0.22
August	R_w	0.80	0.55	0.26	0.30	0.29
	R_t	0.75	0.47	0.28	0.31	0.29
October	R_w	0.64	0.63	0.42	0.34	0.27
	R_t	0.70	0.64	0.46	0.35	0.26

SUN-1, SUN-2, SUN-3, SHADE-4 and SHADE-5 are the same as in Fig.1.

Table 3. Average photosynthesis per unit of dry weight (P_w , mg CO₂ g⁻¹ hr⁻¹), per unit of one half of the total surface area (P_t , mg CO₂ dm⁻² hr⁻¹), and per unit of surface area effective in intercepting light (P_e , mg CO₂ dm⁻² hr⁻¹), at light intensities between 25 and 32 klux, in leaves attached at different positions in the crown of *Cryptomeria japonica* in May, August, and October

		Positions in the crown				
		SUN-1	SUN-2	SUN-3	SHADE-4	SHADE-5
May	P_w	2.43	2.71	2.26	2.44	2.41
	P_t	7.17	7.15	6.65	5.84	5.73
	P_e	14.47	13.27	11.26	8.68	8.06
August	P_w	4.60	4.61	2.03	2.90	3.03
	P_t	7.45	7.90	4.45	6.20	6.17
	P_e	13.73	13.96	7.58	10.19	10.24
October	P_w	4.23	5.02	2.98	2.88	2.36
	P_t	9.91	10.05	6.52	5.97	4.91
	P_e	17.66	17.41	11.67	9.94	7.92

SUN-1, SUN-2, SUN-3, SHADE-4 and SHADE-5 are the same as in Fig.1.

-2 were higher in August than May. This is due to the difference in the leaf area-weight relationships with position and season. On the other hand, the changes in photosynthetic rate per unit of one half of the total area with position and season were almost in accord with the change in photosynthetic rate per unit of light intercepting area.

The maximum photosynthetic rates obtained were 5.02 mg per unit of dry weight, 10.05 mg per unit of one half of the total area, and 17.66 mg per unit of light intercepting area in leaves of SUN-1 and -2 in October. According to ŠESTÁK *et al.* (1971), the maximum net photosynthetic rate at light saturation, optimum temperature and water conditions, and normal content of CO₂ in the air (300 ppm), ranged from 4 to 12 mg per unit of leaf area (single surface) and from 3 to 15 mg per unit of dry weight in evergreen conifers. The photosynthetic rate in *C. japonica* was within these ranges.

2. Changes in response of photosynthesis to light intensity with shading and leaf aging

The results of Experiments 2 and 3 are discussed

in this section. The effect of shading on height growth was small, whereas on dry weight growth it was considerable, especially in roots (Table 4). The total dry weight of seedlings grown in the open was about twice as much as that of seedlings grown under the heaviest shading. The total surface area of leaves per unit of dry weight increased with shading, being largest in seedlings grown under a 22 percent relative light intensity.

The photosynthetic rate at light saturation increased with shading, being highest in seedlings grown under 22 percent relative light intensity followed by 8 and 45 percents in that order (Fig. 7). The seedlings grown under 22, 8 and 45 percent relative light intensities showed increases in photosynthetic rates of 19, 13 and 10 percents respectively, over that of seedlings grown in the open. The photosynthetic rates at lower light intensities also increased with shading, whereas the respiration rates decreased. As is generally known, the photosynthetic organ adapts itself to the light intensity under which it grows. The adaptability differs with different species (BOURDEAU & LAVERICK, 1958;

Table 4. Height, dry weight, and total surface area of leaves per unit of dry weight in *Cryptomeria japonica* seedlings grown under four different degrees of shading

	Shading, relative light intensity (%)			
	100	45	22	8
(1) Height (cm)	102.4	105.6	101.2	95.1
(2) Dry weight, total (g)	92.5	88.1	65.3	53.1
(3) ditto, leaves and branches (g)	35.5	39.5	27.7	19.7
(4) ditto, stem (g)	31.3	28.6	24.6	22.5
(5) ditto, root (g)	25.7	20.0	13.0	10.9
(6) Total surface area of leaves (cm ² g ⁻¹)	89.5	114.2	146.0	138.7

Values in (1) to (5) are the average of five seedlings.

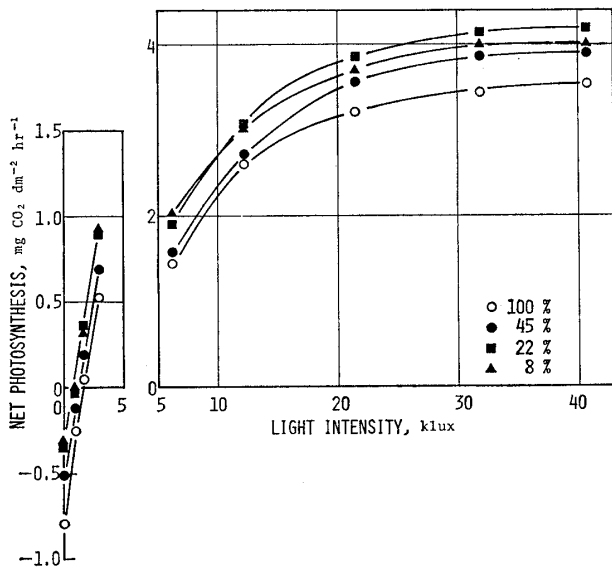


Fig. 7. Effect of light intensity on the net photosynthesis per unit of total surface area in leaves of *Cryptomeria japonica* seedlings grown under different shadings of 100, 45, 22 and 8 percent relative light intensities

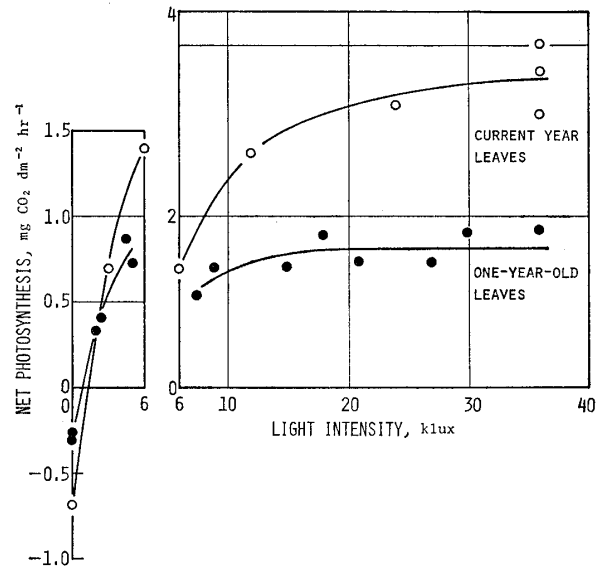


Fig. 8. Effect of light intensity on the net photosynthesis per unit of total surface area in current year and one-year-old leaves of *Cryptomeria japonica*

BJÖRKMANN & HOLMGREN, 1963; LOACH, 1967). The response of photosynthesis in *C. japonica* to shading probably shows that it belongs to the relatively tolerant trees.

The photosynthetic rate at light saturation and the dark respiration rate in one-year-old leaves were only one-half the rates in current year leaves (Fig. 8). Leaves of different ages show a difference in photosynthetic rate, and the rate begins to decrease at a certain age in many plant species (SAEKI, 1959; SMILLIE, 1962; WADA & KURODA, 1968; PEAT, 1970; NISHIOKA *et al.*, 1972).

To study the cause of the difference in photosynthetic rates at light saturation, the diffusive resistances to CO₂ transfer of current year leaves and one-year-old leaves were compared. The total resistance (Σr) to CO₂ transfer from the ambient air of leaves to chloroplasts was divided into $r_a + r_1$ and r_m . The r_a is the boundary air layer resist-

ance. The r_1 is the leaf resistance composed of the stomatal resistance (r_s) and the cuticular resistance (r_c), where $1/r_1 = 1/r_s + 1/r_c$. The r_m is the mesophyll resistance. The r_a was kept constant during the measurements. The increase of resistance in one-year-old leaves over that in current year leaves was 21.99 sec cm⁻¹ in r_1 , 58.41 sec cm⁻¹ in r_m , and 10.7 sec cm⁻¹ in r_c ; it amounted to 80.40 sec cm⁻¹ in total (Table 5). Therefore, the decrease in photosynthesis rate with aging may be due partly to not only the lessening of CO₂ transfer in the mesophyll (an increase of mesophyll resistance), but also to the shrinkage of the stomatal openings and the reduced permeability of the leaf cuticle to CO₂ (an increase of leaf resistance).

From these results, it is apparent that the increase of shading from the apex to the bottom of the crown and the aging of the leaves have considerable effect of the response of photosynthesis to light intensity in leaves attached at different posi-

Table 5. Calculated diffusive resistances to CO₂ transfer in sec cm⁻¹ in current year and one-year-old leaves of *Cryptomeria japonica*

		Σr	r_a+r_l	r_a+r_c	r_m
Current year leaves	1		23.7	75.9	25.6
	2	49.3	18.1	69.1	31.2
	Mean		20.9	72.5	28.4
One-year-old leaves	1		38.4	90.2	91.3
	2	129.7	47.4	76.1	83.3
	Mean		42.9	83.2	86.8

tions in the crown. The degree of change in shading usually was connecting with the leaf age in the crown; for example, older leaves grow under heavier shade than new leaves.

The photosynthetic rates at light saturation were lower in leaves of the inner position (SUN-3) in the conical shaped part of the crown and in leaves in the cylindrical shaped part (SHADE-4 and -5) grown under shading, whereas in the seedlings the rate increased with shading. Leaves attached at these positions in the crown were older than those at the other positions (SUN-1 and -2). The effect of aging on the photosynthetic rate at light saturation seems to predominate over the effect of shading. However, the photosynthetic rates at lower light intensities seem to differ with the degree of shading in the crown. It is supposed that the differences in response of photosynthesis to light intensity with leaf aging have a considerable effect on photosynthetic production in open or lightly shaded parts, whereas the changes with shading plays an important role in photosynthesis of heavily shaded parts of the crown.

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