Spatial and Seasonal Variations in Photosynthetic Properties within a Beech (*Fagus crenata* Blume) Crown

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The light response curve and the intercellular CO_2 concentration response curve of CO_2 assimilation rate were investigated together with the light conditions at the four different heights within the beech crown from 1995 to 1997 on Mt. Fuji in Japan. On the seasonal fluctuation, the CO_2 assimilation rate at light saturated condition increased rapidly in May, and attained to the maximum between the end of June and July, thereafter, slightly decreased until the middle of August and rapidly decreased in September and October. The daily sum of photosynthetic photon flux density attenuated with deeping within the crown, and particularly, the relative value on 2nd position dropped to only 30%. The A_{max} decreased from 10 to 5 μmol m^{-2} s^{-1}, approximately, with deeping within the crown. The light saturation point, quantum yield, light compensation point and dark respiration rate also varied with deeping. These results suggest that the photosynthetic properties vary gradually from sun to shade leaves along the light attenuation within a beech crown. At light saturated condition, the stomatal conductance and mesophyll conductance were strongly correlated with A_{max} among the four different heights ($r > 0.96$, respectively). The C_i/C_a ratio was around 0.8, and there were no remarkable differences among the four different heights. These results suggest that the vertical gradient of A_{max} depends on the variation of mesophyll conductance. The stomatal conductance may be also one of the major factor in the vertical gradient of A_{max}. However the intercellular CO_2 concentration doesn't influence the vertical gradient of A_{max} within the crown.

Key words: CO_2 assimilation, light conditions, mesophyll conductance, Siebold's beech (*Fagus crenata* Bl.) crown, stomatal conductance

To know the mechanism of photosynthesis adaptation to light conditions within a crown is very important as basic knowledge for understanding the productive structure and function within a crown. The vertical gradients in morphological and biochemical changes of leaf characteristics within a beech crown; *e.g.* leaf thickness, chlorophyll contents and N content (Gratani *et al.*, 1987; Kakubari and Hosokawa, 1992; Niinemets, 1995), are generally believed to be related to attenuation of light conditions. These gradients are associated with the vertical variation of photosynthetic properties such as CO_2 assimilation rate at light saturated condition, light saturation point, quantum yield, light compensation point and dark respiration rate.

It's important to confirm whether the vertical variation of photosynthetic properties is continuous or not. In the previous studies, the measurement of photosynthetic properties within a beech crown was limited to the typical sun and shade leaves (Schulze, 1970; Yanagisawa and Maruyama, 1972; Kakubari, 1973; Matsumoto *et al.*, 1982; Kakubari *et al.*, 1985; Kakubari and Harano, 1991; Schulte, 1992). In the case of a maple crown, the vertical gradient of photosynthetic capacity at four different heights was reported (Ellsworth and Reich, 1993). However, this kind of study hasn't been made within a beech crown. Moreover, the vertical variation of photosynthetic properties has been studied less in association with light conditions within a beech crown.

It's also important to find out what kind of physiological functions; *e.g.* stomatal density and activity of carboxylation, causes the vertical variation of photosynthetic properties. A comparison of both stomatal conductance and mesophyll conductance is an available method for understanding their variations. Meanwhile, a comparison of the ratio of intercel-

lular to ambient CO_2 concentration is an effective method, because intercellular CO_2 concentration is a limiting factor to CO_2 assimilation rate.

We investigated the light response curve of CO_2 assimilation rate by detached leaves at the four different heights together with the light condition within a beech crown on Mt. Fuji. The $A-C_i$ response curve was also investigated for comparing with the mesophyll conductance. The objectives of this study were 1) to find out the vertical gradient of photosynthetic properties along the attenuation of light condition within the crown and their seasonal fluctuations, and 2) to make clear the physiological factor at the levels of both stomatal conductance and mesophyll conductance which decide the vertical variation of photosynthetic capacity.

Materials and Methods

The study site is located in the natural beech forest at the altitude of 1,100 m above sea level on the southern slope of Mt. Fuji in Japan (35°20' N, 138°41' E). The climate belongs to cool temperate conditions. The sample tree is 21.0 m high with a bole height of 9.6 m and a diameter of 62 cm at the breast height. The period of the bud break was the early of May, and of fall of leaves was between the end of October and the early of November in 1995, 1996, and 1997. A steel measuring tower of 20 m high was built at the south portion of the sample tree crown, *i.e.* at the middle of the crown. Light conditions and photosynthetic properties of leaves were investigated at four different heights of 20, 17, 15, and 12 m above the ground, and named a top, 2nd, 3rd, and bottom position.

Light measurements at the four different heights of 21, 17, 15, and 12 m were made by using quantum sensors (IKS-25, Koito Co. Ltd., Tokyo) for photosynthetic photon flux density (PPFD). The four sensors were monitored with the battery-operated hand held datalogger (MES-901, Koito Co. Ltd.,

Tokyo). The measurements were taken at the rate of every half hour in 1995 and every 10 min in 1996 and 1997.

The measurements of CO_2 assimilation and transpiration rates were carried out with detached leaves from the middle of June 1995 to the middle of July 1997. The detached method had been established in beech leaves by Yanagisawa and Maruyama (1972), Kakubari (1973), and Koike (1986). The measurements were made during three days from the sampling with an individual leaf under the controlled micro-environmental condition by using a compact mini cuvette system (CMF-400, Walz Co., Germany) with a bypass humidity control unit (CNF-400, Walz Co., Germany). The light source was a halogen lamp using a fiber illuminator (FL-400, Walz Co., Germany) and a special fiberoptics (400-F, Walz Co., Germany). For measuring the C_i response curve of CO_2 assimilation rate, the CO_2 concentration in a measuring chamber was controlled by a CO_2 and N_2 gas mixing unit (GMA-2, Walz Co., Germany).

The light response curve of CO_2 assimilation rate was measured with single leaf ($n = 1$) in 7 steps by decreasing light intensity from 700 to 0 μmol photon m^{-2} s^{-1} at optimal temperature of 21 or 24 °C, optimal vapor pressure deficit of 5.0 Pa kPa^{-1}, ambient CO_2 concentration about 360 $\pm$ 20 ppm and adequate water supply. In addition, the CO_2 assimilation rate at light saturation point was measured by more two leaves of top and bottom positions in 1996 and top, 2nd, 3rd, and bottom positions in 1997. The optimal temperature and water vapor pressure deficit for CO_2 assimilation rate were determined in the other experiments (Saito and Kakubari, unpublished data). The C_i response curve of CO_2 assimilation rate was measured in 10 steps by increasing C_a from 0 to 1,000 ppm. The CO_2 assimilation rate and transpiration rates were determined after the stability for 5 min. The each measurement of light response curve of CO_2 assimilation rate was taken within 5 h. After each measurement, the leaf area without petiole was measured by using the Delta-T image analysis system (DIAS, Delta-T devices Ltd., England).

The light response curves of CO_2 assimilation rate were fitted to a nonlinear least-squares fitting technique (Formula 1; Prioul and Chartier, 1977). The CO_2 assimilation rate at light saturated condition (A_{max}) was defined at 700 μmol photon m^{-2} s^{-1}. The light saturation point was estimated as the light intensity whose assimilation rate is 95% of A_{max} from the light response curve. The quantum yield was estimated as an initial slope of the light response curve (ϕ_A).

The initial slope of the C_i response curve of CO_2 assimilation rate and the C_i compensation point were calculated from a fitted linear line based on the data between 20 and 200 ppm of C_i (Formula 2; Farquhar and Sharkey, 1982).

$$\theta A_g^2 - (\phi_A Q + A_{max}) A_g + \phi_A Q A_{max} = 0 \qquad (1)$$
$$A = \phi_C C_i + A_0 \qquad (2)$$

where θ is shapeness of the bend or convexity of the light response curve of CO_2 assimilation rate. A_g is gross CO_2 assimilation rate calculated as CO_2 assimilation rate plus dark respiration rate. ϕ_A is the slope of initial linear region of the light response curve of CO_2 assimilation rate. Q is irradi-

ance. ϕ_C is the initial slope of C_i response curve of CO_2 assimilation rate. A_0 is the Y-axis intercept in C_i response curve of CO_2 assimilation rate.

For statistical analysis of variance, the significant difference was determined by F-test at 20% level.

Results

1 Seasonal and vertical variations of daily sum of photosynthetic photon flux density

The seasonal fluctuation of the daily sum of photosynthetic photon flux density (PPFD) at the top position and its relative value at the 2nd, 3rd, and bottom positions are shown in Fig.1 A and 1B. In each measuring year, the relative value of the daily sum of PPFD at the 2nd, 3rd, and bottom positions decreased rapidly with leaf flush in May. Between June and August, that value at the 2nd, 3rd, and bottom positions was approximately constant, and its average was 28, 25, and 14% in 1996 and was 33, 29, and 15% in 1997, respectively. After the middle of September, these values increased with the falling of leaves.

2 Seasonal and vertical variations of photosynthetic properties

The light response curves of CO_2 assimilation rate with fitting curves at different measuring years of 1995, 1996, and 1997 are shown in Fig. 2. The coefficient of determination of all fitting nonlinear lines was greater than 0.99, respectively. The oscillation of leaf temperature at different light conditions was less than 1.0 °C in all measurements, and that oscillation has no effect in the analysis of photosynthetic and stomatal response (Saito and Kakubari, unpublished data). The CO_2 assimilation rates at the different positions within the crown were very wide. Light saturation point, light compensation point, quantum yield and dark respiration rate shall be shown in next paragraph and Fig. 4.

Seasonal fluctuations of CO_2 assimilation rate (A_{max}), stomatal conductance to CO_2 vapor (gCO_2), C_i/C_a ratio and A/C_i at light saturation condition are shown in Fig. 3. In the end of May 1996, after 4 weeks from bud break, the A_{max} with standard error at the top, 2nd, 3rd, and bottom positions was 5.8 $\pm$ 0.4, 8.8, 5.7, and 3.9 $\pm$ 0.1 μmol m^{-2} s^{-1}, respectively. Compared with the vertical variation of the A_{max}, the A_{max} at the 2nd position was 1.5-fold greater than that at the top and 3rd positions, approximately. As well as the vertical variation of A_{max}, each value of gCO_2 and A/C_i at the 2nd position was about 1.5-fold greater than that at the top and 3rd positions, respectively. At the bottom position, each value of A_{max}, gCO_2 and A/C_i was the lowest. The C_i/C_a ratio at each position was between 0.81 to 0.86. The differences of the C_i/C_a ratio among the all positions weren't significant.

In the end of June 1996, the A_{max} at the top, 2nd, 3rd, and bottom positions was 10.7 $\pm$ 0.6, 11.4, 9.1, and 4.6 $\pm$ 0.4 μmol m^{-2} s^{-1}, respectively. The A_{max} at the top, 2nd and 3rd positions peaked during this time. The time of the peak at the bottom position was the end of July, and was the latest among the four positions. The A_{max}, in the end of July, at the top, 2nd, 3rd and bottom positions was 10.0 $\pm$ 0.4, 9.0, 7.8, and 5.5 $\pm$
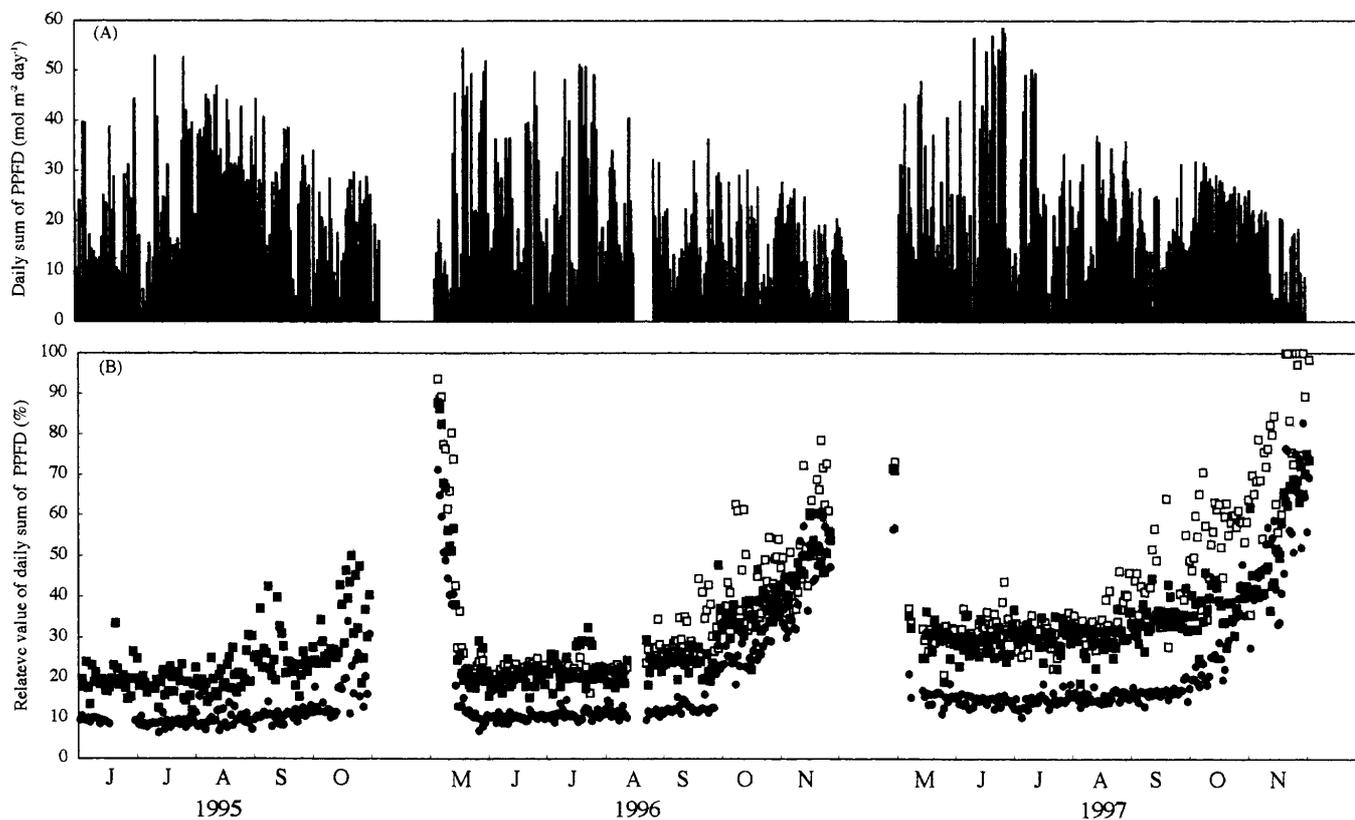
Fig. 1　Seasonal fluctuation of daily sum of photosynthetic photon flux density (PPFD) at the height of 20 m in 1995, 1996 and 1997 (A), and its relative values were measured at the height of 17, 15, and 12 m above the ground (B). Light measurement in 1995 wasn't taken at 2nd position. Symbols of □, ■, and ● mean the relative value of daily sum of PPFD at 2nd, 3rd, and bottom positions.

0.4 μmol m^{-2} s^{-1}, respectively. After peaking, the A_{max} at each position decreased gradually until the middle of August. Compared with the seasonal fluctuations from June to August, the A_{max} at the 2nd and 3rd positions rapidly decreased, on the other hand, the A_{max} at the top and bottom positions slightly decreased. The gCO_2 at each position peaked on the seasonal fluctuation in the end of July. The C_i/C_a ratio at all positions was constant between 0.84 and 0.90, respectively. The seasonal fluctuation of A/C_i at each position decreased such as the fluctuation of A_{max}.

After the middle of August, the A_{max}, gCO_2 and A/C_i at each position rapidly decreased, respectively. The C_i/C_a ratios at all positions were constant between 0.86 and 0.92, respectively.

In 1997, the A_{max} with standard error at the top, 2nd, 3rd, and bottom positions was 8.0 ± 0.8, 9.2 ± 0.8, 6.9 ± 0.2 and 5.8 ± 0.0 μmol m^{-2} s^{-1} on the beginning of June, and was 9.9 ± 0.5, 8.2 ± 0.8, 6.7 ± 0.2, and 5.2 ± 0.1 μmol m^{-2} s^{-1} on the beginning of July. On the beginning of July, the vertical variations of A_{max}, gCO_2, and A/C_i at each position within the crown were significant ($p < 0.2$).

3 Light saturation point, quantum yield, light compensation point and dark respiration

The seasonal fluctuation of light saturation point is shown in Fig.4A. At the top position, the trend of the seasonal fluctuation in light saturation point was constant between 400 and 600 μmol m^{-2} s^{-1}, and was the greatest among the four positions throughout the three growing seasons. At the bottom position, the trend of the seasonal fluctuation was constant between 150 and 300 μmol m^{-2} s^{-1}, and was the lowest among the

four positions. At the 2nd position, although the light saturation point was similar to that at the top position in the end of May, thereafter, the trend of that fluctuation gradually decreased from 600 to 400 μmol m^{-2} s^{-1}, approximately.

The seasonal fluctuation of quantum yield is shown in Fig. 4B. The value of quantum yield at the top position was constant between 0.02 and 0.05 mol CO_2 mol photon^{-1}, and was the lowest among the four positions throughout the three growing seasons. With respect to the trend of vertical variation, the quantum yield increased with deeping the position within the crown, excluding the bottom position.

The seasonal fluctuation of light compensation point is shown in Fig. 4C. At the top position, the value of the light compensation point was between 7 and 32 μmol m^{-2} s^{-1}, and was the greatest among the four positions throughout the three growing seasons. At the 2nd, 3rd, and bottom positions, the values of the light compensation point were between 5 and 12 μmol m^{-2} s^{-1} throughout the three growing seasons.

The seasonal fluctuation of dark respiration is shown in Fig. 4D. At the top position, the value of the dark respiration rate was between 0.4 and 1.3 μmol m^{-2} s^{-1}, and was the greatest among the four positions throughout the three growing seasons. At the bottom position, the value of the dark respiration was between 0.2 and 0.8 μmol m^{-2} s^{-1}, and was the lowest among the four positions throughout the three growing seasons.

4 $A-C_i$ response curve

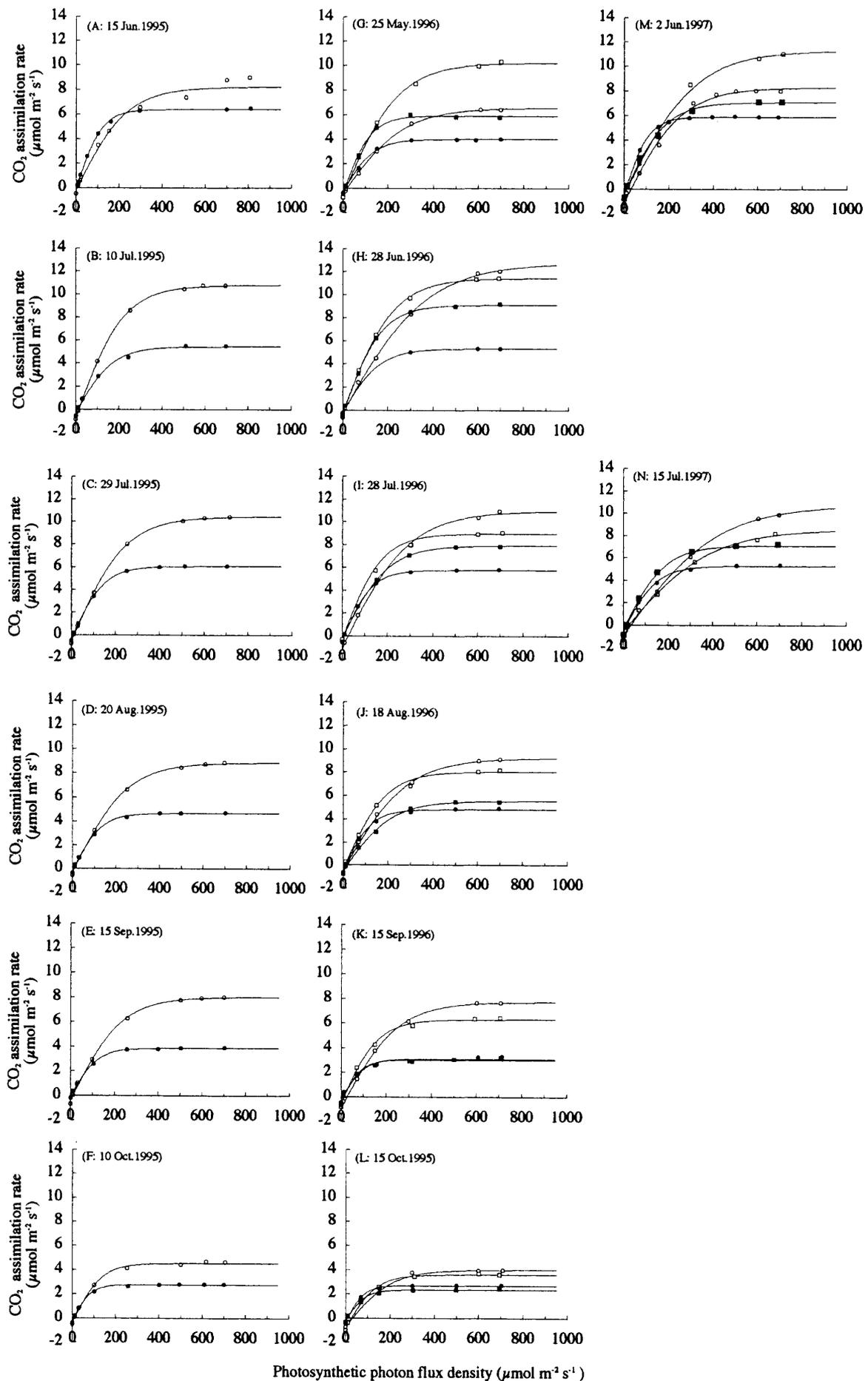The C_i response curves of CO_2 assimilation rate are shown

Fig. 2 Light response curve of CO_2 assimilation rate at the four heights of 20, 18, 15, and 12 m above the ground in the measuring years 1996 and 1997, and that of 1995 is at two positions, 20 and 12 m. The measuring condition was at optimal air temperature of 21 or 24 °C, optimal vapor pressure deficit of 5.0 Pa kPa^{-1}, ambient CO_2 concentration around 360 ppm, and adequate water supply. Symbols of ○, □, ■, and ● mean CO_2 assimilation rate at a top, 2nd, 3rd, and bottom positions. Lines were fitted using a nonlinear least-squares fitting technique ($r^2 > 0.99$).
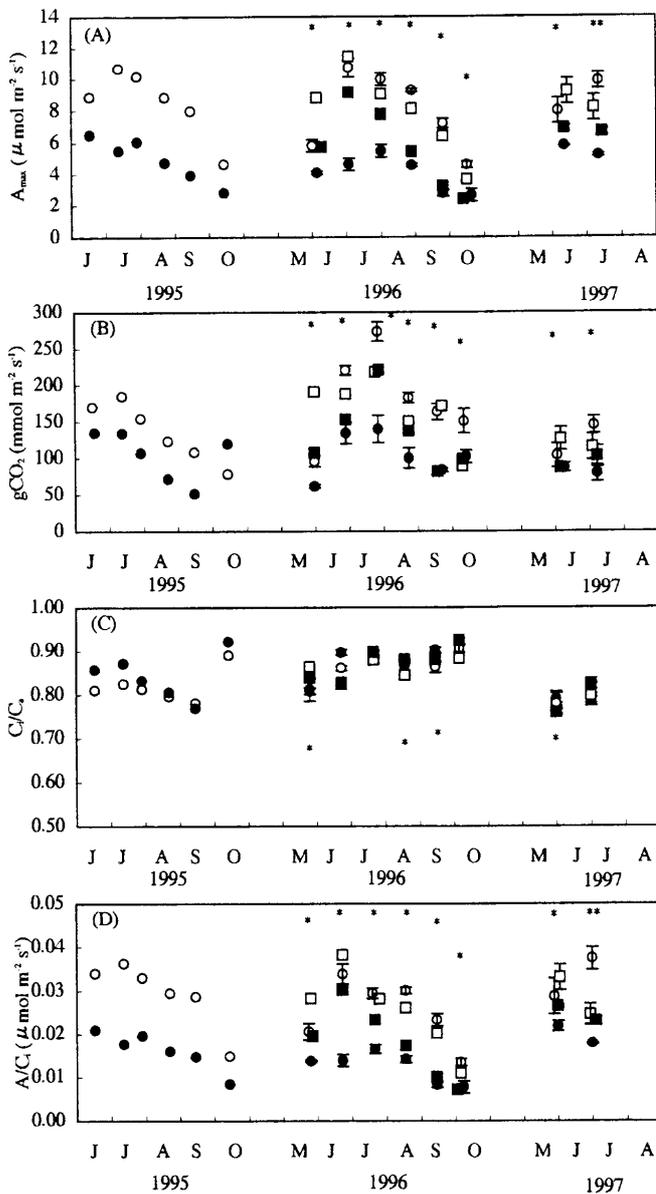
Fig. 3 Seasonal fluctuation of CO_2 assimilation rate (A), stomatal conductance to CO_2 (B), C_i/C_a ratio (C), and A/C_i (D) at the four heights under the light saturated condition of 700 μmol photon m^{-2} s^{-1}. Data was arranged from Fig. 2. About the top and bottom positions in 1996 and the all positions in 1997, the data was added from more two experiments of CO_2 assimilation rate at light saturated condition. Symbols are described in Fig. 2. Error bars mean S.E. ($n \geq 3$). Single asterisk (*) means the significant variance between top and bottom positions at 20% level by F-test. Double asterisk (**) means the significant variances among each position at 20% level by F-test.

Fig. 4 Seasonal fluctuation of quantum yield (A), light saturation point (B), light compensation point (C), and dark respiration rate (D) at the four heights. Data was arranged from Fig. 2. Symbols are described in Fig. 2. Solid lines are used to explain the trends of the photosynthetic properties at the top and 2nd positions, and broken lines are also used at 3rd and bottom positions.

in Fig. 5. The coefficient of determination of all the fitting linear lines was greater than 0.96, respectively. The CO_2 assimilation rate increased linearly with increasing the value of the C_i from 0 to 300 ppm of C_i, approximately.

The value of the initial slope of the C_i response curves at the top and bottom positions was 0.0438 and 0.0167 in June, was 0.0360 and 0.0161 in August, and was 0.0187 and 0.0070 in October 1996, respectively. The initial slope at the top and bottom positions decreased from June to October. In each month, the initial slope at the top position was greater than that at the bottom position.

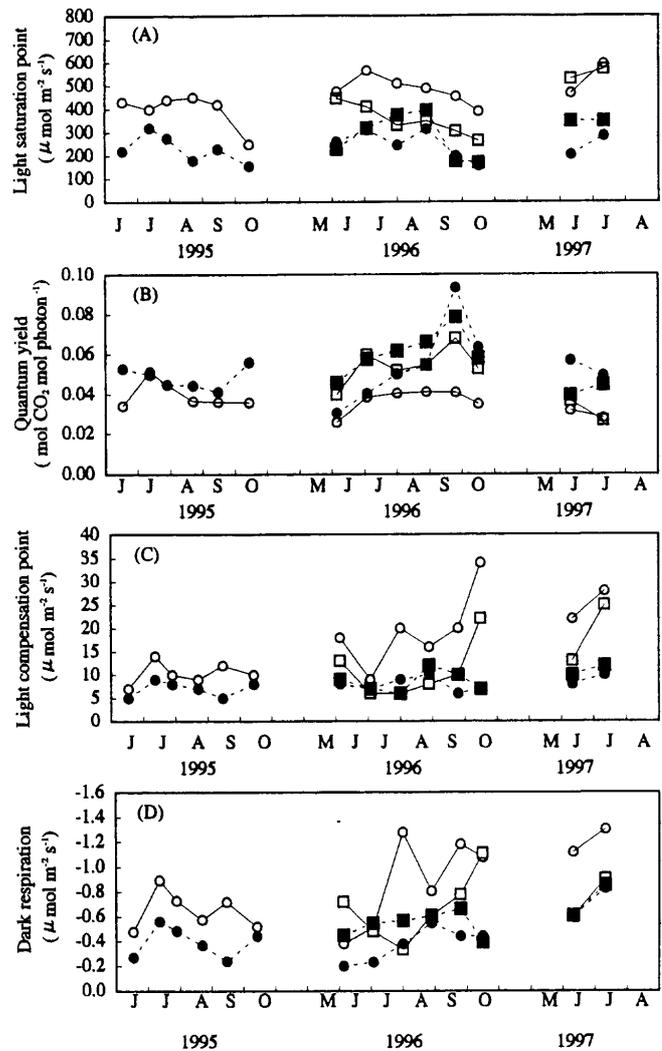The value of the C_i compensation point at the top and bot-

tom positions was 51.5 and 43.2 in June, was 55.2 and 49.5 in August and was 74.4 and 58.5 in October. In each month, the C_i compensation point at the top position was greater than that at the bottom position.

Discussion

For evaluating the vertical variations of photosynthetic properties, we use the values of relative height which was divided into each position with the total crown length instead of a top, 2nd, 3rd, and bottom position (Fig. 6). The discussions of vertical variations were made mainly to focus on the data in July at the different measuring years, taking into consideration the seasonal fluctuations of the relative light condition and photosynthetic capacity.

1 Seasonal and vertical variations of daily sum of photosynthetic photon flux density

The seasonal fluctuation and the vertical gradient of light conditions at the different measuring years were confirmed in Fig. 1B. On the seasonal fluctuation, the relative value of daily sum of PPFD attained stability within a month after bud
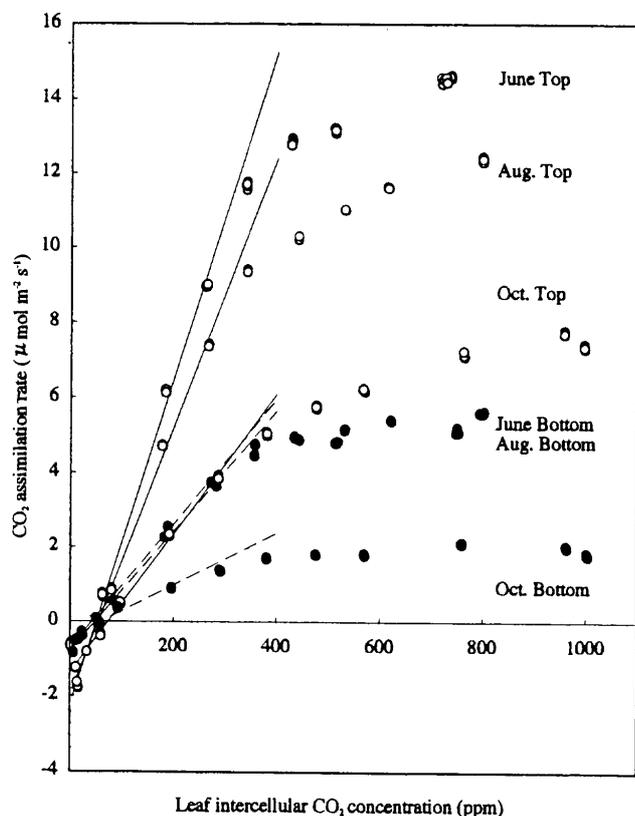
Fig. 5 Intercellular CO_2 concentration (C_i) response curve of CO_2 assimilation rate at optimal air temperature of 21 or 24 °C, optimal vapor pressure deficit of 5.0 Pa kPa^{-1}, and adequate water supply in June, August and September 1996. Symbols of ○ and ● mean CO_2 assimilation rate at a top and bottom positions. Linear lines show the relationship between CO_2 assimilation rate and C_i, and were fitted with the data until 200 ppm of C_i. Solid and broken lines mean the top and bottom positions. The lines support the linearity of the relationship until around 300 ppm of C_i.

break. Compared with the vertical variation in July 1996 and 1997, the relative value of daily sum of PPFD decreased rapidly with deeping from the top to the 2nd position, and decreased slightly from the 2nd to the bottom position. The similar trend of the light attenuation was reported in European beech crown in Solling and Heath, Germany (Schulte, unpublished data).

2 Seasonal and vertical variations of light response curve of CO_2 assimilation rate

We had studied the diurnal fluctuations of CO_2 assimilation and transpiration rates by the direct measurement with intact leaves within the same crown in 1995 (Saito and Kakubari, unpublished data). Our present results of A_{max} were in agreement with the values of the peak in the diurnal fluctuations.

On the seasonal fluctuation, the A_{max} at all positions increased rapidly in May, and attained to the maximum values between the end of June and July, thereafter, decreased slightly until the middle of August and decreased rapidly in September and October.

Compared with the A_{max} in May in both the measuring years 1996 and 1997, the values at the top position were lower than that at the 2nd position. This result points out that the developmental rate of photosynthetic capacity at the top position was more later than that at the 2nd position. The
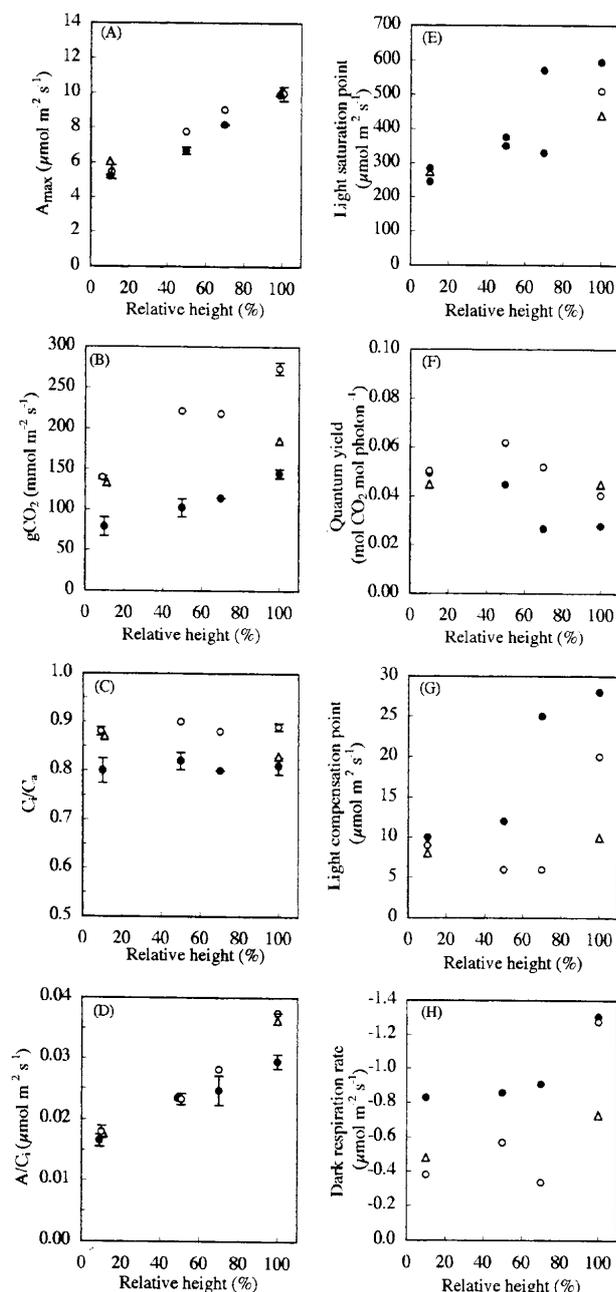

Fig. 6 Relationship between the relative height within the crown and A_{max} (A), stomatal conductance to CO_2 at light saturated condition (B), C_i/C_a ratio at light saturated condition (C), A/C_i at light saturated condition (D), light saturation point (E), quantum yield (F), light compensation point (G) and dark respiration rate (H) in July 1995, 1996, and 1997. Symbols of △, ○, and ● mean the data in 1995, 1996, and 1997. Error bars mean S.E. ($n \geq 3$). The correlation coefficient (r, $p \leq 0.05$) in 1996 and 1997 was 0.99 and 0.99 in panel A, was 0.97 and 0.99 in panel B, was 0.25 and 0.25 in panel C, was 0.97 and 0.93 in panel D, was 0.91 and 0.92 in panel E, was -0.49 and -0.89 in panel F, was 0.61 and 0.91 in panel G and was -0.73 and 0.83 in panel H, respectively.

inversion of the vertical gradient of A_{max} may occur with an inhibition by strong light under the low air temperature and/or frost (Larcher, 1995).

In July, the vertical gradient of A_{max} depends on the crown depth of the crown, *i.e.* from 10.0 to 5.5 μmol m^{-2} s^{-1} in 1996, and from 9.9 to 5.2 μmol m^{-2} s^{-1} in 1997 (Fig. 6A). The relationship between the A_{max} and the relative height within the crown in July in each of the three years was a
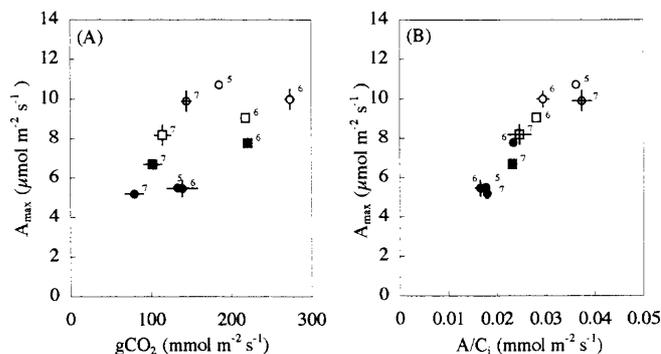
Fig. 7 Relationship between the CO_2 assimilation rate at light saturated condition and stomatal conductance to CO_2 (A), and the A/C_i (B). These graphs were reconstructed from the panel A, B, and D in Fig. 6. Symbols of ○, □, ■, and ● mean CO_2 assimilation rate at a top, 2nd, 3rd, and bottom positions. Numbers of 5, 6, and 7 at shoulder of symbol mean the measuring years of 1995, 1996, and 1997. Error bars mean S.E. ($n \geq 3$). The correlation coefficient ($r, p \leq 0.05$) in panel A was 0.96 in 1996 and 0.99 in 1997, and that in panel B was 0.99 in 1996 and 0.97 in 1997.

strong positive correlation ($r = 0.99$ in 1996 and $r = 0.99$ in 1997; Fig. 6A). Particularly, in 1997, the vertical variance of A_{max} at each position was significant ($p < 0.2$). The vertical gradient of A_{max} within the crown is in agreement with the report in sugar maple crown (Ellsworth and Reich, 1993). Judging from results during three years, the vertical gradient of light saturation point depends on the crown depth of the crown in July (Fig. 6E). In the quantum yield, the vertical gradient of it also depends on the crown depth of the crown, excluding the bottom position. In the light compensation point and dark respiration rate, the trends of vertical gradient of them weakly depend on the crown depth of the crown. The similar trends of photosynthetic properties; i.e. A_{max}, light saturation point, quantum yield, light compensation point and the dark respiration rate, at the top and bottom position were reported in Japanese beech crown (Yanagisawa and Maruyama, 1972; Kakubari, 1973; Kakubari et al., 1985; Kakubari and Harano, 1991).

Generally, A_{max}, light saturation point, light compensation point and dark respiration rate in light-grown leaf are greater than those in shade-grown leaf, and quantum yield in light-grown leaf is smaller than that in shade-grown leaf (Boardman, 1977). In Japanese beech seedlings, the same trend has been reported by Liang et al. (1995). In the present study, the same trend is confirmed along the relative height within the crown. Therefore, we can evaluate that the vertical gradient of photosynthetic properties depends on the attenuation of light conditions.

In addition, on the seasonal fluctuation from the end of June to the middle of August in 1996, the decreasing of A_{max} at the 2nd position was more rapidly than that at the other positions. As well as the seasonal fluctuation of A_{max}, the decreasing of light saturation point at the 2nd position was more rapidly than that at the other positions. These fluctuations are associated with the modification from sun leaf to shade leaf. Although the data of foundation is not enough to discuss this modifi-

cation, we can speculate that this modification from sun leaf to shade leaf caused the change of light conditions from light habitat in May to shade habitat in June, July and August.

3 Vertical variations of stomatal conductance, mesophyll conductance and C_i/C_a ratio at light saturated condition

The A/C_i at the light saturated condition depends on the crown depth of the crown in Fig. 6D. The relationship between A_{max} and A/C_i in the vertical gradient was a strong positive correlation in each of the measuring year ($r = 0.99$ in 1996 and $r = 0.95$ in 1997; Fig. 7B). The A/C_i is understood as mesophyll conductance which depends on resistance of CO_2 diffusion between cell space and inside of chloroplast and/or activity of carboxylation, because the initial slope of the C_i response curves shown in Fig. 5 is similar to the value of A/C_i around 300 ppm of C_i for leaves at the top and bottom positions in June, August and October 1996 (O'Toole et al., 1976; Farquhar et al., 1980). Therefore these results suggest that the mesophyll conductance is a major factor in the vertical gradient of A_{max}.

As shown in Fig. 3C, the differences of C_i/C_a ratio among the four positions were less than 0.1 around 0.8 of C_i/C_a ratio in each measuring month, in spite of the differences of A_{max} and gCO_2. According to the report of von Caemmerer and Evans (1991), the values of C_i/C_a ratio are generally between 0.7 and 0.8, and these values in the present study are the same or a little higher levels in comparison with the other C_3 plants. As shown in Fig. 5, the effect of the difference of 0.1 of C_i/C_a ratio on the CO_2 assimilation rate is less than 10% under the light saturated- and ambient CO_2-conditions at the top and bottom positions. Therefore, these results suggest that the intercellular CO_2 concentration is not a major factor in the vertical gradient of A_{max}.

The vertical gradient of gCO_2 at the light saturated condition depends on the crown depth of the crown in Fig. 6B. As shown in Fig. 7A, the relationship between A_{max} and gCO_2 in the vertical gradient was a strong positive correlation in each of the measuring year ($r = 0.96$ in 1996 and $r = 0.99$ in 1997; Fig. 7A). Although the relationship between stomatal conductance and CO_2 assimilation rate is close in general, stomatal conductance is not always an important limiting factor of CO_2 assimilation rate (Farquhar and Sharkey, 1982). If stomatal conductance dose not vary in the vertical variations of A_{max} and A/C_i, the C_i/C_a ratio may vary, and the intercellular CO_2 concentration may influence on A_{max}. In the vertical variation of A_{max}, however, the C_i/C_a ratio kept relatively constant (Fig. 6C). Thus the vertical variation of stomatal conductance may contribute the constancy of C_i/C_a ratio. These results suggest that the stomatal conductance may be one of the major factor in the vertical gradient of A_{max}.

In the vertical gradient of A_{max}, the both stomatal conductance and mesophyll conductance varied, and the C_i/C_a ratio kept constant around 0.8 (Figs. 6B, C, and D). In general, the C_i/C_a ratio is determined by the balance between stomatal conductance and mesophyll conductance. Thus we can speculate that the changes in stomatal conductance and mesophyll conductance appear to occur in such a way that the C_i/C_a ratio

keeps relatively constant around the value of 0.8 in the vertical gradient of A_{max} within the crown.

In conclusion, photosynthetic properties vary gradually along the light attenuation within a beech crown. The vertical gradient of A_{max} depends on mesophyll conductance. The stomatal conductance may be also one of the major factor in the vertical gradient of A_{max}. However, the intercellular CO_2 concentration doesn't influence the vertical gradient of A_{max} within a beech crown.

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[*] In Japanese with English summary.

[**] Only in Japanese. The titles in parentheses are tentative translation from the original Japanese ones by the author of this paper.