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Growth and maintenance respiration of hinoki cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) branches exposed to long-term CO_2 enrichment in the field

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The CO_2 gas exchange of hinoki cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) branches was measured continuously with an open gas exchange system for 12 (Experiment 1) and 17 months (Experiment 2) in chambers supplied by ambient (370 $\mu molCO_2\ mol^{-1}$) and elevated (800 $\mu molCO_2\ mol^{-1}$) air under field conditions. The daily respiration increased linearly with increasing daily gross photosynthesis in each month. The two-component model was used to examine how maintenance and growth components of respiration were effected by elevated CO_2 enrichment. The partitioning of the respiration into maintenance and growth components was carried out monthly. The slope k of the two-component model did not differ between CO_2 treatments at a significance level of 1%. Both growth and maintenance respiration components tended to increase in elevated CO_2. The growth respiration increment induced by CO_2 enrichment showed a seasonal fluctuation in the ratio (elevated to ambient) from about 1.0 during winter to 1.65-1.80 during summer and seemed to be related to increasing photosynthesis rate. On the other hand, the ratio of maintenance respiration in elevated CO_2 to that in ambient CO_2 increased gradually to an upper limit of around 1.50-1.55 with increasing leaf carbon content and decreasing specific leaf area. N-content per unit leaf area did not increase in elevated CO_2 treatment. The different time-course in the responses altered the balance between growth and maintenance components at the first period of experiments, but this effect disappeared after 4-6 months of CO_2 treatment.

Key words: branch, *Chamaecyparis obtusa*, elevated CO_2, growth respiration, maintenance respiration

Introduction

The concentration of CO_2 in the global atmosphere is steadily rising and the interest of this physiological effect on terrestrial vegetation has focused overwhelmingly on photosynthesis. However, as it has been estimated that about half of the carbon fixed by photosynthesis is lost via respiratory pathways (Amthor 1991), it became clear that photosynthesis alone can not be used to predict long-term plant response to CO_2 enrichment. Therefore, an increasing number of studies is beginning to document the respiratory response of higher plants to atmospheric CO_2 enrichment at the present. The effects of CO_2 enrichment on respiration are still contradictory. That is, with an increase in CO_2, respiration rate increased in some cases and decreased in others. Porter *et al.* (1992) analysing the results of experiments with 46 plant species (including 10 tree species) reported that leaf respiration per unit leaf area shows wide variations ranging from over 50% inhibition to more than 200% stimulation in elevated CO_2.

One approach that yields useful information on the response of respiration to CO_2 enrichment would be to partition respiration into its growth and maintenance components, and subsequently to identify whether CO_2 preferentially affects the cost of either producing or maintaining biomass (Wullschleger and Norby 1992). Growth respiration provides energy for the synthesis of the new phytomass, whereas maintenance respiration supplies energy to keep the existing phytomass in a healthy state. Elevated CO_2 may affect components of respiration differently in different species under contrasting circumstances (Poorter *et al.* 1992). The net result of changes depends on how each of these components is affected.

For separating respiration into maintenance and growth components, several methods have been proposed (McCree 1970; Hesketh *et al.* 1971; Thornley 1976; Yokoi *et al.* 1978; Mariko 1988). In the present study, we measured the respiratory response of hinoki cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) branches to elevated CO_2 for 12 (Experiment 1) and 17 (Experiment 2) months. Using a two-component model (McCree 1970; Paembonan *et al.* 1992) we partitioned the observed results into maintenance and growth components to examine how each of the components is

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affected.

Materials and Methods

Plant materials

The two experiments were carried out on 11-(as of 1994) and 9-year-old (as of 1996) hinoki cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) in experimental stands of the School of Agricultural Sciences, Nagoya University, Japan, from July 1994 to June 1995 (Experiment 1) and from April 1996 to August 1997 (Experiment 2). Two sample branches of a similar size, which were located at similar positions within the crown of a tree, were selected for each experiment. General features of the sample trees and sample branches at the beginning of the experiment are given in Table 1.

CO_2 exchange measurement

Carbon dioxide exchange of the sample branches was measured in the field with an open gas exchange system. Each sample branch was enclosed in a cylindrical assimilation chamber which was made of a 0.2 mm thick transparent film of polyvinyl chloride (Takafuji Chem. Syn. Co., Ltd., Tokyo, Japan) with a transmissivity of ca. 90% of photosynthetically active radiation. The volume of the chamber was 0.02 m^3. The skirt of the chamber was tied to the stem at the base of the branch.

Air temperatures outside and inside the chamber were monitored with platinum resistance thermometers (SHT-01, Koito Ind., Ltd., Tokyo, Japan). Air temperature inside the chamber was adjusted to that of the outside by a temperature controller (MC-K15, Koito Ind., Ltd., Tokyo, Japan). One chamber was supplied with ambient air, which contained approximately 370± 20 $CO_2\mu$mol mol^{-1}, whereas in the other chamber CO_2 concentration was elevated to 800±30 μmol mol^{-1} by adding pure CO_2 to the ambient air. Ambient air was taken from two meters above tree crowns using ducts with a diameter of 20 cm. The ambient air was mixed in 4.0 m^3 buffer tanks using fans to minimize short term fluctuation in CO_2 concentration before being pumped into the chambers. The airflow rate in the chambers were 20 L min^{-1} during daytime and 5 L min^{-1} during the nighttime when CO_2 gas exchange was not so active. Samples of air at the inlet and outlet of the chambers were drawn through vinyl tubes into an infrared gas analyzer (Fuji Electric Co., Tokyo, Japan) for CO_2 concentration analysis at an interval of four minutes. The carbon dioxide concentrations, air temperature and photosynthetic photon flux density were recorded at 4-min intervals during the experimental periods.

Leaf area measurement

Leaf area was measured periodically and nondestructively in order to express the CO_2 gas exchange rate on a leaf area basis. For this nondestructive measurement of leaf area, a light sensitive paper was placed just under leaves and the silhouette of the leaves was taken using a slide projector lamp as the source of light. The measurement was made only in the night. The silhouette was copied onto a transparent film and the area was measured by an area meter (AAC-100, Hayashi Denko Co., Ltd., Tokyo, Japan). Leaf area measurement was carried out at monthly intervals. The leaf area on any day was calculated from the growth pattern, which was

Table 1. General features of the stand, sample trees and sample branches at the beginning of Experiments 1 and 2.

				Exp. 1	Exp. 2
Stand description :	Age		[years]	11	9
	Mean tree height		[m $tree^{-1}$]	4.74	4.20
	Tree density		[no. ha^{-1}]	8800	10000
Sample trees :	Tree height		[m]	5.50	4.85
Sample branches :	Elevation in crown		[m]	4.4	4.4
	Length	(elevated)	[cm]	63	11.9
		(ambient)	[cm]	56	13.1
	Diameter	(at 1 cm from the base)			
		(elevated)	[mm]	3.8	1.90
		(ambient)	[mm]	3.6	1.95
	Leaf area	(elevated)	[cm^2]	430	19.8
		(ambient)	[cm^2]	370	23.4

determined from the monthly measurement of leaf area.

The sample branches were cut down at the end of the experiments and the specific leaf area was calculated from the measured area and the dry weight of the leaves.

Carbon and nitrogen measurement

Samples were taken from dried and blended leafy tissues of the cut branches for C and N measurement at the end of Experiment 1. The C and N contents of the samples were measured by a CN corder (MT-500, Yanagimoto Ind., Ltd., Kyoto, Japan).

Data analysis

Results of CO_2 exchange measurement were expressed in terms of two variables with a dimension of mmolCO_2 dm^{-2} day^{-1}: daily respiratory consumption, R; and daily gross photosynthesis, P. Dark respiration during the daytime was estimated on the basis of the relationship of nighttime respiration rate to air temperature (Nagy *et al.* 1999) and the air temperature observed during the daytime. The daily respiratory consumption was obtained by combining the estimated daytime dark respiration with the observed nighttime respiration. The daily gross photosynthesis was defined as the sum of daily net photosynthesis and the daily respiratory consumption.

The respiration R of each sample branch was divided into growth respiration and maintenance respiration by the following linear equation,

$$R = kP + R_m = R_g + R_m, \quad (1)$$

where k and R_m are coefficients specific to each month. The first term on the right hand side of Eq. (1) represents growth respiration per unit leaf area, $R_g (= kP)$, and the second term, R_m, denotes maintenance respiration per unit leaf area (McCree 1970).

Results

Relationship between daily respiration and daily gross photosynthesis

The relationship between daily respiration R and daily gross photosynthesis P are shown in Fig. 1. There was a trend for R to increase with increasing P. This relationship was well described by Eq. (1). The slope k in Eq. (1) showed a monthly change in value from 0.0 in winter to 0.13 in early summer (Fig. 2), but there was no difference at a significance level of 1% in k-value between CO_2 treatments. Paembonan *et al.* (1992) also

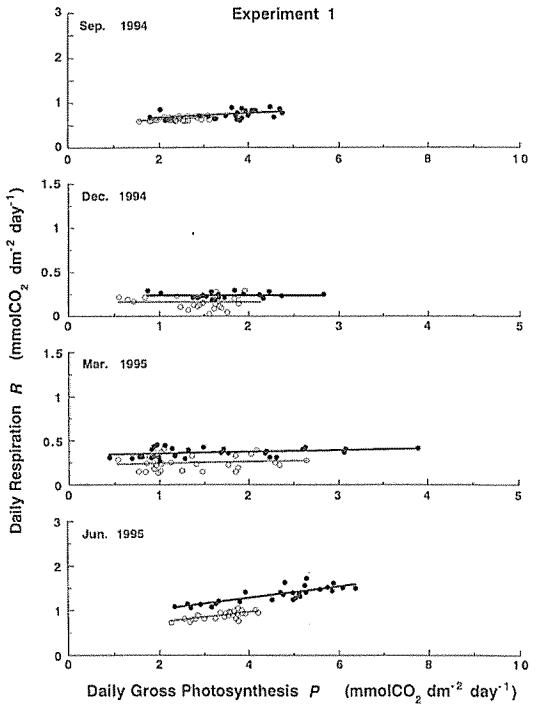

Fig. 1. Dependence of daily respiratory consumption R (mmolCO_2 dm^{-2} day^{-1}) on daily gross photosynthesis P (mmolCO_2 dm^{-2} day^{-1}). The straight line is based on Eq. (1). Symbols mean: (○) ambient CO_2 treatment and (●) elevated CO_2 treatment.

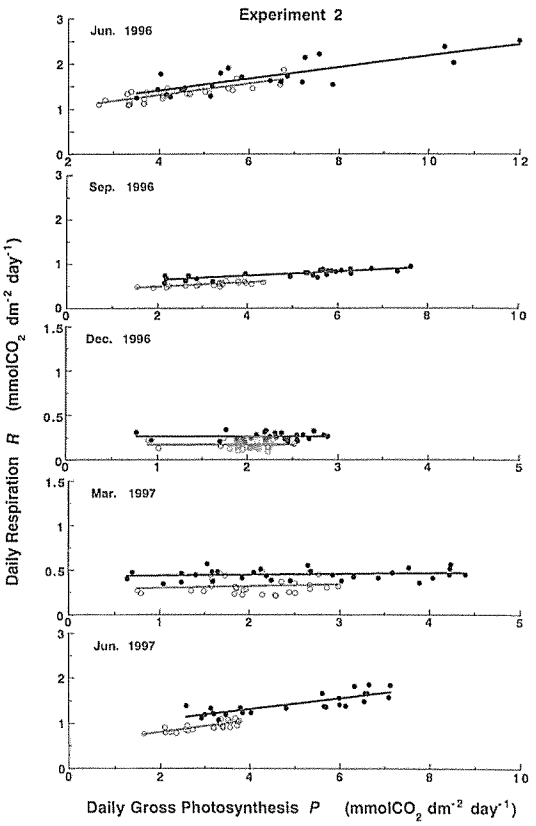

Fig. 1. (continued)

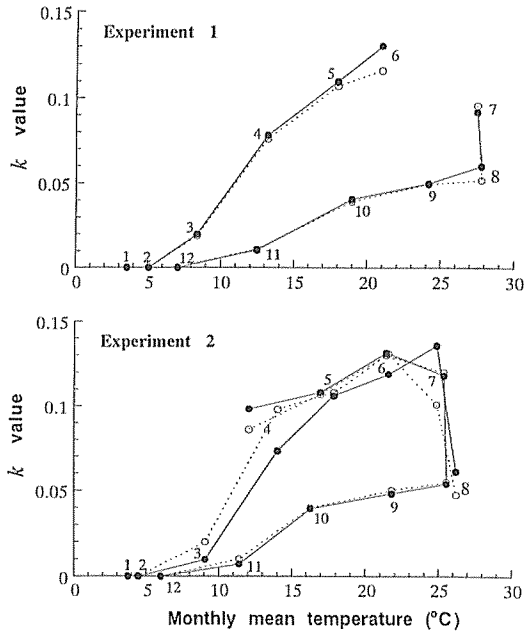

Fig. 2. Relationship between k-value in Eq. (1) and monthly mean temperature. Numerals represent months. Symbols mean; (○) ambient and (●) elevated CO_2 treatments in Experiment 1; (△) ambient and (▲) elevated CO_2 treatments in Experiment 2.

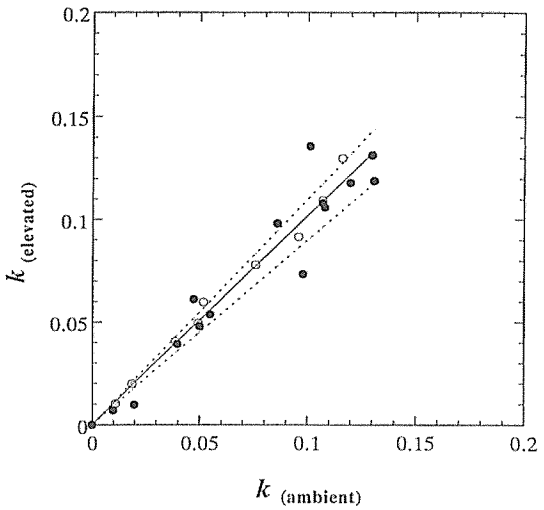

Fig. 3. Relationship between k values in ambient and elevated CO_2 treatments in Eq. (1). Symbols mean: (○) Experiment 1 and (●) Experiment 2. The dotted lines represent a relative error of ±10%.

recognized the monthly change in k value for aerial parts of a hinoki tree. As shown in Fig. 3, the value of $k_{(elevated)}$ agreed with the value of $k_{(ambient)}$ within a relative error of ±10% throughout the entire experimental periods.

The interception R_m was higher in elevated CO_2, especially after the first months, so that R_m differed between treatments at a significance level of 1%.

Seasonal changes in the contribution of maintenance and growth respiration to total respiration

The values of R_m and R_g changed seasonally (Fig. 4). The R_m generally showed higher in summer and lower values during winter. The R_g had the highest values in early summer and was virtually zero during winter. Experiment 2 with younger branches showed somewhat higher R_m and R_g values than Experiment 1 with older branches.

The contribution of monthly growth and maintenance respiration to total respiratory consumption showed a seasonal trend in both experiments and both CO_2 treatments (Fig. 5). The ratio of growth respiration to total respiration increased rapidly in early spring, remained high during the early growing season with a maximum ratio of about 40-45%, decreased abruptly from August and became close to 0 during the winter. The ratio of growth respiration to total respiration was 5-10% as high as in elevated CO_2 treatment as compared with ambient CO_2 treatment in the early period of both experiments. However, this initial deviation between treatments disappeared in 4-6 months after the beginning of the experiments. The annual relative rate of growth respiration to total respiratory consumption was 30.1 and 32.4% in ambient and 31.7 and 33.3% in elevated CO_2 treatments in Experiments 1 and 2, respectively.

CO_2 effect on growth and maintenance respiration

Both growth respiration R_g and maintenance respiration R_m differed between treatments. The seasonal variation of the ratio between elevated and ambient treatments is shown in Fig. 6. The ratio of maintenance respiration ($R_{m(elevated)}/R_{m(ambient)}$) was around 1.0 at the beginning of both experiments. However, this ratio increased rapidly for 5-7 months approaching an upper limit of 1.50-1.55, and then kept a more or less constant level until the end of the experiments. The ratio of growth respiration ($R_{g(elevated)}/R_{g(ambient)}$) showed a seasonal fluctuation with the highest level of 1.65 to 1.80 in August, and then the ratio decreased to 1.0 during winter (Fig. 6). The growth respiration rate was virtually zero in both CO_2 treatments during winter.

Maintenance respiration is associated with the maintenance of the existing plant material, whereas growth respiration is associated with the synthesis of new

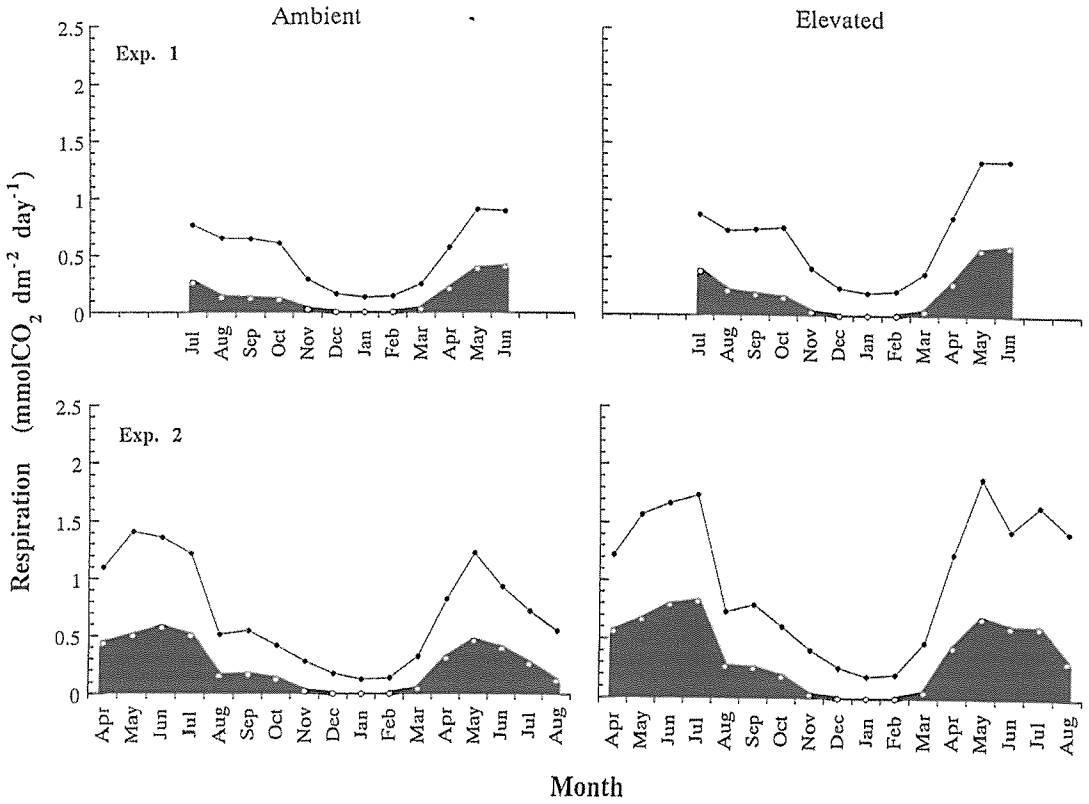

Fig. 4. Seasonal changes in growth respiration, (■) and maintenance respiration, (□).

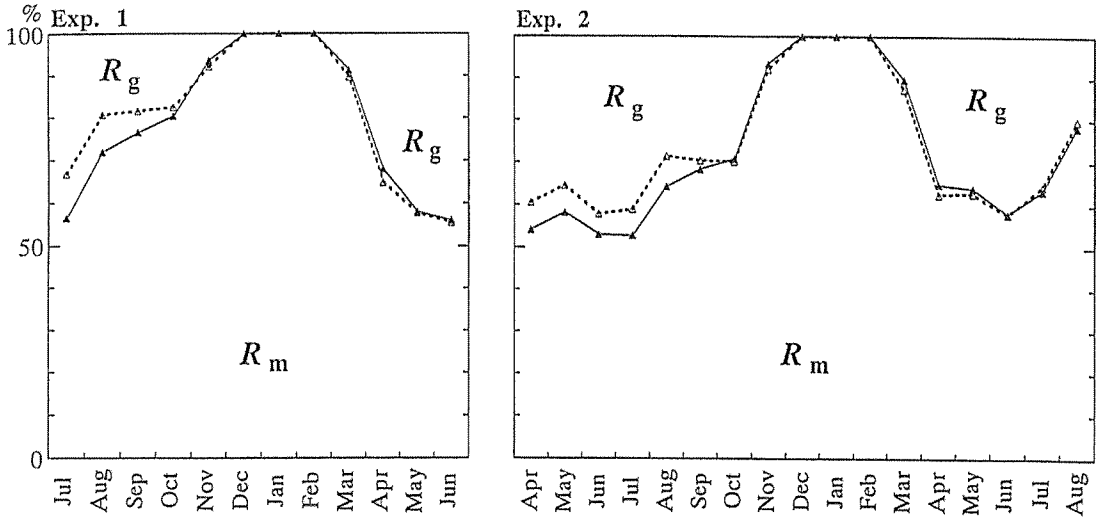

Fig. 5. Seasonal changes in the contribution of growth respiration R_g and maintenance respiration R_m in (△) ambient and (▲) elevated CO_2 treatments.

biomass. Therefore we compared the total growth respiratory cost to total leaf area increment in both CO_2 treatments. The growth respiratory requirement for newly created leaf area in ambient and elevated CO_2 treatments was found to be 0.323 mmolCO_2 cm^{-2} and 0.472 mmolCO_2 cm^{-2} respectively in Experiment 1. The respective values in Experiment 2 were 0.387 mmolCO_2 cm^{-2} and 0.511 mmolCO_2 cm^{-2}. The results suggest that growth respiratory cost per unit newly created leaf area is higher in elevated CO_2 treatment than in younger branches.

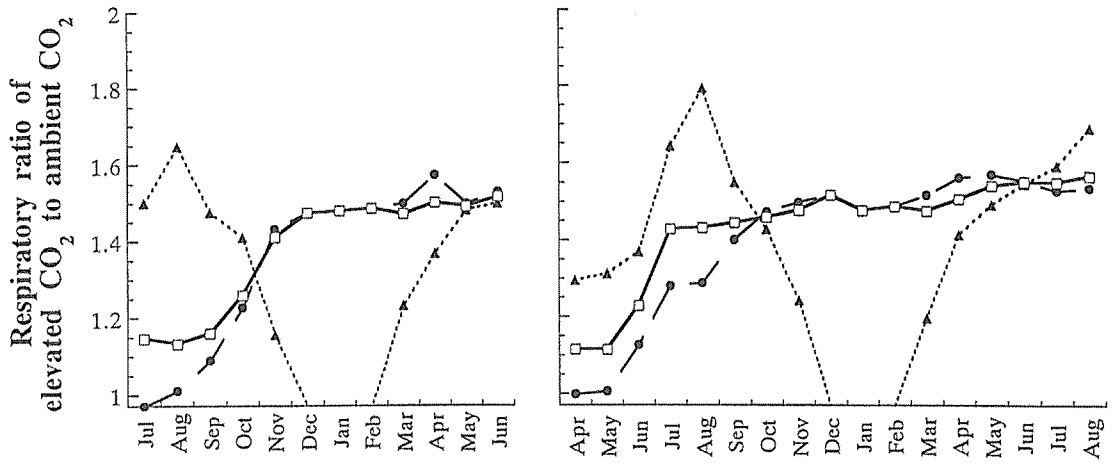

Fig. 6. Seasonal variations of respiratory ratio (as elevated CO_2 to ambient CO_2) in (▲) growth, (●) maintenance and (□) total respiration rates.

Table 2. Leaf area, leaf mass, specific leaf area SLA, and C and N contents of sample branches in ambient and elevated CO_2 treatments at the ends of Experiments 1 and 2.

	Exp. 1							Exp. 2		
	Area (cm^2)	Mass (g)	SLA ($cm^2\ g^{-1}$)	C content ($g\ g^{-1}$)	C content ($mg\ cm^{-2}$)	N content ($g\ g^{-1}$)	N content ($mg\ cm^{-2}$)	Area (cm^2)	Mass (g)	SLA ($cm^2\ g^{-1}$)
Ambient										
Old leaves	370	10.0	36.8					23	0.58	38.7
New leaves	1533	32.5	47.1					781	18.1	43.2
total	1903	42.6	44.7	0.544	12.2	0.0149	0.331	804	18.6	43.1
Elevated										
Old leaves	430	10.8	39.8					19	0.47	39.3
New leaves	1769	48.3	36.6					995	27.1	36.8
total	2199	59.1	37.2	0.531	14.3	0.0122	0.328	1013	27.5	36.8

Specific leaf area

The specific leaf area (i. e., leaf area per unit leaf mass) measured at the end of the experiments was 37.2 and 36.8 $cm^2\ g^{-1}$ for the elevated and 44.7 and 43.1 $cm^2\ g^{-1}$ for the ambient CO_2 treatments in Experiments 1 and 2, respectively (Table 2). This means an approximately 16% decrease of specific leaf area in elevated CO_2 treatment, which indicates that leaves became thicker in elevated CO_2. The particular measurements showed that old and new tissues were not effected in a similar manner. The specific leaf area was approximately 22.5% (Exp. 1) and 15% (Exp. 2) lower in leaf tissues which grew after the experiment had been started, while the previously formed leaf tissues had about the same specific leaf area between the treatments.

Leaf carbon and nitrogen content

There was a strong effect of elevated CO_2 on leaf carbon and nitrogen concentration. The mean carbon and nitrogen concentration in leaves at the end of Experiment 1 were respectively 0.531 g g^{-1} and 0.0122 g g^{-1} in elevated and 0.544 g g^{-1} and 0.0149 g g^{-1} in ambient CO_2 (Table 2). This means an approximately 18% decrease of N in elevated CO_2 treatment. Actually, the carbon increment resulted in a dilution of nitrogen in response to CO_2 enrichment. When the carbon and nitrogen content were calculated on a leaf area basis, only carbon content increased in elevated CO_2 treatment, while nitrogen content appeared not to be affected. The carbon and nitrogen content on a leaf area basis were respectively found to be 14.3 and 0.328 mg cm^{-2} in elevated and 12.2 and 0.331 mg cm^{-2} in

ambient CO_2 treatments.

Discussion

The seasonal fluctuation of the ratio in leaf area-based growth respiration suggested a temperature dependence (Fig. 6). The relationship between growth respiratory ratio ($R_{g(elevated)}/R_{g(ambient)}$) and monthly mean temperature was very similar to the relationship between ratio in gross photosynthesis ($P_{(elevated)}/P_{(ambient)}$) and monthly mean temperature (Fig. 7). This trend results from Eq. (2),

$$\frac{R_{g(elevated)}}{R_{g(ambient)}} = \frac{k_{(elevated)}}{k_{(ambient)}} \cdot \frac{P_{(elevated)}}{P_{(ambient)}} \quad (2)$$

As $k_{(elevated)}$ is not significantly different from $k_{(ambient)}$, Eq. (2) shows that the ratio ($R_{g(elevated)}/R_{g(ambient)}$) is equal to the ratio of $P_{(elevated)}/P_{(ambient)}$.

It has been documented that dark respiration is positively related with different carbohydrate status due to manipulated photosynthesis rate of leaves (Azcon-Bieto and Osmond 1983; Azcon-Bieto *et al.* 1983; Wullschleger *et al.* 1994). This result suggests that the increased growth respiration rate follows the increased carbohydrate content and photosynthesis rate in elevated CO_2, and the elevated CO_2 concentration has only an indirect effect on growth respiration owing to accelerated photosynthesis rate.

Several possible explanations have been shown for altering maintenance respiration. The most often cited explanation is that in many cases maintenance respiration seemed to be positively related with tissue nitrogen (protein) content (Ryan 1991; Amthor 1989) and protein content-based respiration rate might be unaffected (Amthor 1991). Our results did not support this hypothesis, because elevated CO_2 did not alter the N content of leaves on a leaf area basis, but merely C increment caused a dilution of N content. The increased maintenance respiration seemed to be correlated with the increased C content on a leaf area basis.

The ratio ($R_{m(elevated)}/R_{m(ambient)}$) of maintenance respiration on a leaf area basis increased gradually from the initial level of 1.0 to 1.55 with time (Fig. 6), and elevated CO_2 affected specific leaf area only in leaf parts which grew after the beginning of experiment. These facts suggest a correlation between increasing maintenance respiration and increasing proportion of low specific leaf area tissues in elevated CO_2 treatment. This result supports the suggestion of Thomas *et al.* (1993), who reported that the increase in maintenance respiration seemed to be associated with decreased specific leaf area and increased starch level in cotton leaves after 30 days in elevated CO_2 treatment.

In summary, CO_2 enrichment to hinoki stimulated photosynthesis, respiration and area-based carbon content, and decreased specific leaf area. Although both growth and maintenance respiration were stimulated by elevated CO_2, the mechanism and time course of the effects differed between components. The leaf area-based growth respiration in elevated CO_2 was stimulated through accelerated photosynthesis, whereas the maintenance respiration appeared to be increased in accordance with increased carbon content per unit leaf area and decreased specific leaf area. Stimulation to growth component was changing periodically according to the season, whereas stimulation to maintenance component increased gradually until an upper limit with time (Fig. 6). The different time-course of the stimulation to the two components altered the contribution to the total respiration at the beginning (Fig. 5), but within the next few months, the maintenance component in elevated CO_2 treatment increased gradually until the sample branches regained their original balance between components.

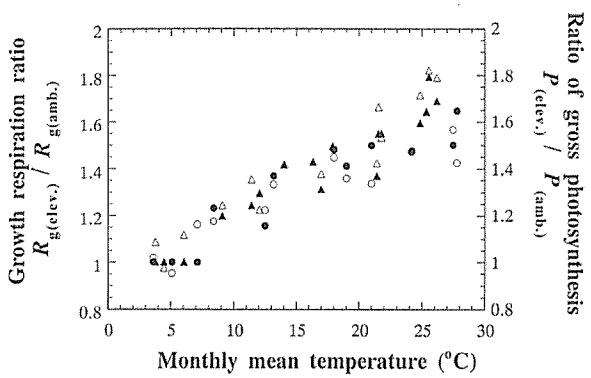

Fig. 7. Temperature dependence of the monthly growth respiration ratio ($R_{g(elev.)}/R_{g(amb.)}$) and the monthly ratio in gross photosynthesis rate ($P_{(elev.)}/P_{(amb.)}$). The temperature means monthly mean temperature. Symbols mean: respiratory ratio, in (●) Experiment 1 and (▲) Experiment 2; photosynthetic ratio, in (○) Experiment 1 and (△) Experiment 2.

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野外での長期に渡る CO_2 高濃度下における ヒノキ枝の成長呼吸と維持呼吸

ミクロシュ ナジ・小川一治・萩原秋男

野外に成育するヒノキの枝のガス交換が外気濃度（370 μmolCO_2 mol^{-1}）と高濃度（800 μmolCO_2 mol^{-1}）で開放系システムのチャンバーを用いて連続的に12ヶ月（実験1）と17ヶ月（実験2）測定された。各月において，日呼吸量は日総光合成量の増加に伴って直線的に増加した。維持呼吸と成長呼吸が高濃度 CO_2 によりどのように影響されるかを調べるために2-コンポーネントモデルが使用された。呼吸量の維持呼吸と成長呼吸への分配は毎月実施された。2-コンポーネントモデルの傾き k は両 CO_2 処理間で有意差1％で差はなかった。成長呼吸，維持呼吸とも高濃度の CO_2 により増加する傾向にあった。高濃度の CO_2 により増加した成長呼吸は季節変化を示し，その比（高濃度区/外気濃度区）は冬期は約1となり，夏期は1.65-1.80となった。この成長呼吸の増加は光合成速度の増加と関係していた。一方，維持呼吸の比（高濃度区/外気濃度区）は葉内炭素含量の増加と比葉面積の減少に伴い上限値1.50-1.55まで徐々に増加した。単位葉面積当たりの葉内窒素量は変化しなかった。成長呼吸と維持呼吸のバランスは実験開始後，両 CO_2 処理間で異なったが，4—6ヶ月後に差はなくなった。

キーワード：枝，ヒノキ，高濃度 CO_2，成長呼吸，維持呼吸