

## Effects of Temperature on CO<sub>2</sub> Dependence of Gas Exchanges in C<sub>3</sub> and C<sub>4</sub> Crop Plants\*

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**Abstract :** The effects of elevated CO<sub>2</sub> in the atmosphere and the accompanied temperature rise predicted for the future on gas exchanges of two summer C<sub>3</sub> (rice, soybean) and two C<sub>4</sub> (Japanese millet, finger millet) crop plants were examined. Plants were grown in artificially illuminated growth cabinets under 350 and 500  $\mu\text{mol mol}^{-1}$  ambient CO<sub>2</sub> (C<sub>a</sub>) and were measured for rates of CO<sub>2</sub> exchange (CER) and transpiration (E) of leaves at 23, 28 and 33°C in terms of C<sub>a</sub> (0—500  $\mu\text{mol mol}^{-1}$ ). The responses of CER to C<sub>a</sub> were slightly lower in plants grown in high C<sub>a</sub> than those in normal C<sub>a</sub> and were largely influenced by temperature. The promotive effect of elevating C<sub>a</sub> on CER was larger at higher temperatures, especially in C<sub>4</sub> crop plants. With the rise of C<sub>a</sub>, the E in C<sub>4</sub> crop plants decreased more than in C<sub>3</sub> crop plants and it was correlated with the decrease in stomatal conductance to CO<sub>2</sub> transfer. The water use efficiency (WUE) of leaves increased with the rise in C<sub>a</sub> but the effect of temperature on WUE was unclear. It is concluded that, within limits, under high C<sub>a</sub>, C<sub>4</sub> crop plants expand their photosynthetic capacity in an environment of high temperature.

**Key words :** C<sub>4</sub> crop plant, CO<sub>2</sub> concentration, CO<sub>2</sub> exchange rate, Stomatal conductance, Temperature, Transpiration rate, Water use efficiency.

C<sub>3</sub>, C<sub>4</sub> 型作物におけるガス交換の CO<sub>2</sub> 濃度依存性に及ぼす温度の影響：今井 勝・岡本-佐藤真奈美（筑波大学農林学系）

**要 旨：**将来予想される高 CO<sub>2</sub> 濃度環境下における，作物葉のガス交換特性に及ぼす温度上昇の効果を知らうとして，光合成の機作を異にする C<sub>3</sub> 型の夏作物（イネ，ダイズ）と C<sub>4</sub> 型作物（ヒエ，シコクビエ）とを用いて研究を行なった．ポット植えの個体を人工光グロースキャビネット内で，CO<sub>2</sub> 濃度 350（標準区）及び 500（高濃度区） $\mu\text{mol mol}^{-1}$  の下に 4～5 週間昼夜連続して処理し，着生したままの最上位完全展開葉のガス交換特性を，開放系の測定装置によって調べた．本実験では，処理期間中の高 CO<sub>2</sub> 濃度がガス交換能を僅かに低下させたが，有意ではなかったもので，高濃度区の作物のみにつき検討を進めた．CO<sub>2</sub> 交換速度の CO<sub>2</sub> 濃度（0～500  $\mu\text{mol mol}^{-1}$ ）依存性は，温度の影響を強く受け，調べた範囲（23, 28, 33°C）では高温ほど高 CO<sub>2</sub> 濃度下での CO<sub>2</sub> 交換速度が大きくなり，C<sub>4</sub> 型作物は C<sub>3</sub> 型作物よりも温度に対する反応が大きかった．蒸散速度は高温ほど大きかったが，CO<sub>2</sub> 濃度上昇に伴ない様に低下し，その低下は C<sub>4</sub> 型作物の方が大きく，気孔コンダクタンスの低下と並行していた．作物葉の水利用効率は C<sub>4</sub> 型が高く，また CO<sub>2</sub> 濃度上昇に伴なって高まったが，温度の影響は明らかではなかった．さらに，作物葉における気孔を介したガス交換の制御に関連して考察を行ない，CO<sub>2</sub> 濃度と温度の上昇が相伴なう環境下では，C<sub>4</sub> 型作物の光合成能力がかなり高まることを推測した．

**キーワード：**温度，気孔コンダクタンス，CO<sub>2</sub> 交換速度，CO<sub>2</sub> 濃度，C<sub>4</sub> 型作物，蒸散速度，水利用効率．

The global increase of atmospheric CO<sub>2</sub> concentration due mainly to the huge consumption of fossil fuels and the clearing of forests will induce climatic change (e.g. the greenhouse effect) in the future<sup>6)</sup>. It will, however, promote both the growth and yield of many crop species through the enhance-

ment of photosynthesis unless water and nutrients are deficient<sup>20,22,29)</sup>. Under CO<sub>2</sub> concentrations higher than the present one (ca. 350  $\mu\text{mol mol}^{-1}$ ), the temperature may be one of the most important environmental factors for photosynthesis<sup>9,11)</sup>. Therefore, it is worthwhile to examine how the elevated temperature affects gas exchanges of crop plants which are grown at elevated ambient CO<sub>2</sub> concentration (C<sub>a</sub>).

In an investigation of CO<sub>2</sub> (1000 vs. 350  $\mu\text{mol mol}^{-1}$ ) effects on the growth of C<sub>3</sub> (rice and soybean) and C<sub>4</sub> (Japanese millet and corn) crop plants in combination with temper-

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Abbreviations : C<sub>a</sub> ; ambient CO<sub>2</sub> concentration, CER ; CO<sub>2</sub> exchange rate, C<sub>i</sub> ; intercellular CO<sub>2</sub> concentration, E ; transpiration rate, g<sub>s</sub> ; stomatal conductance to CO<sub>2</sub> transfer, PPFD ; photosynthetic photon flux density, VPD ; leaf-air vapour pressure difference, WUE ; water use efficiency.

ature (28 vs. 23°C), we have obtained evidence that, at higher temperature, higher  $C_a$  brought about an increased crop growth mainly through the elevation of the net assimilation rate<sup>15)</sup>. We also confirmed the positive  $CO_2$  (700 vs. 350  $\mu\text{mol mol}^{-1}$ ) effect at higher (33°C) than lower (28°C) temperatures in long-term experiments with several  $C_3$  crop plants<sup>17,18,19)</sup>. Similar results were obtained in soybean<sup>4,12)</sup> and aquatic plants<sup>2)</sup>, although there might be an ecotypic difference in the degree of response<sup>25)</sup>. In this paper, we present the  $CO_2$  dependence of gas exchanges in two summer  $C_3$  and two  $C_4$  crop plants at three temperatures as a basis for dry matter production in such environments.

### Materials and Methods

Rice (*Oryza sativa* L. cv. Nipponbare), soybean (*Glycine max* Merr. cv. Bonminori), Japanese millet (*Echinochloa frumentacea* Link cv. Hidaakabie) and finger millet (*Eleusine coracana* Gaertn. cv. Sakase III) were used as materials. The former two and the latter two, respectively, have  $C_3$  and  $C_4$  photosynthetic characteristics.

Seeds of each species were sown in 1 L plastic pots containing 1.2 kg of soil and 3 g of chemical fertilizer ( $N-P_2O_5-K_2O=14-14-14$ , %) in a glasshouse. About a week after the emergence, seedlings were thinned to one plant per pot and transferred into artificially illuminated growth cabinets. Plants were grown under conditions of 450  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD (12-h photoperiod) supplied with metal halide lamps (Toshiba, DR-400), 28/

23°C (day/night) temperatures and about 65% RH. The ambient  $CO_2$  concentrations were kept at 350 (normal) and 500 (high)  $\mu\text{mol mol}^{-1}$  with  $CO_2$  controllers (Fuji, Model ZFP-6) throughout the treatment periods. Rice and Japanese millet were kept submerged and soybean and finger millet, at field moisture conditions. A week before the gas exchange measurements, the chemical fertilizer (2 g/pot) was top-dressed.

During the 4–5 weeks of  $CO_2$  treatments, the attached, uppermost – fully expanded leaves were clumped on two sets of small leaf chambers ( $2 \times 7.3$  cm), which were set inside the growth cabinet and connected with an open-airflow gas exchange measurement system. Carbon dioxide and water vapour concentrations of the inlet and outlet of leaf chambers were measured with an absolute type infrared  $CO_2$  analyzer (Fuji, Model ZRC) and a dewpoint hygrometer (EG & G, Model 911), respectively. Light (950  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) was supplied with the same kind of light source as in growth. The vapour pressure difference between leaf and air (VPD) was kept at 1.0–1.2 kPa by bubbling the air in water in a glass cylinder which was set in a temperature-controlled water bath. Leaf temperature was monitored with a fine copper-constantan thermocouple attached beneath the leaf surface and it was adjusted to the set value (23, 28 or 33°C) by the water jacket of leaf chamber in which water was circulated through another water bath. The  $C_a$  was changed from 500 to 0  $\mu\text{mol mol}^{-1}$  by adding 10%  $CO_2$  from a cylinder to  $CO_2$ -free

Table 1. Rates of  $CO_2$  exchange (CER) and transpiration (E) of soybean and finger millet grown and measured at two  $CO_2$  concentrations.

Crop name	$CO_2$ conc. ( $\mu\text{mol mol}^{-1}$ ) at growth	CER ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) at $CO_2$ conc. of:		E ( $\text{mmol m}^{-2}\text{s}^{-1}$ ) at $CO_2$ conc. of:	
		350	500	350	500
Soybean	350	23.2	29.4	3.1	2.9
	500	22.0	28.9	3.0	2.8
	Difference	1.2ns	0.5ns	0.1ns	0.1ns
Finger millet	350	30.6	34.8	2.3	1.9
	500	30.2	34.1	2.2	1.8
	Difference	0.4ns	0.7ns	0.1ns	0.1ns

ns : Not significant.

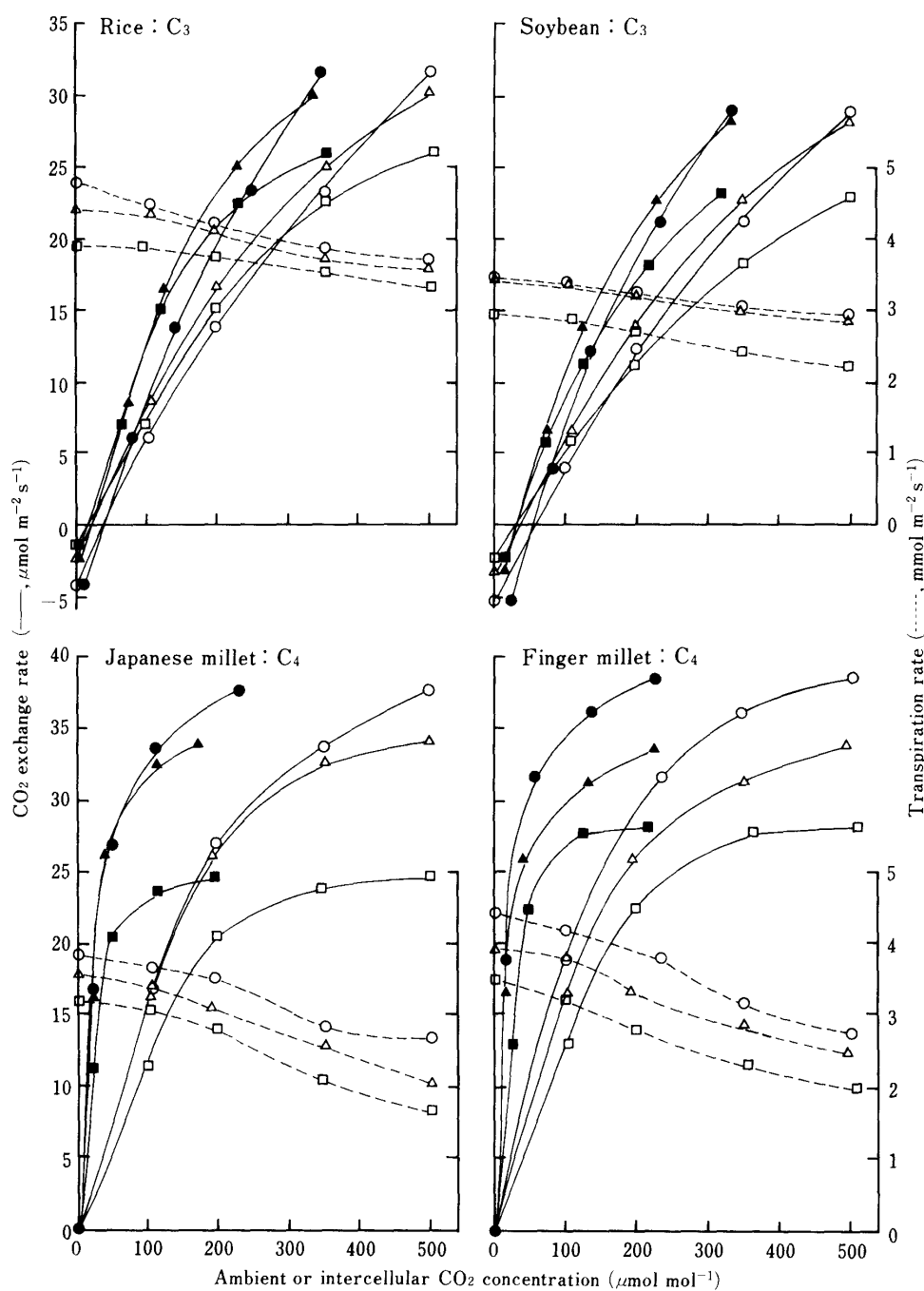


Fig. 1. Effects of CO<sub>2</sub> concentration and temperature on gas exchanges of C<sub>3</sub> and C<sub>4</sub> crop plants.

Open and closed symbols denote responses to ambient and intercellular CO<sub>2</sub>, respectively.

○●, △▲, □■ : 33, 28, 23°C.

air. There was little hysteresis of the CO<sub>2</sub> responses of CO<sub>2</sub> exchange rate (CER) and transpiration rate (E) between the measurements changed from 500 to 0  $\mu\text{mol mol}^{-1}$  C<sub>a</sub> and from 0 to 500  $\mu\text{mol mol}^{-1}$  C<sub>a</sub>.

The water use efficiency of leaf (WUE) was expressed as the ratio of CER to E. Four to five

measurements of gas exchanges at each temperature level with each crop species were carried out in the morning to minimize the decline of photosynthetic capacity in the afternoon due to the accumulation of carbohydrate<sup>3)</sup> and/or imbalance of water status<sup>21)</sup> in leaves. Stomatal conductance to CO<sub>2</sub> transfer

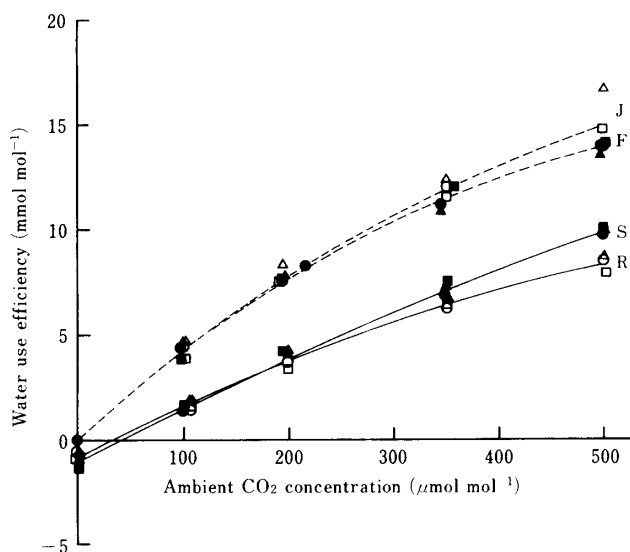


Fig. 2. Effects of ambient  $\text{CO}_2$  concentration and temperature on water use efficiency of crop plants.  
R : rice, S : soybean, J : Japanese millet, F : finger millet.  $\circ, \bullet, \triangle, \blacktriangle, \square, \blacksquare$  : 33, 28, 23°C.

( $g_c$ ) and intercellular  $\text{CO}_2$  concentration ( $c_i$ ) were calculated after Wong et al.<sup>30)</sup>

## Results

### 1. Effects of high $C_a$ during the growth on gas exchanges of leaves

The rates of gas exchanges in leaves of soybean and finger millet to ambient  $\text{CO}_2$  concentrations (350 and 500  $\mu\text{mol mol}^{-1}$ ) at 28°C were always higher in the normal  $C_a$ -grown plants than in the high  $C_a$ -grown plants (Table 1). The differences, however, were not significant and the tendency was similar when measured at 23 or 33°C. These responses were similar in the case of rice and Japanese millet (data not shown).

From the above results, data shown in the latter figures are of high  $C_a$ -grown plants.

### 2. Effects of temperature on gas exchanges of leaves to $C_a$

Figure 1 shows that at 23°C, the CER was lower than at 28°C and 33°C in every crop plant. At the highest  $C_a$  (500  $\pm 3 \mu\text{mol mol}^{-1}$ ), CER was 26.2, 23.3, 24.8 and 28.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in rice, soybean, Japanese millet and finger millet, respectively. The CER of  $C_4$  plants reached saturation at 500  $\mu\text{mol mol}^{-1} C_a$ . The E decreased with the rise in  $C_a$ , with greater depression in  $C_4$  plants than in  $C_3$  plants (Fig.

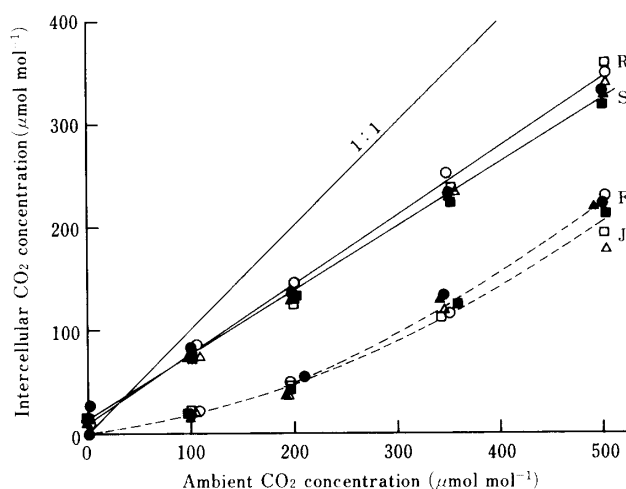


Fig. 3. Relationships between ambient and intercellular  $\text{CO}_2$  concentrations at three different temperatures.  
Symbols are the same with those in Fig. 2.

1). Levels of WUE were higher in  $C_4$  plants than in  $C_3$  plants and increased with  $C_a$  in a quadratic manner (Fig. 2).

At 28°C, values of CER were higher than at 23°C and under 500  $\mu\text{mol mol}^{-1} C_a$ , the CER increased 17–22% and 20–38% in  $C_3$  and  $C_4$  plants than those at 23°C. The levels of E were higher at 28°C than 23°C, but the responses to  $C_a$  were similar in both temperatures (Fig. 1). The patterns of response of WUE to  $C_a$  at 28°C were similar in all the crop plants but the levels were generally higher than at 23°C (Fig. 2).

At 33°C, the levels of CER at 500  $\mu\text{mol mol}^{-1} C_a$  were 21–24% and 36–51% higher than those at 23°C, and 2–4 and 9–13% higher than those at 28°C, respectively, in  $C_3$  and  $C_4$  plants. In  $C_3$  plants at 33°C,  $\text{CO}_2$  fixation efficiency under very low  $C_a$  range was the lowest, but at 500  $\mu\text{mol mol}^{-1} C_a$ , it became the highest among three temperatures. In all the crop plants, the levels of E were higher at 33°C than at 28°C (Fig. 1). The WUE at 33°C was clearly higher in  $C_4$  plants than in  $C_3$  plants but no amelioration occurred when compared with that at 28°C (Fig. 2).

### 3. Response of CER to $C_i$ and relationship between $C_a$ and $C_i$

The response curves of CER in crop plants to  $C_i$  were steeper than those of CER to  $C_a$ . At 23°C, the initial slopes of CER in all the crop plants were lower than those at 28°C and 33°C.

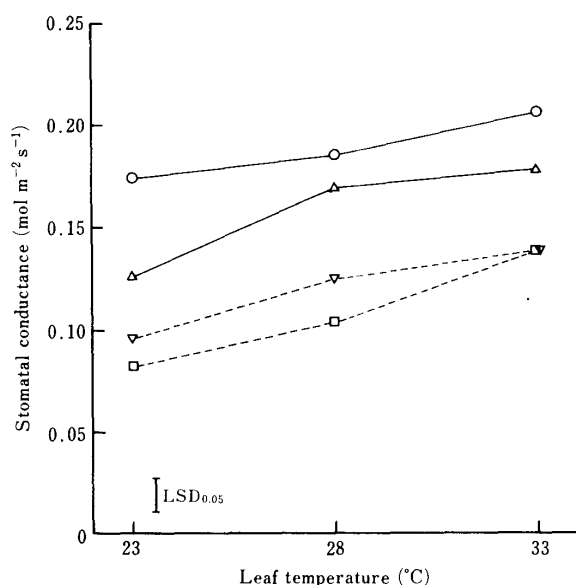


Fig. 4. Effect of temperature on stomatal conductance to CO<sub>2</sub> transfer at 500  $\mu\text{mol mol}^{-1}$ , ambient CO<sub>2</sub>.  
○ : rice, △ : soybean, □ : Japanese millet, ▽ : finger millet.

The difference between  $C_a$  and  $C_i$  at any given temperature was larger in  $C_4$  plants than in  $C_3$  plants (Fig. 1).

When  $C_i$  was plotted against  $C_a$ , the  $C_3$  plants took linear relations, with higher levels of  $C_i$  than those of  $C_4$  plants. When levels of  $C_a$  were at 500 and 350  $\mu\text{mol mol}^{-1}$ , concomitant levels of  $C_i$  in  $C_3$  plants were 320–360 and 220–250  $\mu\text{mol mol}^{-1}$  and those in  $C_4$  plants were 200–230 and 110–130  $\mu\text{mol mol}^{-1}$  but there were no clear effects of temperature (Fig. 3).

#### 4. Effect of temperature on $g_c$ at high $C_a$

At 500  $\mu\text{mol mol}^{-1}$   $C_a$ , the  $g_c$  was plotted against leaf temperature (Fig. 4). Although the  $g_c$  varied among crop plants,  $C_3$  plants had higher and  $C_4$  plants, lower values. All the crop plants increased  $g_c$  with elevating leaf temperature. Over three temperatures, there was a close relationship between  $g_c$  and  $E$  in every crop plant ( $r=0.81^{**}$  for rice and  $r=0.99^{***}$  for soybean, Japanese millet and finger millet, respectively).

### Discussion

The responses of CER and  $E$  to CO<sub>2</sub> concentrations of  $C_3$  and  $C_4$  crop plants grown at normal (350  $\mu\text{mol mol}^{-1}$ ) and high (500  $\mu\text{mol mol}^{-1}$ )  $C_a$  were similar (Table 1)—

probably because the high- $C_a$  plot adopted in the present experiment was too low to induce the negative acclimation of gas exchanges reported by us previously, in which 1000 and 3200  $\mu\text{mol mol}^{-1}$   $C_a$  were referred to high- $C_a$  plots<sup>13,14</sup>.

Under higher levels of  $C_a$  predicted for the future, the growth and yield promotion in  $C_4$  plants was thought to be quite smaller than in  $C_3$  plants because of a lower response of CER in  $C_4$  plants to high  $C_a$  than in  $C_3$  plants<sup>1,7,29</sup>. However, there are accumulating facts indicating that the response of CER and growth of  $C_4$  plants to high  $C_a$  is often fairly large<sup>5,25,26,28</sup>. These responses may be larger under moderate to high temperatures<sup>2,12,15,17,18,19,20</sup> rather than low temperature conditions<sup>27</sup>.

The optimal ranges of temperature for photosynthesis are 25–30°C in  $C_3$  plants adapted to sunny habitats and 30–40°C in  $C_4$  plants, in general<sup>23</sup>. Accordingly, the CER of  $C_4$  crop plants (Japanese millet and finger millet) was saturated at 500  $\mu\text{mol mol}^{-1}$   $C_a$  at 23°C, but at 28°C and 33°C it did not and the rate was highest at the highest temperature (33°C). These responses were larger than those of  $C_3$  plants (rice and soybean), which indicate the decline of enzymatic limitation in  $C_4$  plants with elevating temperature<sup>8</sup>. The difference of photosynthetic response to temperature between  $C_3$  and  $C_4$  plants was apparent at higher  $C_a$  and the effect of temperature was larger at higher  $C_a$ .

The  $C_3$  plants used in the present experiment were adapted to a warm climate and CER did not seem to be largely suppressed by the highest temperature adopted (33°C) when compared the CER at 28°C and 33°C under 350  $\mu\text{mol mol}^{-1}$   $C_a$ . The responses of CER to  $C_a$  were also greater with elevating temperature but the degree was not large when temperature was elevated from 28°C to 33°C. The one reason may be that the high temperature-induced photorespiration is not sufficiently suppressed by the elevation of  $C_a$  (up to 500  $\mu\text{mol mol}^{-1}$ )<sup>16</sup>.

The  $E$  decreased with the rise of  $C_a$  both in  $C_3$  and  $C_4$  plants and the response of  $E$  to  $C_a$  was much larger in  $C_4$  plants than in  $C_3$  plants (Fig. 1). As the VPD was kept at 1.0–1.2 kPa in the present experiment, the direct cause was ascribed to the sensitive stomatal closure in  $C_4$  plants. This was clearer when  $g_c$  was plotted

against  $C_i$  (data not shown) and consistent with the observation by Akita and Tanaka<sup>1)</sup>, but inconsistent with the opinion by Morison and Gifford that stomatal sensitivity of  $C_3$  and  $C_4$  plants to  $CO_2$  was not different<sup>24)</sup>.

As shown in Fig. 4, the  $g_c$  at  $500 \mu\text{mol mol}^{-1}$   $C_a$  increased with the rise of temperature in a similar manner. This may indicate that, within limits, at higher temperatures, plants enlarge a possible gain of  $CO_2$  with the sacrifice of water loss. However, the WUE, which is the product of CER and E, plotted against  $C_a$  varied in response to temperature (Fig. 2). This may reflect the stomatal regulation in optimizing carbon gain and water loss over a broad range of  $C_a$  and temperature<sup>10)</sup>. The higher levels of WUE in  $C_4$  plants were primarily due to higher CER than for  $C_3$  plants but at high  $C_a$  (e.g.  $500 \mu\text{mol mol}^{-1}$ ), the pronounced stomatal closure in  $C_4$  plants could contribute to the WUE at high levels. Then, the stomatal closure with elevating  $CO_2$  may have a limiting effect on  $CO_2$  transfer into leaves. However, according to the calculation introduced by Farquhar and Sharkey<sup>10)</sup>, the stomatal limitation of CER at  $500 \mu\text{mol mol}^{-1}$   $C_a$  (CER at  $500 \mu\text{mol mol}^{-1}$   $C_i$  required for the calculation was obtained by the extrapolation) in all the plants used here was rather low (ranged 4%–20%) and there was no clear effect of temperature nor specific difference between  $C_3$  and  $C_4$ .

As the  $C_a$  increased, the  $C_i$  increased in a similar manner but the regression was different between  $C_3$  and  $C_4$  crop plants (Fig. 3). At the same  $C_a$  with that of  $C_3$  plants, the  $C_4$  plants had higher CER at higher temperatures in spite of the lower  $C_i$ . This could be achieved under a little stomatal limitation coupled with the efficient  $CO_2$  concentrating mechanism in the mesophyll-bundle sheath system<sup>8)</sup>.

Crop plants examined in this experiment were grown at  $28/23^\circ\text{C}$  and the temperature effect on  $CO_2$  dependence of CER and E was a sort of extrapolation. However, the present results partly account for the pronounced dry matter production in  $C_4$  crop plants<sup>5,15,25)</sup> as well as the water use at high  $CO_2$  and high temperature conditions.

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#### References

1. Akita, S. and I. Tanaka 1973. Studies on the mechanism of differences in photosynthesis among species. IV. The differential response in dry matter production between  $C_3$  and  $C_4$  species to atmospheric carbon dioxide enrichment. *Proc. Crop Sci. Soc. Japan* 42: 288–295.
2. Allen, S.G., S.B. Idso and B.A. Kimball 1990. Interactive effects of  $CO_2$  and environment on net photosynthesis of water-lily. *Agric. Ecosyst. Environ.* 30: 81–88.
3. Azcón-Bieto, J. 1986. The control of photosynthetic gas exchange by assimilate accumulation in wheat. In *Biological Control of Photosynthesis*. (Eds.) R. Marcelle, H. Clijsters and M. Van Poucke, Martinus Nijhoff Publishers, Dordrecht. 231–240.
4. Baker, J.T., L.H. Allen, Jr., K.J. Boote, P. Jones and J.W. Jones 1989. Response of soybean to air temperature and carbon dioxide concentration. *Crop Sci.* 29: 98–105.
5. Bazzaz, F.A., K. Garbutt, E.G. Reekie and W.E. Williams 1989. Using growth analysis to interpret competition between a  $C_3$  and a  $C_4$  annual under ambient and elevated  $CO_2$ . *Oecologia* 79: 223–235.
6. Bolin, B., J. Jager and B.R. Doos 1986. The greenhouse effect, climatic change, and ecosystems. A synthesis of present knowledge. In *The Greenhouse Effect, Climatic Change, and Ecosystems*, SCOPE 29. (Eds.) B. Bolin, B.R. Doos, J. Jager and R.A. Warrick, John Wiley and Sons, Chichester. 1–32.
7. Carlson, R.W. and F.A. Bazzaz 1982. Photosynthetic and growth response to fumigation with  $SO_2$  at elevated  $CO_2$  for  $C_3$  and  $C_4$  plants. *Oecologia* 54: 50–54.
8. Edwards, G.E., M.S.B. Ku and R.K. Monson 1985.  $C_4$  photosynthesis and its regulation. In *Photosynthetic Mechanism and the Environment*. (Eds.) J. Barber and N.R. Baker, Elsevier Science Publishers, Amsterdam. 287–327.
9. Enoch, H.Z. and R.G. Hurd 1977. Effect of light intensity, carbon dioxide concentration, and leaf temperature on gas exchange of spray carnation plants. *J. Exp. Bot.* 28: 84–95.
10. Farquhar, G.D. and T.D. Sharkey 1982. Stomatal conductance and photosynthesis. *Ann. Rev. Plant Physiol.* 33: 317–345.

11. Hellmuth, E.O. 1971. The effect of varying air-CO<sub>2</sub> level, leaf temperature, and illuminance on the CO<sub>2</sub> exchange of the dwarf pea, *Pisum sativum* L. var. Meteorol. Photosynthetica 5 : 190—194.
12. Hofstra, G. and J.D. Hesketh 1975. The effect of temperature and CO<sub>2</sub> enrichment on photosynthesis in soybean. In Environmental and Biological Control of Photosynthesis. (Ed.) R. Marcelle, Dr. W. Junk b.v., Publishers, The Hague. 71—80.
13. Imai, K. and Y. Murata 1978. Effect of carbon dioxide concentration on growth and dry matter production of crop plants. IV. After-effect of carbon dioxide-treatments on the apparent photosynthesis, dark respiration and dry matter production. Japan. Jour. Crop Sci. 47 : 330—335\*.
14. ——— and ——— 1978. ———. V. Analysis of after-effect of carbon dioxide-treatment on apparent photosynthesis. Japan. Jour. Crop Sci. 47 : 587—595.
15. ——— and ——— 1979. ———. VII. Influence of light intensity and temperature on the effect of carbon dioxide-enrichment in some C<sub>3</sub>- and C<sub>4</sub>-species. Japan. Jour. Crop Sci. 48 : 409—417.
16. ———, F. Ogura and Y. Murata 1982. Photosynthesis and respiration of papaya (*Carica papaya* L.) leaves. Acta Oecol./Oecol. Plant. 3 : 399—407.
17. ——— and D.F. Coleman 1983. Elevated atmospheric partial pressure of carbon dioxide and dry matter production of konjak (*Amorphophallus konjac* K. Koch). Photosynthesis Res. 4 : 331—336.
18. ———, ——— and T. Yanagisawa 1984. Elevated atmospheric partial pressure of carbon dioxide and dry matter production of cassava (*Manihot esculenta* Crantz). Japan. Jour. Crop Sci. 53 : 479—485.
19. ———, ——— and ——— 1985. Increase in atmospheric partial pressure of carbon dioxide and growth and yield of rice (*Oryza sativa* L.). Japan. Jour. Crop Sci. 54 : 413—418.
20. ——— 1988. Carbon dioxide and crop production. Japan. Jour. Crop Sci. 57 : 380—391\*\*.
21. Ishihara, K. and K. Saito 1987. Diurnal courses of photosynthesis, transpiration, and diffusive conductance in the single-leaf of the rice plants grown in the paddy field under submerged condition. Japan. Jour. Crop Sci. 56 : 8—17\*.
22. Kimball, S.A. 1983. Carbon dioxide and agricultural yield : An assemblage and analysis of 430 prior observations. Agron. J. 75 : 779—788.
23. Larcher, W. 1980. Physiological Plant Ecology, 2nd ed. Springer, Berlin-Heidelberg-New York. 112—117.
24. Morison, J.I.L. and R.M. Gifford 1983. Stomatal sensitivity to carbon dioxide and humidity. A comparison of two C<sub>3</sub> and two C<sub>4</sub> grass species. Plant Physiol. 71 : 789—796.
25. Potvin, C. and B.R. Strain 1985. Effects of CO<sub>2</sub> enrichment and temperature on growth in two C<sub>4</sub> weeds, *Echinochloa crusgalli* and *Eleusine indica*. Can. J. Bot. 63 : 1495—1499.
26. Rogers, H.H., G.E. Bingham, J.D. Cure, J.M. Smith and K.A. Surano 1983. Responses of selected plant species to elevated carbon dioxide in the field. J. Environ. Qual. 12 : 596—574.
27. Sionit, N., B.R. Strain and H.A. Beckford 1981. Environmental controls on the growth and yield of okra. I. Effects of temperature and of CO<sub>2</sub> enrichment at cool temperatures. Crop Sci. 21 : 885—888.
28. ——— and D.T. Patterson 1984. Response of C<sub>4</sub> grasses to atmospheric CO<sub>2</sub> enrichment. I. Effect of irradiance. Oecologia 65 : 30—34.
29. Warrick, R.A., R.M. Gifford and M.L. Parry 1986. CO<sub>2</sub>, climatic change and agriculture. In The Greenhouse Effect, Climatic Change, and Ecosystems. SCOPE 29. (Eds.) B. Bolin, B.R. Doos, J. Jager and R.A. Warrick, John Wiley and Sons, Chichester. 393—473.
30. Wong, S.C., I.R. Cowan and G.D. Farquhar 1978. Leaf conductance in relation to assimilation in *Eucalyptus pauciflora* Sieb. ex Spreng : Influence of irradiance and partial pressure of carbon dioxide. Plant Physiol. 62 : 670—674.

\* Japanese with English summary.

\*\* Japanese only.