Elevated Atmospheric Partial Pressure of Carbon Dioxide and Dry Matter Production of Cassava (*Manihot esculenta* Crantz)*

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The global increase in partial pressure of carbon dioxide (CO_2), about $1 \mu\text{bar}$ per year, is well recognized (now greater than $340 \mu\text{bar}$)^{3,17}. Further increases are inevitable as long as we continue to use organic fuels (petroleum, coal, wood, etc.) and clear vegetation without developing alternative energy sources or providing appropriate sinks for CO_2 by reestablishing forests on a large scale. The increase may induce changes of climate, e.g. a rise in mean surface temperature of the earth (greenhouse effect)¹⁷, which may have adverse effects on agricultural systems and natural vegetation^{3,15}.

While the effects of CO_2 on climate are uncertain, it is well known that the enrichment of CO_2 of the ambient air promotes growth and yield of many C_3 species^{3,12,14} even if they grow under some water shortage⁷, although other factors such as nutrient deficiency may reduce the positive effect^{8,16,18}. Within limits, the temperature optimum for photosynthesis increases with increasing partial pressure of CO_2 ⁵. Because higher temperatures have been predicted for a future high CO_2 environment, we are interested in the combined effects of high CO_2 and high temperature on photosynthesis and production processes of crop plants^{10,12}.

In this paper we showed some results for cassava, a tropical root crop. Because cassava grows vigorously at high temperature and

has a relatively simple source-sink relationship¹¹, we expected that doubling CO_2 partial pressure coupled with a high temperature would promote its dry matter production through increasing net CO_2 assimilation as had been observed for konjak plants¹².

Materials and Methods

Growth experiments

Experiment 1 : On 1 August 1981, scions of cassava (*Manihot esculenta* Crantz cv. Izu-kei), of about 11 g of fresh weight and 10cm in length, were planted singly in 1/2,000are Wagner pots containing 12kg of soil and 10g of compound chemical fertilizer. They were placed outdoors in light shade. On 20 August, when plants had five expanded leaves, they were transferred to glasshouses, at the Center of Environment Regulation System for Biology (CERES) of the University of Tokyo, and the combined treatments of CO_2 and temperature were applied. As the air sampled from 8m high at CERES contained 350 to 360 μbar CO_2 on average (KANDA and IMAI, unpublished) we chose partial pressures of CO_2 in the glasshouses at 350 (control) and 700 ($2 \times$ control) μbar and maintained the levels continuously with CO_2 -controllers (Fuji, ZFP-6, Tokyo). Air temperature was set at 28°C 12h-day/ 21°C 12h-night. A third group of plants was maintained at 700 μbar CO_2 and $33/26^\circ\text{C}$. Saturation deficits for water vapour were kept at about 20 mbar during the day and 14 mbar at night. The plants had additional

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Table 1 Plant characters of cassava grown under different CO₂ and day/night-temperature regimes (1981).

Items	350 μ bar CO ₂ 28/21°C	700 μ bar CO ₂ 28/21°C	700 μ bar CO ₂ 33/26°C
Stem length (cm)	52.4 a	71.9 b	126.0 c
Number of leaves	22.0 a	23.5 a	46.6 b
Leaf area (cm ²)	2,140.0 a	2,520.1 a	7,083.4 b
Number of thick roots	3.4 a	5.5 b	6.4 b
Dry weight (g)			
Leaf blade	8.11 a	10.68 b	26.74 c
Petiole	2.37 a	2.71 a	9.42 b
Stem	5.56 a	8.71 b	35.63 c
Old scion	6.96 a	8.02 b	11.25 c
Root	5.32 a	13.38 b	44.75 c
Whole plant	28.32 a	43.50 b	127.79 c
Top/root ratio	4.32 c	2.25 b	1.86 a

- 1) Treatments were applied from 20 August to 19 November.
- 2) Values are expressed as per plant basis.
- 3) Several dead leaves were not recovered at harvest.
- 4) Thick roots are those larger than 5 mm in diameter.
- 5) In each row figures followed by a different letter are significantly different ($p = 0.05$).

fertilizer (5g per plant on 1 and 29 October) and were well-watered. All the plants grew with little mutual shading and without branching. On 19 November, three months from the start of treatments, eight plants were harvested, sorted into leaf blade, petiole, stem, old scion (which was planted on 1 August) and root fractions, and then oven dried at 85°C for three days and weighed.

Experiment 2: On 29 May 1982, plants of similar size to those used in 1981 were potted and on 15 June, when they had three expanded leaves, CO₂ treatments (350 vs 700 μ bar) were applied. Day/night temperatures were 33/26°C and saturation deficits were 20/14 mbar. On 24 July, plants had additional fertilizer (5 g per plant) and on 17 August, two months from the start of treatments, eight plants were harvested, oven dried and weighed.

The average solar radiation outside the glasshouses during treatments in 1981 and 1982 was 11.2 and 13.4 MJ m⁻² day⁻¹, respectively (data from the Tokyo Meteorological Observatory near the university). The average transmittance of light into the glasshouses was about 60%.

Measurements of gas-exchange characteristics

During the CO₂ treatments in 1982, CO₂ and water vapour exchanges of attached, fully expanded leaves were measured as a function of partial pressure of CO₂ using a semi-closed gas-exchange measurement system (Koito, KMC-1000-K001, Yokohama)¹³⁾. The data processing part of the system was used to calculate stomatal and mesophyll conductances. A photon flux density of 650 μ E m⁻² sec⁻¹ (400–700 nm) was supplied by metal halide lamps (Toshiba, Yōkō Lamp DR-400, Tokyo). Leaf temperature was kept at 33°C and monitored with a fine chromel-almel thermocouple pressed to the lower leaf surface. Vapour pressure difference between leaf and air was 20 mbar and wind velocity was 1.70 m sec⁻¹.

Results

Plant growth

Table 1 shows the effects of CO₂ and temperature. At 28/21°C, the stem length and number of thick roots (larger than 5 mm in diameter) increased when CO₂ was doubled, but neither the number of attached leaves (with blades longer than 1 cm) nor

Table 2 Plant characters of cassava grown under different CO₂ at 33/26°C, day/night-temperature (1982).

Items	350 μ bar CO ₂	700 μ bar CO ₂
Stem length (cm)	80.9	128.3
Number of leaves	31.8	36.9
Leaf area (cm ²)	5,155.1	8,644.6
Number of thick roots	4.6	12.5
Dry weight (g)		
Leaf blade	14.89	29.28
Petiole	4.97	11.88
Stem	9.04	27.97
Old scion	4.19	9.14
Root	5.59	18.59
Whole plant	38.68	96.86
Top/root ratio	5.92	4.21

- 1) Treatments were applied from 15 June to 17 August.
- 2) Values are expressed as per plant basis.
- 3) Thick roots are those larger than 5 mm in diameter.
- 4) All the differences between treatments are significant ($p = 0.001$).

leaf area was significantly different from the controls. A combination of high CO₂ and high temperature (33/26°C) increased shoot growth considerably but there was little effect on the number of thick roots.

At 33/26°C (Table 2), the promotive effect of doubling the CO₂ on growth, especially on the number of thick roots, was bigger than at 28/21°C (Table 1).

Table 3 shows values for length, area and specific weight of leaves at several nodes. For leaves at the same position, those developed in high CO₂ were larger and thicker than the control.

Dry matter production

At 28/21°C (Table 1), the relative shoot dry weight was increased slightly by doubling the CO₂ for three months but dry weight of roots more than doubled that of the controls. Cassava plants accumulated dry matter vigorously at the high temperature and high CO₂. The enhancement of total dry matter at high CO₂ was 54% at 28/21°C (in three months, Table 1) and 150% at 33/26°C (in two months, Table 2). Top (=shoot)/root ratio was reduced by doubling the CO₂ but the decline was smaller at the high temperature (1982) because of more active shoot

growth. In 1982 (two months' growth), the higher solar radiation might have accelerated the dry matter production of shoot (Table 2) when compared with plants of three months' growth in 1981 (Table 1).

Gas-exchange characteristics

During the early stage of growth (30 days), leaves developed at normal and high CO₂ showed similar responses of net CO₂ assimilation, transpiration, stomatal and mesophyll conductance to changing ambient partial pressure of CO₂ except in the lower CO₂ range (Fig. 1A). About 55 days from the start of treatments the capacity of the youngest, fully expanded leaves of high CO₂ grown plants to fix CO₂ declined. This was associated with a decline in stomatal conductance (Fig. 1B). From Figs. 1A,B, we calculated the water use efficiency (ratio of photosynthesis to transpiration) of leaves, giving ranges of 3.3–4.5 and 10.5–17.1 mg CO₂/g H₂O for those developed and measured at 350 and 700 μ bar CO₂, respectively.

Discussion

Recently KIMBALL¹⁴⁾ examined more than 430 prior observations on CO₂-enrichment

Table 3 Leaf characters of cassava developed under different partial pressure of CO₂ at 33/26°C, day/night-temperature (1982).

Leaf position	CO ₂ treatment (μ bar)	Leaf area (cm ²)	Length of:		Dry weight of:		Specific leaf weight (mg/cm ²)
			Leaf blade (cm)	Petiole	Leaf blade (mg)	Petiole	
8	350	310.1	17.8	26.2	896	282	2.89
	700	357.3	19.3	31.0	1,206	539	3.38
9	350	287.7	17.4	27.6	864	286	3.00
	700	351.8	19.0	32.0	1,244	543	3.54
10	350	261.8	16.8	26.8	798	262	3.05
	700	380.6	19.6	33.5	1,342	568	3.53
11	350	246.8	16.6	27.0	774	259	3.14
	700	391.9	19.9	34.3	1,387	579	3.54

- 1) The first leaf is that with a leaf blade about 1 cm long, which is 10th or 11th from the growing point.
- 2) All the differences between treatments, except that for the area of 8th leaf, are significant ($p = 0.01$).

and found that the average increase of yield by doubling the CO₂ was about 33%. We found little data on crops harvested for underground organs. Growth at high CO₂ increased yield by about 50% in sugar-beet⁶⁾, 75% in potato²⁾ and 100% in konjak¹²⁾. Cassava grew vigorously under the condition of high CO₂ and high temperature as we had expected. Doubling the CO₂ partial pressure increased the total dry matter of cassava by 150% at most, although this may depend on the duration of growth. Judging from comparative data available so far, the yield of crops harvested for underground organs, including cassava, at high CO₂ exceeds the average for cereals and other agricultural crops¹⁴⁾, possibly because of their relatively simple storage forms of carbohydrates and continuing vegetative growth.

Increase in the number of leaves was associated with increasing temperature (cf. IMAI et al.¹¹⁾) rather than increasing CO₂ partial pressure, but that of thick roots, though we could not distinguish whether they actually became storage roots, was associated with CO₂ possibly because of the increased photosynthate supply (Tables 1 and 2).

The notable result in the current experiments was the decline of the top/root ratio at high CO₂ irrespective of temperature. This resulted from greater partitioning of dry matter to the root fraction than that to the

leaf and stem fractions, and led to a larger Harvest Index (the weight of yield relative to that of whole plant) as found in other crops^{7,12)}.

During the CO₂ treatments, the gas-exchange characteristics of the youngest, fully expanded leaves were modified (Fig.1). Similar responses have been shown for *Nerium*⁴⁾, rice⁹⁾, maize^{9,18)} and cotton¹⁸⁾. We found a large decline in stomatal conductance of leaves from plants grown for 55 days at 700 μ bar CO₂ (Fig. 1B). As the leaves on plants (30-day-treatment, Fig. 1A) were active, except in the lower CO₂ range, and showed no evidence of having developed a decrease in mesophyll conductance during growth in high CO₂, the decline of net CO₂ assimilation in leaves of older plants (55-day-treatment, Fig-1B) can be attributed mainly to the closure of stomata. IMAI and MURATA⁹⁾ concluded, from plots of resistances against intercellular partial pressure of CO₂, that the relative decline of photosynthetic capacity of rice leaves, developed at higher than normal CO₂, was due to increased sensitivity of stomatal resistance (reciprocal of conductance) to CO₂ rather than an increase in mesophyll resistance. Nevertheless, several other factors may have contributed to the observed decline of net CO₂ assimilation in cassava. It is possible that a decline in ribulose-1,5-bisphosphate carboxylase activity induced an increase in the intercellular

Fig. 1 Effects of ambient partial pressure of CO_2 on gas exchange characteristics of cassava leaves obtained from plants grown for 30 (A) and 55 (B) days at 350 ($\circ\Delta\Box$) and 700 ($\bullet\blacktriangle\blacksquare$) μbar CO_2 .

CO_2 which brought about the closure of stomata^{4,18}). On the other hand, AZCÓN-BIETO¹⁾ examined wheat leaves and suggested that the decline of photosynthetic rate of leaves exposed to high CO_2 for a long time was due to the accumulation of carbohydrates in the leaves. Both the bigger specific weight (Table 3) and higher carbon contents (unpublished) of leaves developed at high CO_2 in our sample might support the above observations.

The limited volume of soil might have affected the production processes, especially of the bigger plants, in our experiments. For example, part of the decline in net CO_2 assimilation may have been due to a reduction in demand following root restriction, or

to a reduced supply of nutrients to the leaves. These factors remain to be solved.

Doubling the CO_2 increased the water use efficiency^{7,15)} of cassava irrespective of the duration of treatments, because the decline of transpiration was larger than that of net CO_2 assimilation.

In short, the elevated atmospheric partial pressure of CO_2 promotes the dry matter production of cassava plants considerably and especially stimulates root development. However, the degree of promotion may decrease with time due to the partial suppression of photosynthetic rates.

Summary

Cassava plants were grown for two or three

months in glasshouses at 350 (control) and 700 μ bar CO₂, and the growth attributes and gas-exchange characteristics were compared.

High CO₂ increased total dry matter production by 54% of the control at 28/21°C (three months' growth) and by 150% at 33/26°C (two months' growth). The high CO₂ grown plants had bigger leaves but lower top/root ratios.

Gas-exchange characteristics of both the control and high CO₂ plants were similar at 30 days but the rate of net CO₂ assimilation declined after 55 days of growth at high CO₂. The decline was associated with a decrease in stomatal conductance. Irrespective of the duration of CO₂-treatments, leaves from the high CO₂ plants had higher water use efficiency than those from the controls.

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〔和 文 摘 要〕

大気中二酸化炭素分圧の上昇とキャッサバの乾物生産

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将来予想される大気中の二酸化炭素 (CO₂) 分圧の上昇がキャッサバの生産過程に与える影響を知る一助として本研究を行った。自然光ファイトロンを用いて、1/2000 アールポットに土耕した材料を、3 か月 (1981 年) 及び 2 か月 (1982 年) 間 350, 700 μ bar CO₂ 下で栽培し、乾物生産を比較した。また CO₂ 処理 30, 55 日目に葉の CO₂—光合成特性を測定した。

1981 年は気温が 28/21℃ の場合 700 μ bar CO₂ により全乾物重が 350 μ bar CO₂ 区の 54% 増加した。1982 年は 33/26℃ で行い、150% の増加をみた。地上部/地下部比は温度に拘らず高 CO₂ により低下した。光合成特性は 30 日目では処理間の差が小さかった。55 日目では高 CO₂ 区の見かけの光合成速度の低下がみられ、気孔コンダクタンスの低下と並行していた。しかしながら、光合成と蒸散の比から求めた水利用率は常に高 CO₂ 区の方が高かった。