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Effects of Long term Exposure to Atmospheric Carbon Dioxide Enrichment on Flowering and Podding in Soybean

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It is known that increasing atmospheric carbon dioxide (CO₂) concentration resulted in the enhancement of vegetative growth and an increase in seed yield in Soybean (*Glycine max* (L.) Merrill). However, the way this increase in seed yield comes about is not well known. The objective of this study was to make clear the effects of CO₂ enrichment on flowering and podding, since these are the factors which directly limit the seed yield in soybean. Cultivar 'Fukuyutaka' were grown in the ambient CO₂ concentration (AC: 350 μ mol CO₂ mol⁻¹ Air) and an enriched CO₂ concentration (EC: 700 μ mol CO₂ mol⁻¹ Air) throughout the growth period. The effects of EC on the flowering were significantly different among the individual racemes. On the terminal racemes and the primary racemes, there was no difference in the total number of flowers between AC and EC, although the number of flowers at the peak of flowering differed slightly with the CO₂ regime used. On the secondary racemes with compound leaves, EC condition increased the number of flowers compared with AC. The opposite effect was seen on the secondary racemes without compound leaves. Furthermore, large number of flowers on the tertiary racemes appeared in EC throughout the flowering period. The number of pods and the pod-setting ratio in EC condition on the secondary racemes, the secondary racemes with compound leaves and the tertiary racemes were larger than those in AC condition. Therefore, enrichment of CO₂ increased seed yield because of the increase in the number of flowers and the high pod-setting ratio on the high order racemes (the secondary racemes, the secondary racemes with compound leaves and the tertiary racemes), which appeared at later time during the flowering period.

INTRODUCTION

Since the Industrial Revolution, atmospheric carbon dioxide (CO₂) concentration has been increasing. This increase is almost certainly due mainly to the continued burning of fossil fuels. According to the IPCC (1995), the atmospheric CO₂ concentration is predicted to double by the end of this century. The steady increasing level of CO₂ is expected to enhance plant growth and to increase seed yield in grain crops. Kimball (1983) reported that vegetative growth was enhanced significantly by doubling the atmospheric CO₂ concentration. Longer term experiments have generally shown that

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enriched CO₂ concentration have brought about high photosynthetic rates, rapid rates of biomass accumulation, and therefore high yields (Kimball, 1983; Zelitch, 1982). However, the morphological developmental process by which this increase in seed yield come about is not well known.

Flower and pod shedding are the limiting factors for seed yield in soybean. This might be because of the overlap of vegetative and reproductive growth, namely nutrient competition between both growths. Therefore, an investigation of the number of flowers and the pod-setting ratio on individual raceme orders is considered to be an effective way of estimating the effect of enhanced CO₂ concentration (EC) on seed yield in soybean. Some preliminary data on planting date and planting density illustrated that the total number of flowers and the change in the number of flowers opening each day on each raceme order also different among cultivars (Kuroda *et al.*, 1992; Fujita, 1995).

The objective of this study was to determine the effects of CO₂ enrichment on flowering and podding, in order to clarify whether and how could CO₂ enrichment increase the seed yield in soybean.

MATERIALS AND METHODS

Soybean (*Glycine max* (L.) Merrill cv. Fukuyutaka, maturity type IVc) seeds were inoculated with *Bradyrhizobium japonicum* and planted in plastic pots (20 cm diameter by 20 cm in height) filled with fine sand on 19 July, 2000 in the institute of Agricultural Electrification Testing Center of Kyushu Electric Power Co., Inc. at Saga (Long. 130° 34' E, Lat. 33° 27' N). After emergence, plants were moved into the natural light growth chambers where the CO₂ concentrations were maintained at 350 µmol CO₂ mol⁻¹ Air (Ambient CO₂ concentration (AC)) and 700 µmol CO₂ mol⁻¹ Air (enriched CO₂ concentration (EC)). Day/night air temperatures were controlled at about 28/22 °C, except at 25 °C for 2 hours during sunrise (from 7:00 to 9:00) and sunset (from 18:00 to 20:00). Nutrient solution (Table 1) was given every day for 5 minutes at 9:00 and 14:00 by an automatic watering system. After flowering started on 26 August, the date and raceme position of flowers that had opened that day were recorded in both treatments every 2 days on a small label 8 mm in width and 21 mm in length. The labels were then wrapped around the pedicel of

Table 1. Composition of nutrient solution

Nutrient	Concentration (ppm)
N	88.5
P ₂ O ₅	69.0
K ₂ O	110.3
CaO	89.7
MgO	35.2
Fe	2.90
Zn	0.04
Cu	0.02
B	1.00
Mo	0.02
Mn	1.00

flowers. Flowers were distinguished at each node and each raceme order according to Torigoe et al (1982) as follows,

Terminal racemes – formed at the top of main stem and branches.

Primary racemes – formed at the leaf axils of main stem and branches directly.

Secondary racemes – formed at both sides of the primary racemes axils.

Secondary racemes with compound leaves – formed at the same position as the secondary racemes with a few nodes like branches.

Tertiary racemes – formed at both sides of the secondary racemes and the secondary racemes with compound leaves. The racemes which start flowering after the tertiary racemes were included as the tertiary raceme.

The investigation continued until 23 September when the flowering was almost finished. Matured plants were harvested on 17 November. The vegetative growth, yield components and seed yield were measured after being dried naturally in a room. Six plants were investigated in each chamber.

RESULTS

Fig. 1 shows the change in the total number of flowers affected by CO₂ enrichment. From 0 to 16 days after flowering (DAF), the change in the number of flowers opening daily under enriched CO₂ concentration (EC) was almost the same as that under ambient CO₂ concentration (AC). However, from 16 DAF, more flowers opened under EC condition. By the end of flowering therefore, the total number of flowers in EC were significantly greater than that in AC at the end of flowering.

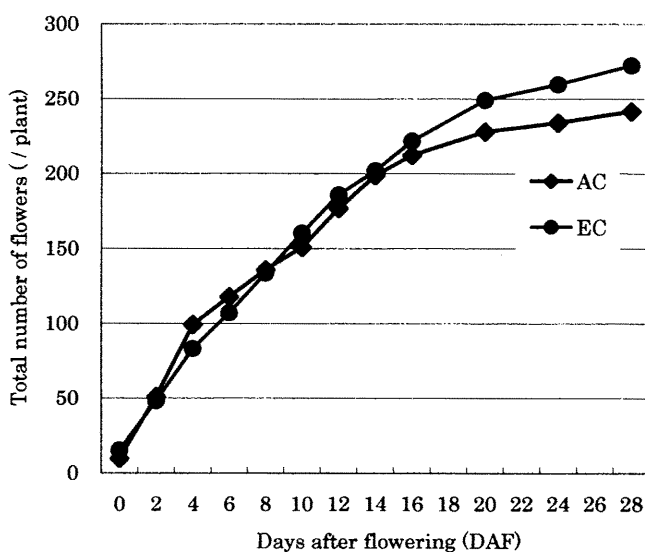


Fig. 1. Changes in flowering pattern of the total number of flowers
AC: 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ EC: 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$

Fig. 2 shows the change in the number of daily opened flowers on individual order racemes. In both EC and AC, the flowering started on the primary racemes. It was followed by the terminal racemes after 2 days, the secondary raceme with compound leaves after 6 days, the secondary racemes after 8 days, and finally the tertiary racemes after 14 days. The peaks in the number of daily opened flowers on the primary and the terminal racemes were broad in EC but sharp in AC. Under EC condition, there was a slight decrease in the number of flowers opening each day on the secondary racemes, and an increase on the secondary racemes with compound leaves. On the tertiary racemes, the number of flowers opening each day was always greater in EC than in AC.

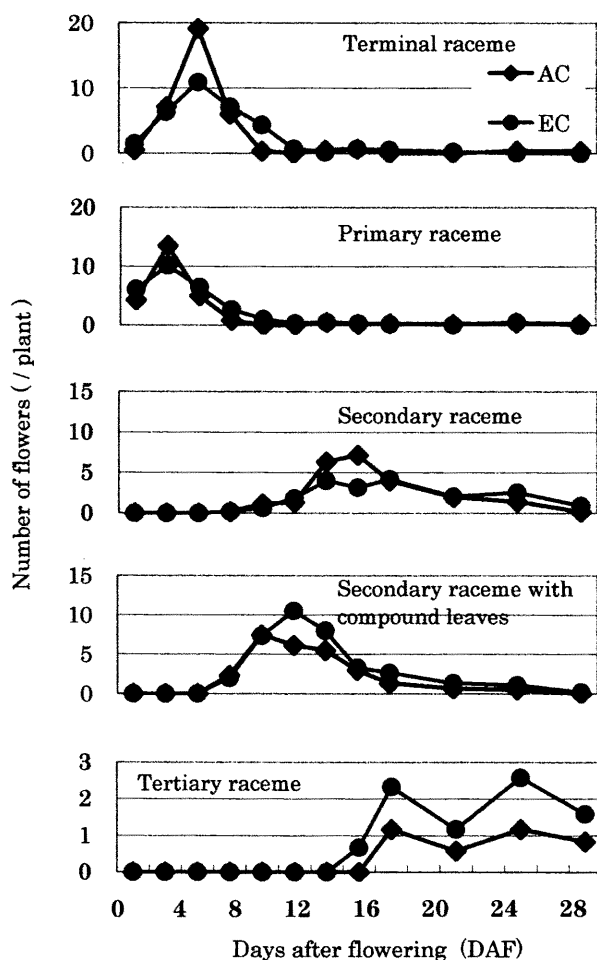


Fig. 2. Changes in flowering pattern of the number of daily flowers on the individual racemes.

AC: 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ EC: 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$

The number of flowers, pods and pod-setting ratio on the individual raceme orders are shown on Table 2. There were no significant differences in the number of flowers on the primary and the terminal racemes between AC and EC. In EC, there were less flowers on the secondary racemes and significantly more on the secondary racemes with compound leaves and the tertiary racemes. Therefore, the increase in the total number of flowers in EC was contributed by the increase in the number of flowers on the high order racemes (consisting of the secondary racemes, the secondary racemes with compound leaves and the tertiary racemes). The number of pods on the terminal and the primary

Table 2. Effects of CO₂ enrichment on the number of flowers, pods and pod-setting ratio on individual racemes per plant in 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (AC) and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (EC) after harvest

	350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (AC)				700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (EC)			
	number of flowers	number of pods	PR*(%)		number of flowers	number of pods	PR(%)	
terminal raceme	73.3 \pm 5.51 (29.8)	45.7 \pm 6.03 (24.0)	62.3		69.7 \pm 9.07 (23.7)	27.7 \pm 11.80 (13.2)	39.7	
primary raceme	52.3 \pm 3.51 (21.3)	45.3 \pm 4.62 (23.8)	86.6		52.7 \pm 7.09 (17.9)	28.0 \pm 11.85 (13.3)	53.2	
secondary raceme	55.7 \pm 3.21 (22.7)	47.0 \pm 4.58 (24.6)	84.4		44.0 \pm 7.21 (14.9)	40.0 \pm 4.00 (19.1)	90.9	
secondary raceme with compound leaves	47.3 \pm 5.69 (19.2)	41.3 \pm 6.66 (21.7)	87.3		81.7 \pm 4.73 (27.7)	75.0 \pm 9.64 (35.8)	91.8	
tertiary raceme	17.3 \pm 8.62 (7.0)	11.3 \pm 5.51 (5.9)	65.4		46.7 \pm 20.53(15.8)	39.0 \pm 23.07 (18.6)	83.6	
lower order raceme	125.7 \pm 4.73 (51.1)	91.0 \pm 7.94 (47.7)	72.4		122.3 \pm 15.00(41.5)	55.7 \pm 19.22 (26.6)	45.5	
high order raceme	120.3 \pm 7.23 (48.9)	99.7 \pm 5.51 (52.3)	82.8		172.3 \pm 22.81(58.5)	154.0 \pm 26.21 (73.4)	89.4	
total	246.0 \pm 3.0 (100.0)	190.7 \pm 12.50(100.0)	77.5		294.7 \pm 9.45(100.0)	209.7 \pm 25.02(100.0)	71.2	

*: Pod-setting ratio

Values in () are relative values in the each raceme orders of the total. (n=3).

The lower order racemes include the terminal and the primary racemes.

The high order racemes include the secondary, the secondary with compound leaves and the tertiary racemes.

Table 3. Vegetative growth, yield components and yield per plant in both treatments after harvest

	350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (AC)	700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (EC)
Main stem length (cm)	70.7 \pm 4.1 (100)	69.8 \pm 4.4 (98.8)
Number of nodes on main	13.5 \pm 0.8 (100)	13.8 \pm 0.4 (102.5)
Total number of nodes	69.8 \pm 7.1 (100)	82.0 \pm 10.4 (117.4)
Number of branches	11.2 \pm 1.3 (100)	12.0 \pm 2.5 (107.5)
Number of filled pods	168.7 \pm 25.9 (100)	192.5 \pm 34.3 (114.1)
Number of filled seeds	323.7 \pm 27.1 (100)	351.8 \pm 76.4 (108.7)
Stem dry weight (g)	19.6 \pm 4.5 (100)	25.3 \pm 6.0 (129.1)
Seeds yield (g)	101.9 \pm 19.6 (100)	114.9 \pm 29.6 (112.8)
Weight per 100 seed (g)	31.3 \pm 3.8 (100)	32.5 \pm 2.7 (104.1)

Values in () are relative values as against AC. (n=6).

racemes were smaller in EC than in AC, while the number on the secondary racemes in EC was almost the same as in AC. On the secondary racemes with compound leaves and the tertiary racemes were greater in EC than in AC. Hence, the pod-setting ratio under EC was lower on the terminal and the primary racemes but was higher on the other racemes compared with those in AC.

Vegetative growth, yield components and seed yield after harvest are shown in Table 3. Significant increases were observed in the total number of nodes, stem dry weight, the number of matured pods and seeds in EC. As a result, seed yield per plant was about 13% higher in EC than in AC, but there was no significant difference in seed size between AC and EC. Therefore, CO₂ enrichment increased the number of matured pods by increasing the number of flowers and causing a high pod-setting ratio on the high order racemes compared with those in AC.

DISCUSSION

It was revealed in this study that enriched of CO₂ increased seed yield because of the increase in the number of flowers and the high pod-setting ratio on the high order racemes (the secondary racemes, the secondary racemes with compound leaves and the tertiary racemes), which appeared at later time in the flowering period. An increase of 30% in stem dry weight and 13% in seed weight with CO₂ enrichment seemed to be lower than that reported by Allen *et al* (1987). One major factor could be the approximately 40% shading by two layers of vinyl in the roof of our chambers, so that the vegetative growth was not too much affected by EC.

The remarkable result of this study is that CO₂ enrichment caused a low pod-setting ratio on lower order raceme (the terminal and the primary racemes). Yoshida *et al* (1983) classified flowers by DAF and found that the flowers which opened from 0 to 10 DAF in determinate type and from 0 to 15 DAF in inter- or indeterminate types are important for pod set and seed yield. Moreover, it was also important for seed yield to maintain high pod-setting ratio on the lower order racemes (Isobe *et al*, 1995; Yoshida *et al*, 1983). In this study, the pod-setting ratio derived from the lower order racemes was 46% in EC, which is relatively lower than any other reports (Fujita, 1995; Kuroda *et al*, 1992; Yoshida *et al*, 1983). Those results could be caused by either the difference in cultivar, or the distributive competition of assimilates between vegetative and reproductive organs. However, further experiments are needed to clarify this, such as investigating the change in flowering patterns and the number of flowers on the individual raceme orders when plant is exposed to enriched CO₂ during different growth periods.

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