

Effects of Carbon Dioxide Enrichment during Different Growth Periods on Flowering, Pod Set and Seed Yield in Soybean

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Abstract : The objective of this study is to elucidate the effects of CO₂ enrichment during different growth periods on flowering, pod set and seed yield in soybean (*Glycine max* (L.) Merr.). Soybean cultivar 'Fukuyutaka' was grown in a growth chamber of the Institute of Bioresources Research Center of Kyushu Electric Power Co., Inc. at Saga, Japan (33°17'-N, 130°18'-E) under natural light. The CO₂ concentrations were maintained at 350 μmol mol⁻¹ for ambient CO₂ and at 700 μmol mol⁻¹ for CO₂ enrichment. CO₂ concentration was elevated during the whole growth period (WP), vegetative growth period (VP) or reproductive period (RP). Seed yield was increased by CO₂ enrichment during RP or WP due to the increase of pod number, but not by CO₂ enrichment during VP. Although CO₂ enrichment had no effect on the number of flowers, CO₂ enrichment during RP increased the pod number on all raceme orders and that during WP increased the pod number in the secondary and tertiary racemes. It is suggested that an increase of seed yield by CO₂ enrichment is mostly brought by the improvement of pod set, mainly on the high-order racemes that opened later during flowering period, and that the response of seed yield to CO₂ enrichment is mainly attributed to the response during RP.

Key words : CO₂ enrichment, Growth stage, Flowering, Pod set, Raceme order, Soybean.

Since the Industrial Revolution, the concentration of carbon dioxide (CO₂) in the atmosphere has been increasing. This increase is almost certainly due primarily to the continued burning of fossil fuels. According to the Intergovernmental Panel on Climate Change (IPCC, 2001), the atmospheric CO₂ concentration is predicted to double by the end of this century. The steadily increasing level of CO₂ is expected to enhance plant growth and to increase seed yield in grain crops. Long-term experiments have generally shown that an elevated CO₂ concentration (CO₂ enrichment) brings about high yields through high photosynthetic rates and rapid biomass accumulation (Zelitch, 1982; Kimball, 1983).

In soybean, CO₂ enrichment has been reported to increase the photosynthetic rate (Jones et al., 1984; Rogers et al., 1984) and leaf area (Ziska and Bunce, 1995), and therefore the total dry weight (Cooper and Brun, 1967; Allen et al., 1991). These results suggest that the stimulation of vegetative growth by CO₂ enrichment is important for the increase of seed yield. On the other hand, some researchers reported that seed yield was increased by CO₂ enrichment during the reproductive growth period when vegetative growth was almost completed (Hardman and Brun, 1971; Ackerson et al., 1984). Thus, the response of seed yield to CO₂ enrichment is not always

correlated with vegetative parameters. Recently, Ziska et al. (2001) reported that the seed yield response to CO₂ enrichment is associated with plasticity in the ability to set additional pods on branches in a CO₂ enriched environment. However, the morphological developmental process by which this increase in seed yield comes about is not well known.

Abortion of flowers and young pods is an important limiting factor of seed yield in soybean (Van Schaik and Probst, 1958). Although soybean flowers are produced abundantly, a large number of flowers and young pods abscise rather than develop into mature pods. The flowering period varies from 18 to 50 days in soybean, and the seed yield depends on the pods set on various racemes which flowered at different times. Therefore, an investigation of the number of flowers and the pod set on individual raceme orders may be an effective way of estimating the effect of elevated CO₂ concentrations on the seed yield in soybean.

The objective of this study was to determine the effects of CO₂ enrichment during various growth periods on flowering and pod set to clarify whether and how CO₂ enrichment causes an increase in seed yield in soybean.

Materials and Methods

The experiments were conducted at the

Table 1. Composition of nutrient solution.

Nutrient	N	P ₂ O ₅	K ₂ O	CaO	MgO	Fe
Concentration (ppm)	88.5	69.0	110.3	89.7	35.2	2.9
Nutrient	Zn	Cu	B	Mo	Mn	
Concentration (ppm)	0.04	0.02	1.00	0.02	1.00	

The composition was modified based on Matsunaga et al. (1983).

Bioresources Research Center of Kyushu Electric Power Co., Inc. in Saga, Japan (33°17'-N, 130°18'-E). Soybean (*Glycine max* (L.) Merr. cv. Fukuyutaka) seeds were inoculated with *Bradyrhizobium japonicum* (A1018) and planted in plastic pots (20cm in diameter and 21cm in height) filled with fine sand on 19 July, 2000 and 18 July, 2001. After emergence, the plants were moved into the growth chambers under natural light and with CO₂ concentrations maintained at 350 μmol mol⁻¹ (Control) and 700 μmol mol⁻¹ (CO₂ enrichment). The chambers were constructed with steel frames and covered with a layer of plastic film (about 40% shade in 2000, and about 25% shade in 2001 because of the change of film). The day/night air temperature was controlled at about 28/22°C, except for 2 hours at sunrise (from 0700 to 0900) and 2 hours at sunset (from 1800 to 2000), when it was set at 25°C. Nutrient solution (Table 1) was given automatically twice every day at 0900 and 1400 five minutes each, but the concentration of the nutrient was maintained at 50% of the standard until flowering. The CO₂ concentration was elevated through whole growth period (WP, from emergence to maturity) in 2000, but in 2001 during the vegetative growth period (VP, from emergence to the onset of flowering), the reproductive growth period (RP, from flowering to maturity), and WP. Before and after the CO₂ enrichment, the plants were exposed to the same as control. Each treatment consisted of six plants and a half of them were used to record flower number. After the first flower opened, the raceme order of the flowers that had opened that day were recorded every two days. Flowers were distinguished at each node and each raceme order following the method described by Kuroda et al. (1992). The flowers that had been counted were marked by giving a cut injury through into the standard vexillum of the flower. All of the plants were harvested after matured, and the vegetative growth parameters, yield components and seed yield were measured after the plants were dried naturally in a room.

Results

1. Growth parameters and seed yield

Table 2 shows the growth parameters of the plants

Table 2. Influence of CO₂ enrichment during the different growth periods on the vegetative growth parameters after harvest.

Period of CO ₂ enrichment	Length of main stem (cm)	Number of nodes on main stem	Total number of nodes	Dry weight of stem (g)	Dry weight of root (g)
2000					
C	70.7	13.5	69.8	19.6	-
WP	69.8	13.8	82.0	25.3	-
	ns	ns	*	ns	
2001					
(C)	44.0 a	13.7 a	65.2 a	26.8 b	14.7 b
VP	43.6 a	13.2 a	66.2 a	27.7 b	13.6 b
RP	48.3 a	14.0 a	70.2 a	28.5 b	14.4 b
WP	45.3 a	13.5 a	69.5 a	35.7 a	38.6 a

The values are means of 6 plants. * indicated a significant difference, and ns no significant difference at 5% level according to Student's t-test. Treatments followed by the same letter are not significantly different at 5% level according to One-way ANOVA and Bonferroni's multiple range test.

C, Control; WP, whole growth period; VP, vegetative growth period; RP, reproductive growth period.

Table 3. Influence of CO₂ enrichment during the different growth periods on the seed yield and the yield components after harvest.

Period of CO ₂ enrichment	Number of flowers	Number of matured pods	Rate of pod set (%)	Number of matured seeds	100-seed weight (g)	Seed yield (g)
2000						
C	246.0	168.7	77.6	323.7	31.3	101.9
WP	294.7	192.5	71.1	371.6	32.5	114.9
	*	ns	ns	ns	ns	ns
2001						
(C)	285.0 a	170.2 b	64.7 a	307.8 b	44.0 a	135.2 b
VP	231.7 a	161.8 b	70.1 a	290.2 b	45.1 a	130.8 b
RP	268.7 a	210.2 a	76.5 a	384.8 a	43.8 a	168.2 a
WP	253.0 a	210.3 a	77.1 a	393.0 a	43.2 a	169.4 a

The values of the number of flowers and the rate of pod set are means of 3 plants. Other notes are the same as in Table 2.

exposed to elevated CO₂ concentrations at various developmental stages. In 2000, CO₂ enrichment during WP increased the dry weight of the stem and the total number of nodes. In 2001, it significantly increased the dry weights of the stem and root, but did not increase the total number of nodes. CO₂ enrichment during VP or RP had no effect on growth parameters.

In 2000, CO₂ enrichment during WP increased the seed yield per plant about 13%, and it also increased the pod number and seed number by about 12% (Table 3). In 2001, CO₂ enrichment during WP and RP increased seed yield by about 25%, but that during VP had no effect. CO₂ enrichment during WP and

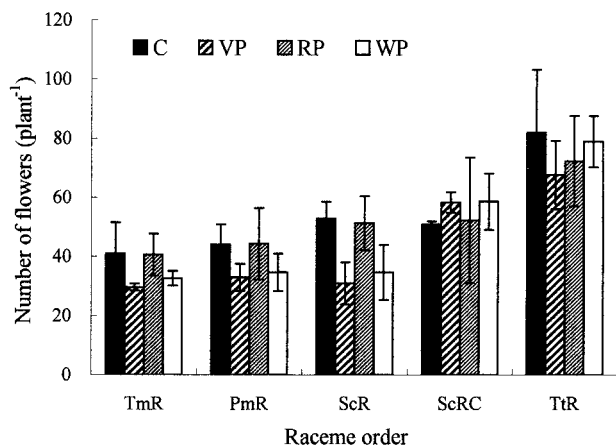


Fig. 1. Number of flowers on each raceme order of the plants exposed to elevated CO₂ concentrations during the different growth periods in 2001. Data are means of 3 plants \pm S.D.

C, Control; VP, CO₂ enrichment during the vegetative growth period; RP, CO₂ enrichment during the reproductive growth period; WP, CO₂ enrichment during the whole growth period.

TmR, terminal raceme; PmR, primary raceme; ScR, secondary raceme; ScRC, secondary raceme with compound leaves; TtR, tertiary raceme.

RP increased the number of matured pods and seeds. However, seed size was unaffected by that during any of the periods (WP, VP or RP). Thus, CO₂ enrichment increased seed yield not by increasing seed size but by increasing the number of matured pods per plant.

2. Flowering and pod set

The number of flowers on each raceme order was not affected by the CO₂ enrichment during any of the periods (Fig. 1). Although CO₂ enrichment during VP and WP slightly decreased the number of flowers on the terminal, primary and secondary racemes, CO₂ enrichment during any periods had no significant effect on the total number of flowers in 2001 (Table 3).

Fig. 2 shows the effects of CO₂ enrichment during different growth periods on the number of pods on the individual raceme order. CO₂ enrichment during RP slightly increased the numbers of matured pods on the terminal, primary and secondary racemes, but that during VP and WP decreased them. However, CO₂ enrichment during any period increased the pod number on the secondary racemes with compound leaves and the tertiary racemes, although that during VP did not increase the pod number of tertiary racemes. Thus, CO₂ enrichment during RP increased the pod number on all racemes and that during WP increased the pod number on the secondary and tertiary racemes.

The effect of CO₂ enrichment on the rate of pod set varied with the raceme order (Fig. 3). CO₂ enrichment during RP increased the rate of pod set on all

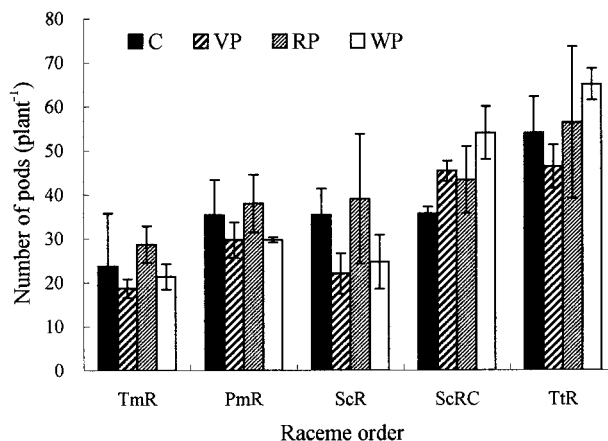


Fig. 2. Number of matured pods on each raceme order of the plants exposed to elevated CO₂ concentrations during the different growth periods in 2001. Data are means of 3 plants \pm S.D.

Other notes are the same as in Fig. 1.

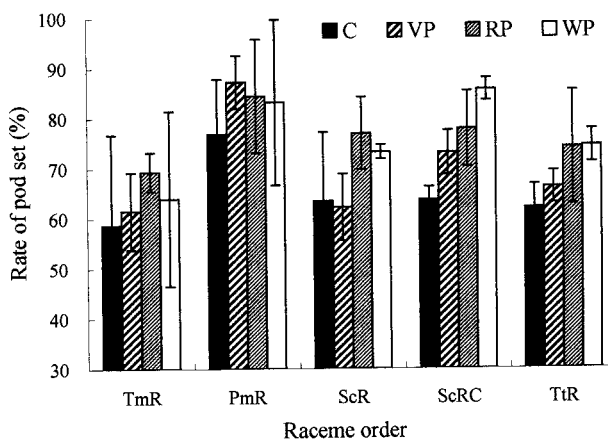


Fig. 3. Rate of pod set on each raceme order in the plants exposed to CO₂ enrichment under the different growth periods in 2001. Data are means of 3 plants \pm S.D.

Notes are the same as in Fig. 1.

raceme orders. On the other hand, CO₂ enrichment during WP greatly increased the rate of pod set on the secondary racemes, the secondary racemes with compound leaves and the tertiary racemes; that is, on the higher-order racemes. Since only the CO₂ enrichment during RP and WP increased the number of pods, we suggest that seed yield can be most effectively increased by CO₂ enrichment during the reproductive growth period.

Discussion

In 2000, CO₂ enrichment brought about a 13% increase in seed yield. However, since the light condition of the growth chambers was improved by a change of the film, the seed yield was increased by about 25% in 2001. The increase in agricultural yield by a doubling of atmospheric CO₂ concentration is

estimated to range from 24% to 43% in 37 crop species (Kimball, 1983). Ziska et al. (2001) found that a doubled CO₂ concentration brought about an increase in seed yield by 20-90%, averaging about 40%, in nine soybean cultivars. Our results were roughly consistent with these previous reports.

Some reports indicated that the seeds derived from the lower-order racemes, which bloom early during flowering, account for most of the yield (Torigoe et al., 1982; Isobe et al., 1995). Although a large number of flowers are produced on the higher-order racemes, most of them abort due to photosynthate deficiency (Saitoh et al., 1998). In the present experiment, the number of seeds derived from the high-order racemes was significantly increased by CO₂ enrichment (Fig. 3), suggesting that photosynthesis stimulated by CO₂ enrichment could provide enough assimilate for the pod growth not only on the lower-order but also on the higher-order racemes. Therefore, the seed production on the higher-order racemes may be important for the development of a cultivar which can adapt to the future climate.

The rate of pod set observed in this experiment was about 70% (Table 3). It seemed to be very high compared with the reports of Kuroda et al. (1992) or Zheng et al. (2002) who reported the increase of 40 to 50%. Huff and Dybing (1980) described that the proportion of soybean flowers developing into mature pods ranges from 20 to 70%, depending upon environmental factors. Since the flower number per plant was 265 on the average in this experiment, but was more than 119 in the experiment of Jiang and Egli (1993) and more than 126 in the experiment of Zheng et al. (2002), although it was less than 388 in the experiment of Kuroda et al. (1992). The high rate of pod set in this experiment might be resulted from the unique cultivation system. The plants were grown in the pot filled with fine sand and were given the nutrient solution twice a day. The cultural system might provide a good condition for the pod set of soybean in this experiment.

According to Hardman and Brun (1971) and Ackerson et al. (1984), increase in seed yield is caused principally by an increase in the number of matured pods. However, there is no further discussion about the increase in pod number. In the present experiments, the increase in seed yield by CO₂ enrichment during RP and WP corresponded to an increase in pod number. Furthermore, we found that CO₂ enrichment increased the pod number mostly by improving the rate of pod set on the high raceme orders (Fig. 3). Because the higher-order racemes differentiates after the onset of flowering (Saitoh et al., 1998), our data suggests that CO₂ enrichment during the reproductive growth period enhanced the translocation of photosynthate to the higher-order racemes and prevented the abortion of flowers or young pods from

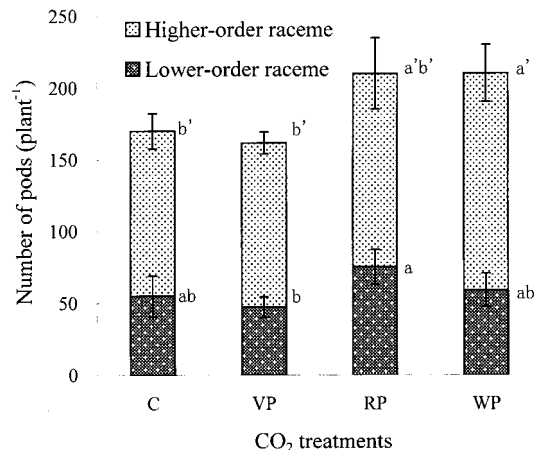


Fig. 4. The number of matured pods originating from the lower- or higher-order raceme in 2001. Data are means of 6 plants \pm S.D. Data followed by the same letter are not significantly different at 5% level according to One-way ANOVA and Bonferroni's multiple range test.

C, control; VP, CO₂ enrichment during the vegetative growth period; RP, CO₂ enrichment during the reproductive growth period; WP, CO₂ enrichment during the whole growth period.

on these racemes.

CO₂ enrichment during RP increased the rate of pod set on all racemes, but that during WP increased the rate of pod set only on the higher-order racemes (Fig. 3), although CO₂ enrichment either during RP or WP increased the seed yield (Fig. 4). Since CO₂ enrichment during RP had no significant effect on stem dry weight or total number of nodes (Table 2), it might have contributed mostly to the increase of reproductive growth improving the pod set on both the lower- and higher-order racemes. On the other hand, CO₂ enrichment during WP promoted vegetative growth from the early growth stage allocating a large amount of assimilate to vegetative organs than to the reproductive organs. It may reduce the promoting effect of CO₂ enrichment on the pod set on the lower-order racemes, which develop earlier, but increase the rate of pod set on the higher-order racemes, which develops after completion of vegetative growth, allocating the photosynthate exclusively to the pod set.

In conclusion, CO₂ enrichment may increase seed yield by improving pod set on the higher-order racemes. Moreover, the response of seed yield to CO₂ enrichment is mainly attributed to the response during the reproductive growth stage. However, further research on the accumulation and translocation of assimilate is necessary to clarify the physiological mechanism of the response to CO₂ enrichment in the higher-order racemes.

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