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Effects of continuous and intermittent carbon dioxide enrichment on fruit set and yield of sweet pepper (*Capsicum annuum* L.)

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Abstract

The effects of carbon dioxide (CO_2) enrichment on vegetative growth, fruit set and yield of an autumn crop of sweet pepper (*Capsicum annuum* L., cv. Bolero) were studied. In 12 greenhouse compartments of 9.6 m × 6 m each, 6 CO_2 treatments were tested: 3 continuous CO_2 levels, setpoints 200, 340 and 500 ppm ($\mu l\ l^{-1}$), 2 intermittent dosings (8 minutes per 40 and per 104 minutes, respectively) and a control (without dosing or filtering). It was not possible to maintain the setpoints of the continuous CO_2 levels throughout the experiment, therefore the measured CO_2 concentrations were used to explain the effects.

The results show a positive effect of elevated CO_2 concentrations on fruit set and yield. The number of fruits harvested per m^2 was 60 % higher at the 500 ppm treatment than at the 200 ppm treatment, whereas the average fruit weight was not significantly affected. The dry matter content of the leaves increased, the SLA and LAR were smaller at higher CO_2 concentrations. The vegetative growth tended to decrease at higher CO_2 levels, which was ascribed to competition between vegetative and generative organs. The results with respect to the setting and yield were less favourable at intermittent CO_2 enrichment than at continuous CO_2 levels, if plotted versus the measured, average CO_2 concentration.

Introduction

Carbon dioxide (CO_2) has a strong positive effect on the productivity of greenhouse crops (Kimball, 1986). Not much specific literature is available however, about the effect of CO_2 on sweet pepper under greenhouse conditions, especially in an autumn crop. The planting date of such a crop in the Netherlands varies from the end of June to August. A problem in this growing period is the poor fruit set and low yield. Fruit set is especially problematic during periods of calm, dull weather, which are not unusual in autumn.

The hypothesis is that the supply with assimilates may be limiting for fruit set as suggested by various authors (Calvert & Slack, 1975; Acock & Pasternak, 1986). Under dull weather conditions, the CO_2 concentration can become very low due to a low CO_2 influx. The question to be answered was whether CO_2 enrichment stimulates the setting and the productivity of autumn greenhouse sweet pepper.

Since several years it is common practice in modern greenhouse crop production to enrich the greenhouse air with carbon dioxide. In the Dutch greenhouse industry this is mostly done with exhaust gases from the (central) heating system (van Berkel, 1986). CO_2 enrichment is then connected with the production of heat, which is a disadvantage in the warmer seasons. Moreover, when ventilation increases, the efficiency of CO_2 enrichment decreases. Due to these two conditions, the CO_2 supply is at a low level during late summer and early autumn.

In order to reduce the costs and increase the efficiency of enrichment, a technique with pulsed or intermittent dosing was suggested by Enoch (1984). According to Mortensen (1984), plants respond more efficiently to intermittent CO_2 enrichment than to a continuous CO_2 level, probably because adaptation of the plants to high CO_2 levels is prevented.

In the experiment reported here, different CO_2 treatments were chosen, such that the effect of CO_2 shortage (200 ppm) as well as of CO_2 enrichment (500 ppm) could be compared with the average ambient CO_2 level (340 ppm) and with a treatment without enrichment or filtering. In addition, the principle of intermittent enrichment was tested, although in a different set-up than suggested by Enoch (1984).

To be able to study the CO_2 effect under various weather types (including the unfavourable conditions), fruit set was allowed on several dates in the cultivation.

Materials and methods

Experimental set-up

The experiment has been carried out in twelve compartments of a Venlo-type greenhouse of 9.6 m × 6 m each. Sweet pepper (*Capsicum annuum* L., cv. Bolero), was planted in soil on 15 July 1985. Carbon dioxide enrichment started on 1 August. Harvesting started on 1 October and was finished on 19 November. The young plants were first kept vegetative by weekly defloration/defruiting (removing all set flowers and young fruits) until the date that fruit set was allowed. Four different dates for the start of fruit set were applied at four different groups of plants: 5, 13, 21 and 29 August (in each compartment the same four fruit set dates in duplicate). The results on fruit set (Table 3) are given separately per fruit set date and the results on yield (Table 4, Figs. 1 and 2) are given for all fruit set dates combined.

Climate control was done by a minicomputer. Except for the CO_2 concentrations, the climatic conditions maintained in the experimental greenhouse were comparable to those in commercial greenhouses and equal in all compartments. Setpoint for heating was 21 °C by day and 15 °C at night. The temperatures at which ventilation started, were set two degrees above the heating setpoint. This relatively high dead zone was applied in order to decrease (unnecessary) CO_2 losses. During the whole period, a small ventilation (minimum of 5 % of the window opening) was maintained.

Carbon dioxide treatments

In the experiment the following six CO_2 treatments were applied:
(1) continuous CO_2 level of 200 ppm ($\mu l\ l^{-1}$);
(2) continuous CO_2 level of 340 ppm;
(3) continuous CO_2 level of 500 ppm;
(4) intermittent CO_2 dosing, one CO_2 pulse of 8 minutes per 40 minutes;
(5) intermittent CO_2 dosing, one CO_2 pulse of 8 minutes per 104 minutes:
(6) control treatment, without dosing or filtering.
In the treatments with pulsed CO_2, the flux of CO_2 was adapted, so that in 8 minutes the concentration rose to about 400 to 800 ppm (depending on the ventilation).

The six CO_2 treatments were applied in duplicate: one replicate in a compartment with the front wall facing north, the other replicate in a south orientated compartment. In all treatments, CO_2 was supplied and controlled only during daytime.

The CO_2 concentration was measured with a CO_2 analyser (Siemens), combined with a multiplexer. Eight compartments were measured by one device with a measuring cycle of 8 minutes. The dosing of liquid CO_2 from a storage tank and, in the treatment with 200 ppm, filtering of the air through a chemical filter (NaOH + $Ca(OH)_2$) to remove CO_2, were controlled by a minicomputer.

Observations

Recorded data on environmental conditions were: CO_2 concentration, temperature and window aperture of each compartment, windspeed and light intensity (Photosynthetically Active Radiation) outside. Except for the CO_2 concentration which had a measuring cycle of 8 minutes, the other factors were measured and recorded each minute. Observations on the crop were:
- fruit set: removed set flowers were counted on 13, 21 and 29 August;
- yield: every week the ripe, red fruits were harvested, weighed and counted. At the end of the season (19 November) all mature fruits were harvested (green or red/green mature fruits separated from the red ones);
- vegetative plant parameters: on five dates two plants per compartment were sampled. Number of leaves, leaf area, fresh and dry weights of leaves and stems were recorded.

Results

CO_2 concentration

Table 1 shows the average, measured CO_2 concentrations during daylight hours. It

Table 1. CO_2 concentrations ($\mu l\ l^{-1}$) measured at the six CO_2 treatments during daylight hours, averaged per period and averaged over the two replicates.

Date	Continuous CO_2 levels				Intermittent		Control	LSD[2] ($P < 0.05$)
	200 ppm	340 ppm	500 ppm	ANOVA[1]	8/32 min	8/96 min		
04-12 Aug.	329	325	431	q	378	387	371	58.2
13-20 Aug.	296	333	462	q	461	399	337	36.7
21-29 Aug.	310	332	458	q	464	398	327	38.2
01-31 Aug.	314	332	450	q	428	396	350	38.6
01-30 Sept.	271	331	453	q	476	423	332	26.0
01-31 Oct.	299	345	458	q	478	442	341	18.5
01-15 Nov.	343	379	432	l	432	411	353	48.5
01 Aug.- 15 Nov.	306	346	448	q	453	418	344	27.5

[1] ANOVA: analysis of variance on the differences between continuous CO_2 concentrations (treatments 200, 340 and 500 ppm): l = linear component significant, q = quadratic component significant, n = no significance at $P = 0.05$.
[2] Least significant difference, calculated over all treatments.

is clear that it was not always possible to maintain the setpoints, especially the setpoint of 200 ppm. This was due to the high ventilation in the autumn period and the insufficient capacity of the CO_2 filtering installations. Remarkable and unexpected was the high average CO_2 level in the control treatment, especially in early August. This can be explained partly by CO_2 release from the soil and partly by influx of CO_2 from the environment. In this region, close to the industrial area of Rotterdam, the ambient level of CO_2 is regularly high.

Vegetative growth

The vegetative growth was determined on five dates during the experiment. The results of the last observation (22 October), when the differences were most obvious, are given in Table 2.

Some parameters which are calculated from the observed vegetative data show clear differences: the dry matter content of the leaves increased at higher CO_2 levels; the Specific Leaf Area (leaf area per dry weight of leaves) and the Leaf Area Ratio (leaf area per dry weight of plant), decreased with increasing CO_2 levels.

Some observed data (number of leaves, leaf area) showed a decrease with increasing CO_2 levels, especially if only the continuous CO_2 treatments were considered. Other parameters (fresh and dry weights of leaves and stems) only indicated a tendency towards less vegetative growth at higher CO_2 levels. A statistical analysis could not confirm the tendency however, since the number of plants (two per compartment) and the number of replicates (two compartments) were too small. Moreover, the differences between treatments in realized CO_2 levels (Table 1) were relatively small and the variances between individual sweet pepper plants are great.

Table 2. Vegetative plant parameters of sweet pepper, measured on 22 October at six CO_2 treatments, averaged over two compartments and two plants per compartment. Leaf area in dm^2 per plant; weights in g per plant; dry matter (DM) content in %. Specific Leaf Area (SLA) and Leaf Area Ratio (LAR) in $cm^2 g^{-1}$.

Parameter	Continuous CO_2 levels				Intermittent		Control	LSD[2] ($P < 0.05$)
	200 ppm	340 ppm	500 ppm	ANOVA[1]	8/32 min	8/96 min		
Number of leaves	204.8	173.3	159.5	l	200.3	171.8	163.8	n.s.
Leaf area	130.8	110.8	99.6	l	113.4	109.1	94.8	n.s.
Fresh wt leaves	289.0	247.3	235.5	n	259.0	239.9	216.8	n.s.
Fresh wt stem	400.3	325.3	328.8	n	396.0	340.3	324.5	n.s.
Dry wt leaves	40.2	36.3	35.8	n	39.8	34.3	32.9	n.s.
Dry wt stem	51.3	45.8	45.6	n	55.3	44.5	46.2	n.s.
DM leaves	13.9	14.7	15.2	l	15.3	14.3	15.2	0.95
DM stem	12.8	14.1	13.9	n	13.9	13.1	14.2	n.s.
SLA	326.0	305.0	278.1	l	285.7	318.6	288.3	20.4
LAR	143.7	135.2	122.3	l	120.3	138.6	120.0	15.2

[1,2] See Table 1.

Table 3. Fruit set of sweet pepper (numbers of flowers set per m^2) at six CO_2 treatments, counted at three dates of defloration/defruiting, averaged per treatment (= two compartments).

Date	Continuous CO_2 levels				Intermittent		Control	LSD[2] ($P < 0.05$)
	200 ppm	340 ppm	500 ppm	ANOVA[1]	8/32 min	8/96 min		
Non-cumulative								
13 Aug.	5.8	8.8	13.3	n	7.8	8.9	9.0	n.s.
21 Aug.	13.5	18.3	26.0	l	22.8	19.7	16.8	6.2
30 Aug.	8.0	11.6	15.9	n	17.8	12.9	9.8	n.s.
Cumulative								
21 Aug.	19.3	27.2	39.4	l	30.6	28.6	25.8	10.5
30 Aug.	27.3	38.8	55.3	l	48.4	41.5	35.6	17.2

[1,2] See Table 1.

Generative growth

Fruit set was increased by elevated CO_2 concentration, as shown in Table 3. Per date of defloration/defruiting, the results were not always significantly different if all treatments were considered, but the differences over the three continuous CO_2

concentrations (200, 340 and 500 ppm) were significant, as follows from the probabilities. Also the accumulated fruit setting data differed significantly. In Fig. 1 the fruit set in each compartment is related to the average CO_2 level, measured in the compartment during the corresponding period (mentioned in the figure), the period which probably is important for the fruit set.

Also with respect to the yield, the favourable effect of CO_2 is obvious. The number of harvested fruits increased with increasing CO_2 concentrations (Table 4), while the average fruit weights were not significantly different. The second-class fruits are not included in the data in Table 4. The amounts of second-class fruits ranged from 1.5 to 2.7 % of the total yield and they were not significantly related to the CO_2 concentrations. In Fig. 2, for each compartment, the number of fruits harvested per m^2 is related to the average measured CO_2 concentration in the preceding period.

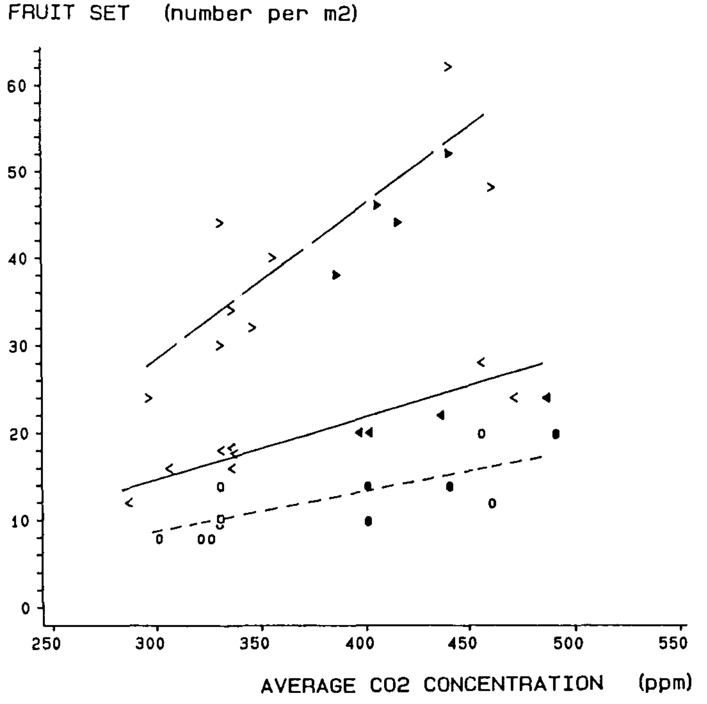

Fig. 1. Fruit set of sweet pepper (number per m^2) versus average, measured CO_2 level (ppm) in the corresponding period, data per compartment. Linear regression lines ($Y = a X + b$) are fitted through the observations at continuous CO_2 treatments (200, 340 and 500 ppm) and control only. Open symbols: continuous CO_2 treatments (200, 340 and 500 ppm) and control. Filled symbols: intermittent CO_2 treatments.

1. —— < ◀ setting 14-21 Aug. vs. CO_2 of 13-20 Aug.; $a = 0.072$, $b = -6.9$, $r = 0.62$.
2. - - - ○ ● setting 22-30 Aug. vs. CO_2 of 21-29 Aug.; $a = 0.046$, $b = -5.0$, $r = 0.77$.
3. — - > ▶ cumulative setting until 30 Aug. vs. CO_2 of 4-29 Aug.; $a = 0.177$, $b = -24.9$, $r = 0.68$.

Table 4. Cumulative yield of sweet pepper (number of red fruits per m^2) at six CO_2 treatments, averaged per treatment (= two compartments).

Date	Continuous CO_2 levels				Intermittent		Control	LSD[2] ($P < 0.05$)
	200 ppm	340 ppm	500 ppm	ANOVA[1]	8/32 min	8/96 min		
1 Oct.[3]	0.8	3.4	4.2	1	1.8	1.9	1.6	n.s.
29 Oct.[4]	7.4	10.5	14.5	1	12.9	9.5	8.9	4.26
19 Nov.[4]	13.4	16.3	21.3	1	20.0	17.9	15.5	2.24
19 Nov. all[5]	16.2	18.4	23.6	1	22.4	20.4	18.3	2.14

[1,2] See Table 1.
[3] Only fruits from the first fruit set treatment.
[4] Data from all fruit set treatments.
[4,5] All mature fruits, including green and red/green.

In both figures (1 and 2) the positive correlation between CO_2 concentration and fruit set and yield, respectively, is visible, especially for the non-intermittent CO_2 treatments, through which the linears are fitted (treatments 200, 340 and 500 ppm, and the control treatment).

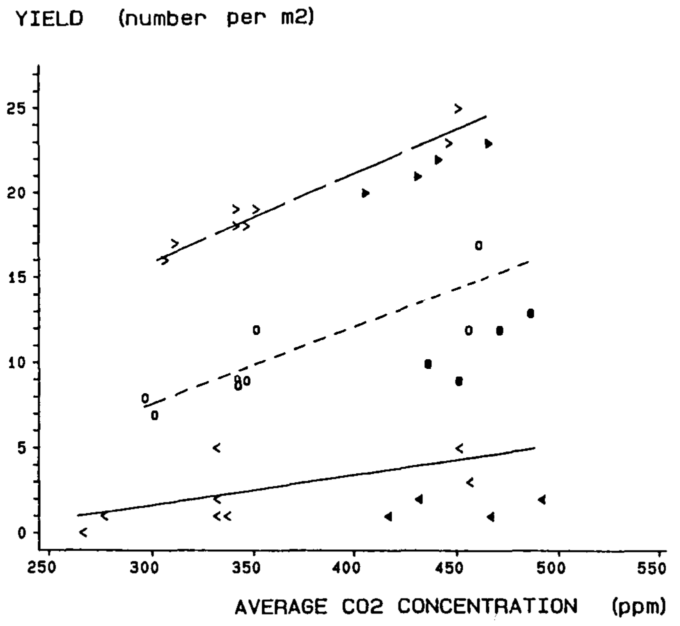

Fig. 2. Yield of sweet pepper (number of fruits per m^2) versus average, measured CO_2 concentration (ppm) in previous period. Observations per compartment. Symbols and linears as in Fig. 1.
1. —< ◀ yield at 1 Oct. vs. CO_2 in Sept.; $a = 0.018$, $b = -3.7$, $r = 0.65$.
2. - - -○● yield until 29 Oct. vs. CO_2 in Oct.; $a = 0.045$, $b = -5.9$, $r = 0.86$.
3. — - > ▶ yield until 19 Nov. vs. CO_2 of 1 Aug.-15 Nov.; $a = 0.053$, $b = 0.1$, $r = 0.96$.

Discussion

Crop response

A positive effect of carbon dioxide on fruit set was observed and this may be explained by a direct positive effect of CO_2 on photosynthesis. An increased photosynthesis rate makes more assimilates available for the flowers and fruits, which are strong sinks for assimilates. This explanation is based on the work of other authors: Calvert & Slack (1975) found a clear correlation between CO_2 concentration and average number of fruits per truss at the first ten trusses of tomato. The authors ascribe this phenomenon to enhanced rates of net assimilation and of carbon transport from leaves to fruits (sinks) of CO_2-enriched plants. Acock & Pasternak (1986), referring to a number of literature sources, described an increase of number of flowers and fruits of some crops at elevated CO_2 levels, caused by increase of photosynthesis.

The increase of yield at higher CO_2 levels, as found in this experiment, is thought to be partly a result of the better fruit set and partly of a better supply with assimilates of the fruits during the fruit growth period.

An increase in dry matter content of leaves at high CO_2 concentrations, which was observed in this study, has also been reported by Klapwijk & Wubben (1984) for young tomato, cucumber and sweet pepper plants. The observation that the leaf area per unit dry weight (both of leaves and of total plant: SLA and LAR) was significantly smaller at higher CO_2 concentrations, implies that the plants had thicker leaves and heavier stems, relative to the leaf area, at higher CO_2 levels. This was also found by other authors (Hurd, 1968, for tomato, and Jolliffe & Ehret, 1984, for bean). Acock & Pasternak (1986) ascribe the decrease of SLA at higher CO_2, as observed in some crops, to accumulation of carbohydrates in leaves.

A tendency to a decreased vegetative growth at elevated CO_2 levels was observed and this may be explained by competition between vegetative and generative organs (Hall, 1977). Since fruits are strong sinks, it is perceptible that in crops with a high fruit load (grown at higher CO_2 levels), the vegetative growth is hampered more than in crops where less fruits are set (grown at lower CO_2 levels).

Intermittent CO_2 enrichment

From the results on fruit set and yield related to the average carbon dioxide concentrations, it appeared that intermittent enrichment seemed slightly less effective than enrichment to a constant CO_2 level. This can be seen in Fig. 2 (and less clearly in Fig. 1), where the yield (respectively fruit set) at intermittent dosing treatments was below the linears fitted through the continuous dosing treatments. So the suggestion of Mortensen (1984) that the crop responds more efficiently to intermittent CO_2 than to continuous enrichment, was not confirmed in this experiment. The papers of this author were based on experiments with *Chrysanthemum* and *Saintpaulia* in growth chambers.

Our negative results are also in contrast with the expectation of Enoch (1984), although the method proposed by this author was not applied in the same way in our experiment. According to Enoch (1984) also the ventilation should be intermittent. In order to avoid possible side effects caused by this measure (e.g. on temperature) and regarding a practical application, we applied continuous ventilation. The saving on use of CO_2 was not recorded exactly. The concept of optimal use of CO_2, which was the reason for Enoch (1984) to apply intermittent enrichment, was studied further under practical conditions in other work (Challa & Schapendonk, 1986; Nederhoff, 1988).

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