

Effect of variable CO₂ enrichment on greenhouse production in mild winter climates

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Abstract

Variable CO₂ enrichment was evaluated under the autumn–winter climatic conditions prevailing in a coastal zone of southern Spain. Two adjacent identical greenhouses were used: control (without CO₂ enrichment) and enriched. Pure CO₂ was supplied to a greenhouse cucumber crop, maintaining in the greenhouse the air CO₂ concentration at close to 700 μmol mol⁻¹ when the greenhouse was closed and 350 μmol mol⁻¹ when the vents were open. CO₂ dynamics, efficiency of radiation and CO₂ use, and crop responses were determined over the growing season and compared to those of a similar cucumber crop grown in a non-enriched greenhouse. While the average diurnal concentration remained above 400 μmol mol⁻¹ in the enriched greenhouse, significant CO₂ depletion was observed in the unenriched compartment, where the CO₂ concentration fell below 300 μmol mol⁻¹ during 60% of the daytime when the crop was fully developed (leaf area index (LAI) ≈ 3). In the unenriched greenhouse, the average diurnal CO₂ depletion as well as the average mean concentration were highly correlated to the radiation intercepted by the crop, i.e. to the potential for biomass production. The average efficiency of CO₂ enrichment, i.e. the ratio of the amount of CO₂ sequestered in the crop to the amount of artificial CO₂ delivered, was about 2% with respect to vegetative biomass, and about 6% with respect to fruit biomass. CO₂ enrichment affected mainly fruit biomass and had only a slight effect on leaf area index and vegetative biomass. The average increase in fruit production for both dry and fresh matter due to CO₂ enrichment was 19%, which agrees well with previous results on the agricultural response of cucumber to moderate CO₂ enrichment.

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1. Introduction

The lack of climate control in many greenhouse of Mediterranean countries results in an inadequate micro-

climate that negatively affects yield components and input-use efficiency. A better control of the greenhouse aerial environment can improve marketable yield and quality, and extend the growing season (Baille, 1999). Air CO₂ concentration is a relevant climate variable to be controlled in greenhouses as it has a marked effect on plant CO₂ assimilation. The atmospheric level limits the potential photosynthesis of most plant species and their productivity (Boves, 1993). Inside an unenriched

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greenhouse, the CO₂ concentration drops below the atmospheric level whenever the CO₂ consumption rate by photosynthesis is greater than the supply rate through the greenhouse vents. CO₂ depletion depresses the daily photosynthetic rate, which is estimated to be about 15%, integrated over 29 days of simulation, when the concentration drops below 340 μmol mol⁻¹ (Schapendonk and Gaastra, 1984). The poor efficiency of ventilation systems of the low-cost greenhouses in Mediterranean countries, coupled with the use of insect-proof nets (Muñoz et al., 1999) explains the relatively high CO₂ depletion (about 20% or more) reported in southern Spain (Lorenzo et al., 1990). The solution is to increase the ventilation rate through forced air, to improve design and management of the ventilation system, or to provide CO₂ enrichment. The latter is common in the greenhouse industry of Northern Europe as a means to enhance crop photosynthesis under the low radiation conditions that prevail during winter in those regions. Enrichment reportedly increases crop yield and quality under a CO₂ concentration of 700–900 μmol mol⁻¹ (Kimball, 1986; Mortensen, 1987; Nederhoff, 1994). This situation explains why most of the present information on the effects of CO₂ enrichment on horticultural crops was gathered under climatic conditions and production systems (computerized climate-controlled greenhouses) typical of Northern Europe. Such knowledge and technology are not directly transferable to the environmental and socio-economic conditions of the Mediterranean countries, where CO₂ enrichment is not a common practice for several reasons. One of the main restrictions is the short time duration available for an efficient use of CO₂ enrichment, due to the need to ventilate for temperature control (Enoch, 1984). The fact that greenhouses have to be ventilated during a large proportion of the daytime makes it uneconomical to maintain a high CO₂ concentration during the daytime. However, some authors advise supplying CO₂ even when ventilation is operating (Nederhoff, 1994) to maintain the same CO₂ concentration in the greenhouse as outside and enriching to levels of about 700–800 μmol mol⁻¹ during the periods when the greenhouse is kept closed, usually in the early morning and the late afternoon.

The aim of this study was to compile more information concerning the performance, over the growing season, of a dynamic strategy that combines CO₂ enrichment to 700 μmol mol⁻¹ when the vents were closed with enrichment to the equivalent of the ambient concentration (350 μmol mol⁻¹) when the vents were open, and to do so under the typical conditions of Mediterranean countries. The interest was focused on the

mean and long-term evaluation of this strategy based on crop response. The main goals of this paper are to (i) compare the trend of CO₂ consumption by the crop (estimated from dry-matter production) with the amount of CO₂ injected into the greenhouse, and (ii) determine the trend of CO₂ efficiency when applying the proposed strategy of CO₂ enrichment. Cucumber was chosen as the test crop because, besides its economical importance in greenhouse horticulture, it is known to present a significant and positive response to CO₂ enrichment (Nederhoff, 1994; Akilli et al., 2000).

2. Materials and methods

2.1. Greenhouse and climate control

The experiment was conducted in two adjacent identical multispan plastic greenhouses of 720 m² located at the CIFA experimental station, near Almería, Spain (36°30'N, 2°18'W). The greenhouses were equipped with a pipe heating system, roof and side vents, and a system for the injection of pure CO₂. All ventilators were permanently covered with insect-proof nets (25% of porosity). The greenhouse ventilation rates with full open vents were estimated, using a theoretical model described by Muñoz et al. (1999), to be between 5 and 16 m³ s⁻¹ under low to moderate wind speed (≈1 m s⁻¹), for leeward and windward directions, respectively. Ventilation started at 25 °C. To prevent high humidity, roof vents opened to 25% of full opening when relative humidity exceeded 85%. The pre-fixed heating set points (day/night) were: 22 °C/20 °C during the germination period, 18 °C/16 °C to the first fruit set and 16 °C/14 °C during fruit harvest. From 5 days after sowing onwards, pure CO₂ was supplied in one greenhouse, distributed through a network with one outlet below each plant. CO₂ enrichment was applied during the daytime according to two set points: 700 μmol mol⁻¹ when the roof and side vents were closed and 350 μmol mol⁻¹ when the roof vent opening was greater than 20% of full opening. The CO₂ concentration was continuously monitored and controlled through an infrared gas analyser (Siemens Corp., Mainz, Germany). The CO₂ injected into the enriched greenhouse was quantified indirectly by using the time (days) for CO₂ container depletion (27 and 35 kg) and referred to the greenhouse area. The other greenhouse was not CO₂ enriched but rather was maintained at the same temperature and humidity set points as the enriched one, and served as the control. The climatic variables (temperature, humidity and CO₂ concentration) were controlled by means of a commercial

climate-control system (LCC-900, DGT-Volmatic, Soendersoe, Denmark) connected to a PC.

2.2. Crop and cultural techniques

Cucumber seeds (*Cucumis sativus*, L.), cv. 'Marumba', were sown on 9 October 1997 directly in perlite bags placed in a gutter. Crop density was 1.33 plants m^{-2} in north–south oriented rows. According to the standard commercial practice, all axillary shoots were removed weekly and fruit pruning was carried out in order to leave only a single fruit per node. In both greenhouses, the same nutrient solution was used, provided by an automatic drip irrigation system (AMI-1000, DGT-Volmatic, Soendersoe, Denmark). Water and nutrient supplies were scheduled to maintain the same electrical conductivity (EC) in the root environment (about 4.5 dS m^{-1}).

2.3. Measurements and statistical analysis

2.3.1. Climate measurements

Data of dry and wet bulb air temperature, measured by means of aspirated psychrometers (DGT-Volmatic, Soendersoe, Denmark), and CO_2 concentration in each greenhouse were recorded every 15 min. Periodically, the outside CO_2 concentration was measured by means of a portable infrared gas analyser (IRGA LCA-2, ADC, Herts, UK). The incident photosynthetically active radiation (PAR) was measured every minute by a quantum sensor (Delta T Devices, Cambridge, UK) placed above the canopy in both greenhouses and the 5 min. averages were registered by a data-logger (DL2, Delta T Devices, Cambridge, UK).

2.3.2. PAR interception measurements

The PAR intercepted by the canopy (i) in both greenhouses was measured throughout the growing period, using a linear quantum sensor (LI-191, SB, Nebraska, USA) positioned at six different points above the plants and at bag level. The extinction coefficient for PAR radiation (k) was calculated using the expression: $i = 1 - \exp(-kL)$ (Russell et al., 1989), where L is the LAI. The best correlation was found for $k = 0.61$ ($R^2 = 0.81$). Daily incident PAR was multiplied by the above expression to calculate the daily intercepted PAR, PAR_{int} .

2.3.3. Biomass measurements

The experimental design for fresh- and dry-biomass determination followed a single-factor model, with sampling of shoot biomass during the crop cycle, on: 31

October, 11 November, 25 November, 15 December, 7 January and 13 February. The samples consisted of six plants randomly selected from homogeneous zones in each greenhouse. Each plant was separated into three fractions: leaf, stem (plus petioles and flowers) and fruit. Fresh weight was determined for each fraction. Leaf area was derived by means of a leaf area meter (Delta T Devices, Cambridge, UK). Dry weight was determined after drying for 48 h at 80 °C in a forced-air oven. All axillary stems and young fruits, removed till the sample date, were included in the corresponding fraction.

Fruit yield was routinely surveyed (total number of fruits and fresh weight) on three complete rows of each treatment. Ripe fruits were harvested twice a week from 1 December to 13 February, and weighed. Dry weight was determined on fruit samples of each row.

The efficiency of CO_2 enrichment with respect to the increase of assimilated CO_2 , defined as the ratio ε of the increase in C-assimilates content in the aerial part, due to CO_2 enrichment, δA ($\text{g}_{\text{CO}_2} \text{m}^{-2} \text{d}^{-1}$), relative to the amount of CO_2 supplied in the greenhouse, δQ ($\text{g}_{\text{CO}_2} \text{m}^{-2} \text{d}^{-1}$), was evaluated during the crop cycle and for periods between the biomass determinations. The δA was calculated from the difference in dry biomass produced by the two crops during each period, which was converted into assimilated CO_2 using the following conversion factors: 0.7 for the ratio of structural dry weight formed per amount of glucose consumed, and 0.68 for the conversion factor from gram of assimilated CO_2 to gram of glucose (Ehler and Karlsen, 1993).

3. Results

3.1. Climate characterization

During the experiment, no differences were observed between the amounts of incident radiation measured in each greenhouse. At the beginning of the growth cycle (mid-October), the daily PAR integral was around 6 $\text{MJ m}^{-2} \text{d}^{-1}$, decreasing progressively until values ranging between 3 and 4 $\text{MJ m}^{-2} \text{d}^{-1}$ in December and January.

The evolution of temperature and vapour pressure deficit was similar inside the CO_2 -enriched and control greenhouses. The average over the growth cycle for maximum, mean, and minimum values were, respectively: 27 °C, 1.6 kPa; 19 °C, 0.5 kPa and 15 °C, 0.2 kPa.

Fig. 1a and b plot the daytime evolution of CO_2 concentration inside the two greenhouses, for two single

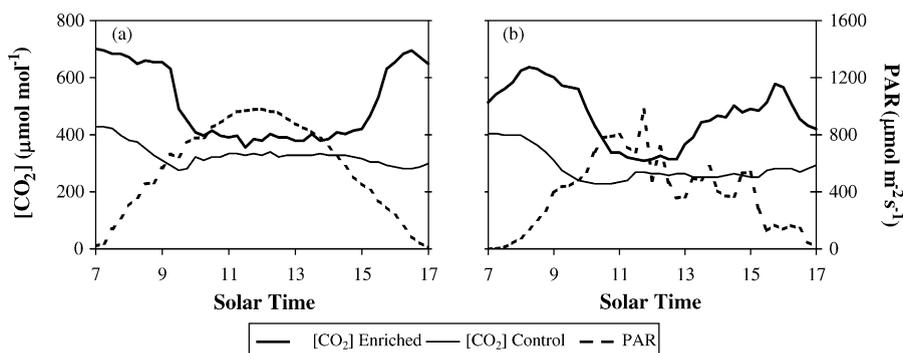


Fig. 1. Daytime course of the incident PAR and the CO₂ concentration inside enriched ([CO₂] Enriched) and control ([CO₂] Control) greenhouses, for two single days representative of two growth stages: (a) vegetative phase, LAI = 0.8 (12 November); (b) generative phase, LAI = 3 (8 January).

days as representative of two growth stages corresponding to values of LAI of 0.8 (12 November) and 3.0 (8 January). When the vents were closed and PAR was near or above 200 μmol m⁻² s⁻¹, the CO₂ concentration in the control greenhouse dropped significantly below the outside level, which was generally stable around 355–360 μmol mol⁻¹ in this agricultural (non-industrial) area. The minimum CO₂ concentrations inside the greenhouses were about 270 and 230 μmol mol⁻¹ for LAI = 0.8 and 3.0, respectively, corresponding to maximum depletions of 25% and 35%. When ventilation was operating, the minimum CO₂ concentration reached values near 300 μmol mol⁻¹, still indicating a significant depletion. In the enriched greenhouse, the CO₂ supply enabled maintenance of a concentration near 600–700 μmol mol⁻¹ when vents were closed. During the ventilation period, the CO₂ concentration was slightly above the outside level for the low LAI stage, and slightly below during the high LAI stage. Values close to 500 μmol mol⁻¹ were registered on the afternoon of 8 January (Fig. 1b) due to the alternating

CO₂ set point as a consequence of the ventilation operational changes on days with clear and overcast periods as represented.

Fig. 2 presents the frequency distribution of daytime CO₂ concentration inside the non-enriched greenhouse and its evolution with the crop development and time of year. When LAI was between 0.5 and 1, the CO₂ concentration was within the range 300–350 μmol mol⁻¹ during about 70% of the daytime. As the crop developed, the period with a CO₂ concentration below 300 μmol mol⁻¹ increased to 60% at LAI = 3–3.5, with 50% between 250 and 300 μmol mol⁻¹ and 10% between 200 and 250 μmol mol⁻¹.

The diurnal variation of the CO₂ concentration inside the enriched greenhouse (Fig. 3) changed over time. From 8 November onward, the daytime period with 400–600 μmol mol⁻¹ CO₂ levels extended, due to changes in the ventilation requirements to control the maximum levels of temperature and humidity.

Analysis of the 10-day average values of mean, maximum and minimum daytime CO₂ concentrations

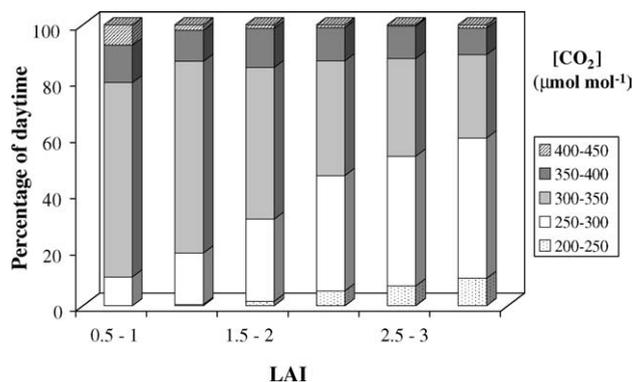


Fig. 2. Distribution per class of CO₂ concentration (average during daytime) in the unenriched greenhouse for different values of leaf area index (LAI).

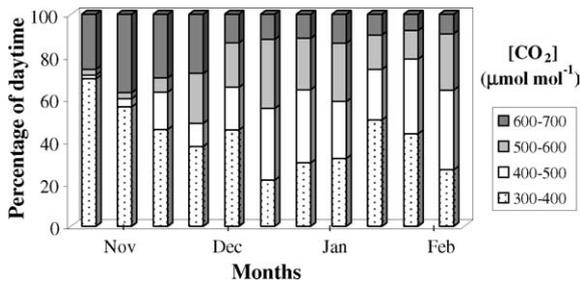


Fig. 3. Distribution per class of CO₂ concentration (average during daytime) in the enriched greenhouse for 10-day periods.

(C_m , C_{max} and C_{min} , respectively) revealed that, during the first half of the crop cycle, the mean values in the non-enriched greenhouse gradually decreased to about $285 \mu\text{mol mol}^{-1}$, later to increase slightly and stabilise near $300 \mu\text{mol mol}^{-1}$ during the second half. Average minimum levels were between 230 and $250 \mu\text{mol mol}^{-1}$. In the enriched greenhouse, the mean values remained in the range 400 – $500 \mu\text{mol mol}^{-1}$, and maximum and minimum levels, i.e. about 600 and $340 \mu\text{mol mol}^{-1}$, respectively, were close to the two pre-established set points.

3.2. LAI and intercepted radiation

3.2.1. Leaf area

The CO₂ supply did not significantly affect the final values of LAI and SLA (specific leaf area) (Table 1). However, there was a statistically significant difference on 25 November, as observed for leaf dry matter, when LAI was slightly augmented (+9%) and SLA slightly diminished (–5%) by CO₂ enrichment. The LAI evolution (Fig. 4) closely matched a sigmoidal curve, such as the logistic or Gompertz functions.

3.2.2. Intercepted radiation

The time evolution of 10-day average intercepted PAR was similar in the enriched and control crops

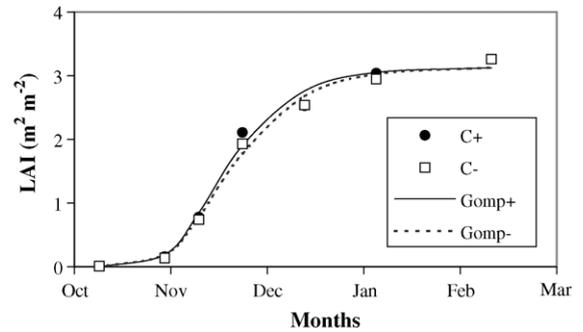


Fig. 4. LAI evolution in the enriched (C+) and control (C–) crops, with the corresponding fitted curves to the Gompertz function.

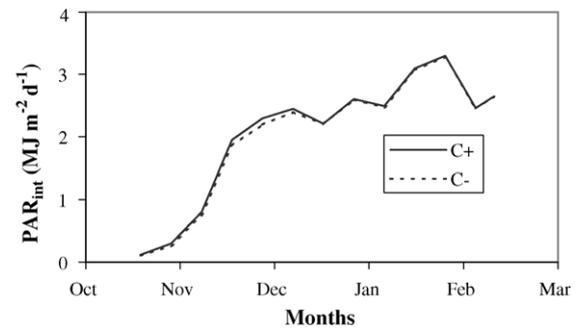


Fig. 5. Ten-day averaged values of intercepted PAR (PAR_{int}) for the two crops, enriched (C+) and control (C–).

(Fig. 5), with a maximum value of about $3 \text{ MJ m}^{-2} \text{ d}^{-1}$ between 27 January and 6 February.

3.3. Biomass production

3.3.1. Aerial biomass production

The evolution of the accumulated aerial dry biomass (without roots), M_D (g m^{-2}), is presented in Fig. 6. Differences were significant from 25 November onwards that is, throughout the entire harvest period.

Table 1

Leaf area index (LAI) and specific leaf area (SLA) of enriched (C+) and control (C–) crops

	31 October	11 November	25 November	15 December	7 January	13 February
LAI ($\text{m}^2 \text{ m}^{-2}$)						
C+	0.16	1.78	2.11	2.53	3.04	3.26
C–	0.14	0.74	1.93	2.54	2.95	3.26
LSD _{0.05}	n.s.	n.s.	0.17	n.s.	n.s.	n.s.
SLA ($\text{m}^2 \text{ g}^{-1}$)						
C+	0.037	0.037	0.032	0.034	0.030	0.027
C–	0.038	0.037	0.033	0.034	0.032	0.028
LSD _{0.05}	n.s.	n.s.	0.001	n.s.	n.s.	n.s.

LSD_{0.05} = least significant difference at $P < 0.05$; n.s.: no significance.

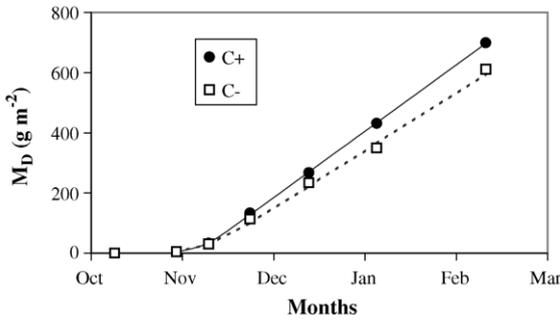


Fig. 6. Dry-matter accumulation in the aerial part of the plant (M_D , $g\ m^{-2}$) throughout the crop cycle, enriched (C+) and control (C-).

3.3.2. Fruit biomass

The total fresh yield for the enriched crop ($13.7\ kg\ m^{-2}$) was higher than for the unenriched one ($11.5\ kg\ m^{-2}$) by about 20% (Fig. 7a). The rate of yield increase of the control crop was reduced between 26 December and 2 January due to abortion of some young fruits, more pronounced than in the enriched crop as a consequence of self-regulatory processes.

The evolution of the relative gain G in cumulated yield expressed as

$$G(\%) = \frac{Y^+ - Y^-}{Y^-}$$

where Y^+ and Y^- are the cumulated yield of the enriched and unenriched crop, respectively, is presented in Fig. 7b. It can be seen that the maximum gain from CO_2 enrichment was obtained during the first half of the harvest period (between 1 December and 9 January) with a relatively constant value of 30% for G , and a rapid decrease from 9 January until the end of the cycle, when the final value of G was about 20%.

3.3.3. Radiation-use efficiency

The average radiation-use efficiency (RUE, $g\ MJ^{-1}$) was derived from the slope of the linear relationship

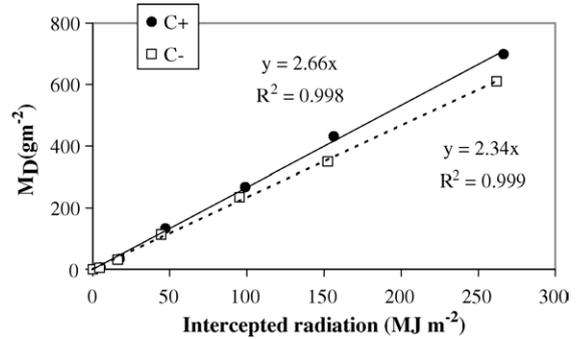


Fig. 8. Relationship between accumulated aerial dry biomass (M_D , $g\ m^{-2}$) and intercepted radiation. The points refer to each biomass determination.

between cumulated aerial dry biomass and cumulated intercepted radiation (Monteith, 1977; Gosse et al., 1986). The slope was $2.34\ g\ MJ^{-1}$ for the unenriched crop and $2.66\ g\ MJ^{-1}$ for the enriched crop (Fig. 8), i.e. a 14% increase in RUE due to CO_2 enrichment.

3.4. CO₂ supply and efficiency

3.4.1. CO₂ supply

The total amount of CO_2 injected over the whole cycle was $2.2\ kg_{CO_2}\ m^{-2}$. Fig. 9 shows the evolution of the 10-day average of the amount of CO_2 (Q , $g\ m^{-2}\ d^{-1}$) injected in the enriched greenhouse. The maximum Q value was reached (about $27\ g\ m^{-2}\ d^{-1}$) between 19 and 28 November, coinciding with the onset of the generative stage and high assimilate demand.

The CO_2 supply required for maintaining the target CO_2 concentrations increased gradually with the intercepted PAR, until PAR_{int} reached a value of $2\ MJ\ m^{-2}\ d^{-1}$ (Fig. 10), after which the CO_2 consumption became more or less stable, around a mean value of $22\ g\ m^{-2}\ d^{-1}$.

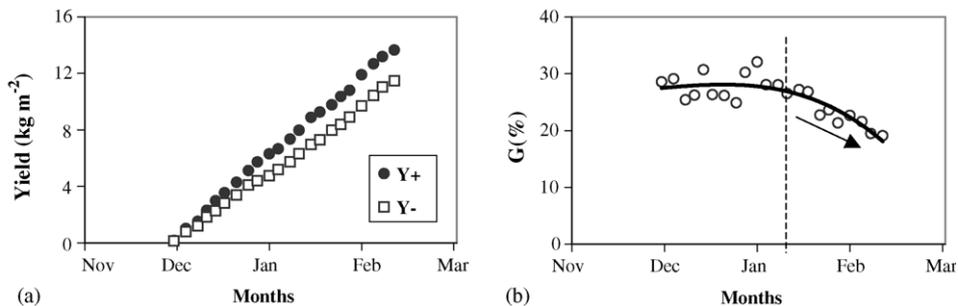


Fig. 7. (a) Cumulated yield of enriched crop Y^+ ($kg\ m^{-2}$) and control crop, Y^- . (b) Relative gain in yield, $G(\%) = (Y^+ - Y^-)/Y^-$.

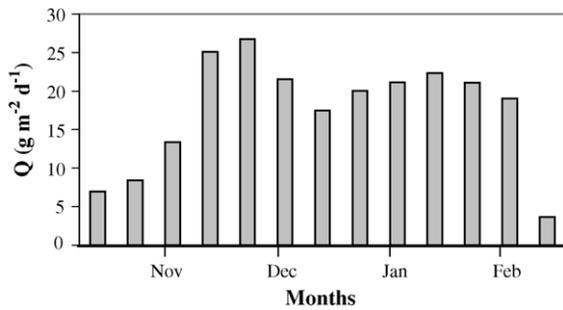


Fig. 9. Ten-day averaged CO₂ input (Q) in the enriched greenhouse.

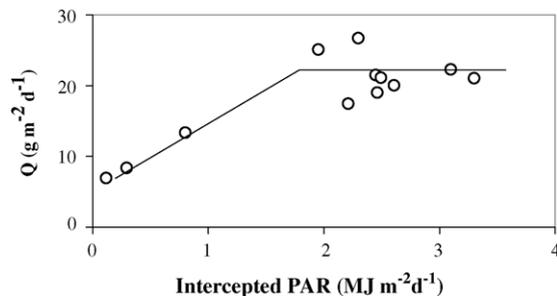


Fig. 10. Relationship between CO₂ input (Q) and intercepted PAR (10-day averaged values).

3.4.2. CO₂ efficiency related to biomass

Fig. 11 shows the evolution of the CO₂-enrichment efficiency, $\epsilon = \Delta A/Q$, at different phases of crop development, distinguishing between vegetative (ϵ_{veg}) and harvested (ϵ_{fruit}) biomass components. The evolution was very different for each component, the highest efficiency being registered for fruit biomass (up to 16% during the period: 16 December–7 January). After the onset of the generative phase, values of ϵ_{veg} were much lower than during the vegetative phase, and even negative, as observed between 26 November and 15 December, i.e. during the period with the highest

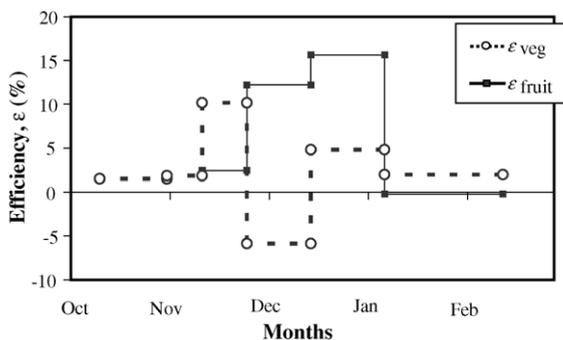


Fig. 11. Evolution of vegetative and fruit CO₂-enrichment efficiency, ϵ_{veg} and ϵ_{fruit} . Average values between each biomass determination.

Table 2

Fruit-production rate (g m⁻² d⁻¹) in enriched and control crops

	Period		
	I	II	III
Yield rate (g m ⁻² d ⁻¹)			
Enriched	205	175	178
Control	156	139	161

Values are calculated over periods between two fruit-biomass determinations: I (26 November–15 December), II (16 December–7 January), III (8 January–13 February).

fruit load and production rate in the enriched crop (Table 2). At the end of the cycle, both vegetative and fruit CO₂ efficiencies sharply decreased. Calculated over the whole cycle, ϵ was three times higher for fruit (6%) than for vegetative (2%) biomass.

4. Discussion

4.1. CO₂ levels and consumption

As reported in several studies (e.g. Heij and de Lint, 1984), the CO₂ concentration in unenriched greenhouses, when closed, declined in proportion to the radiation intensity and to the leaf area of the crop that is, in proportion to the photosynthetic activity of the canopy. The values found in our study confirmed the important role of the leaf area in determining the CO₂ concentration in the greenhouse, with average minimum values of 270 and 230 $\mu\text{mol mol}^{-1}$ for LAI = 0.8 and 3.0, respectively. From 18 December (LAI = 2.5) onwards, the minimum CO₂ levels were between 230 and 250 $\mu\text{mol mol}^{-1}$ in the control greenhouse. When vents were open, this greenhouse did not maintain the inside concentration at the level of the outside, with differences generally between 50 and 60 $\mu\text{mol mol}^{-1}$. This could be ascribed to the low ventilation rate of the greenhouse and to the presence of the insect-proof screens, which can considerably reduce the air-exchange rate (Muñoz et al., 1999). The amount of CO₂ absorbed by the crop was not offset by an equivalent supply of atmospheric CO₂ from the outside atmosphere, resulting in CO₂ depletion within the greenhouse, until some level of equilibrium was reached between the supply and demand.

The period during which the CO₂ concentration was lower than 350 $\mu\text{mol mol}^{-1}$ was long, going from 70% of the daylight period for LAI = 0.5–1, to 90% for LAI = 3–3.5. These values, much higher than the value of about 30% reported by Heij and de Lint (1984) for well-ventilated Venlo glasshouses in the Netherlands,

can be ascribed to the relatively high photosynthetic activity of the crop and probably also to the presence of the insect-proof nets. An analysis of the correlation in the unenriched greenhouse between the 10-day average values of intercepted radiation on one hand, and the 10-day average diurnal average CO₂ concentration and depletion on the other hand, gave significant positive R^2 values ($R^2 = 0.57$ and 0.63 , respectively for concentration and depletion). The latter result highlights the link between the internal CO₂ concentration and the photosynthetic activity of the crop in an unenriched greenhouse.

In the enriched greenhouse, CO₂ consumption increased rapidly with the intercepted PAR during the period corresponding to the foliar-development stage ($\text{PAR}_{\text{int}} < 2 \text{ MJ m}^{-2} \text{ d}^{-1}$), and was more or less stable ($\approx 22 \text{ g m}^{-2} \text{ d}^{-1}$) during the generative phase (Fig. 9). This result appears to be logical, given that the net assimilation of a crop follows a similar asymptotic pattern with respect to radiation.

4.2. Yield response to CO₂ enrichment

The overall values for radiation-use efficiency (2.34 g MJ^{-1} for the unenriched crop and 2.66 g MJ^{-1} for the enriched crop) were within the range of values reported for greenhouse fruit–vegetable crops (Lorenzo, 1994; Nederhoff, 1994). The relative increase (14%) in RUE due to CO₂ enrichment can be ascribed mainly to the stimulation of fruit-biomass production, which contributes to the major part of the increase in plant aerial biomass observed for the enriched crop.

The relative increase of final yield due to CO₂ enrichment was 19%, a value which is in the lower range of Kimball's (1986) reported values for C3 species (14–61%). However, it should be taken into account that the latter range covers very different enrichment strategies, and includes low to high CO₂ levels (Slack and Hand, 1985; Nederhoff, 1994). The greatest influence of CO₂ enrichment on yield occurred during the first half of the harvest period, with about 30% gain in yield from 1 December to 9 January with respect to the unenriched crop. This is in accordance with previous results indicating higher increases during the early generative period (Ito, 1978; Yelle et al., 1990; Peñuelas et al., 1995). The high sink strength during this period may have enhanced the photosynthetic capacity of the leaves, thereby enabling them to sustain the higher productivity registered. However, this increase was not observed in the second half of the harvest period, where the plants appeared to respond less positively to CO₂ enrichment, and the production was

rather similar in the two greenhouses, suggesting some type of source-sink regulation.

4.3. CO₂ efficiency

The artificial CO₂ supply was more efficiently used for increasing fruit (6%) than vegetative (2%) biomass production. This is due to the fact that the increase in assimilate production induced by CO₂ enrichment was allocated mainly to fruit growth, as Peñuelas et al. (1995) reported. The average value for ϵ was 8%, which is similar to the values given by Hand (1984), who reported an average value of 5% for crops enriched to $1000 \mu\text{mol mol}^{-1}$ under winter conditions in England; thus, it could be inferred that the suggested dynamic supply does not reduce the CO₂ efficiency when compared to the current strategy. A reduction would probably be expected in the case that higher CO₂ levels are maintained with the vents open.

In relation to vegetative biomass, the CO₂-supply efficiency reached its maximum value ($\approx 10\%$) before the start of the harvest period, and decreased significantly afterwards, when fruits became the major sink for assimilates. At that time, fruit CO₂-enrichment efficiency rose to 15%. These results are consistent with other studies concerning a differential response of vegetative and generative growth to CO₂ enrichment during crop development (Aoki and Yabuki, 1977; Nederhoff, 1994).

In the last period of the crop cycle, both vegetative and generative biomass gains in response to CO₂ supply were limited, leading to a drastic reduction in CO₂ efficiency. This observation supports the assumption of an acclimation process of the crop to CO₂ enrichment, as reported in earlier studies (Aoki and Yabuki, 1977; Ito, 1978).

In the present study, the relative yield response with respect to the average increase of daytime CO₂ concentration over the whole crop duration was found to be about 0.1% per $\mu\text{mol mol}^{-1}$, in agreement with the results at higher CO₂ levels reported by Nederhoff (1994).

5. Concluding remarks

In this study, the effects on the efficiency of radiation and CO₂ use in relation to variable CO₂ enrichment were investigated for a cucumber crop, and compared to the results under unenriched winter conditions prevailing in Mediterranean greenhouses. In the unenriched greenhouse, CO₂ depletion was substantial, being highly correlated to the radiation intercepted by the

crop. The variable CO₂ enrichment improved the efficiency of radiation use in the crop, resulting in a significant increase in yield, ascribed mainly to the stimulation of fruit-biomass production. The values of CO₂ efficiency were of the same order of magnitude, or higher, than values for CO₂-enriched crops at higher latitudes and in cooler climates.

Overall, the results confirmed the agricultural interest of the proposed strategy of CO₂ enrichment for greenhouses located in Mediterranean climates, where ventilation requirements are relatively high during winter. These data also enable a more precise assessment of the economic benefits that Mediterranean greenhouse growers can expect from CO₂ enrichment, taking into account the specificity of the winter climatic conditions and greenhouse characteristics.

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