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The Effect of CO_2 Concentration on the CO_2 Exchange Rate in a Small Plant Stand of Cucumber during Different Periods of the Day

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Summary

The effect of CO_2 concentration on the carbon dioxide exchange rate (CER) was studied in small plant stands of cucumber for 12 hours a day^{-1} in three experiments (Exp.) conducted in summer. A photon flux density (PFD) of 300 µmol m^{-2} s^{-1} of supplementary light was provided in addition to daylight, except for during the middle of the day (12.00–17.00). The photoperiod was 20 hours per day^{-1} (02.00–22.00). In Exp. 1, an increase in CO_2 concentration from 380 to 800 µmol mol^{-1} from 08.00 until 20.00 increased CER by about 30 % during the period, irrespective of the PFD. In Exp. 2, a decrease in CO_2 concentration from 380 to 210 µmol mol^{-1} during the same period reduced the CER by 20–36 %, with an increasingly negative effect towards the end of the period. Measured at the same CO_2 concentration during the first hours of the photoperiod (02.00–08.00) and at end of the photoperiod (20.00–22.00), the CER was the same in both plant stands in both experiments. In Exp. 3, an increase in the CO_2 concentration from 800 to 1200 µmol mol^{-1} during the same 12-hour period increased CER much more early in the period (28 %) than late in the period (7 %). Measured at the same CO_2 concentration, the CER of the 1200 µmol mol^{-1} exposed plants was 12 % lower at end of the photoperiod (20.00–22.00) compared with the control plants, but the same during the first part of the photoperiod (02.00–08.00). CER increased with increasing PFD in all three experiments. In a fourth experiment, CER was measured at three different temperatures throughout the day in three different plant stands. Supplementary light (300 µmol m^{-2} s^{-1} PFD) was provided for 20 hours per day^{-1}. When 800 µmol mol^{-1} CO_2 was combined with moderate PFD levels (about 300 µmol m^{-2} s^{-1}), the CER was the same at 25 and 30 °C, decreasing at 35 °C. At a high PFD level (about 750 µmol m^{-2} s^{-1}) and intermediate CO_2 level (500 µmol mol^{-1}), the CER was the same irrespective of temperature. When the CO_2 concentration decreased to 300 µmol mol^{-1}, the CER decreased with increasing temperature.

Key words. CO_2 concentration – cucumber – light culture – photon flux density – photosynthesis – supplementary light – temperature

Introduction

High carbon dioxide (CO_2) concentrations in the greenhouse atmosphere are necessary if the growth and yield of many crops, including cucumber (Kläring et al. 2007), are to reach the optimum level. A concentration of 800–1000 µmol mol^{-1} is normally recommended, but it is difficult to maintain in practice because of ventilation needs and it can sometimes decrease to around 200 µmol mol^{-1} (Nederhoff and Vegter 1994). High concentrations can be maintained even at high ventilation rates using a large amount of CO_2 (> 50 kg m^{-2} h^{-1}). However, in semi-closed and closed greenhouses, a high concentration can be maintained using small amounts of CO_2 gas (Qian et al. 2011). This new greenhouse technology may be the solution in future, but it is still not economically feasible. Much information is already available about the relationship between CO_2 concentration and photosynthesis and cucumber growth (Aoki and Yabuki 1977; Nederhoff and Vegter 1994; Aguera et al. 2006). Most measurements of the CO_2 gas exchange rates (CER) of greenhouse plants have been performed on single leaves, and few continuous studies appear to have been carried out on whole plants or plant stands under variable climate conditions (Mortensen and Moe 1983; Nederhoff and Vegter 1994; Körner et al. 2007). Reduced photosynthetic rates over time are well known in plants exposed to high concentrations, but they vary between species (Aoki and Yabuki 1977; Mortensen 1983; Hao et al. 2006; Aranjuelo et al. 2008; Reddy et al. 2010). Today, good control of the CO_2

concentration is recognised as perhaps the most important single factor in relation to further increasing crop growth and yield in the greenhouse industry. In order to obtain more detailed information about the diurnal effect of CO_2 concentration, CER was therefore monitored continuously in small cucumber stands. This study included elevated CO_2 concentrations as well as lower- than-ambient concentrations that often occur even with full ventilation when CO_2 gas is not supplied. Since CO_2 control during early morning and late evening is generally easy to maintain due to low solar radiation and little ventilation, the effect of CO_2 was studied during 12 daytime hours in a photoperiod of 20 hours per day^{-1}. In a traditional greenhouse, a stepwise decrease in the CO_2 concentration is often used when the irradiance level and need for ventilation increase during the day. One experiment was therefore designed to study the effect of temperature at different CO_2 concentrations arising during the day. Increased knowledge about the dynamic pattern of how CO_2 concentration affects the photosynthesis of cucumbers will hopefully contribute to a better CO_2 control strategy.

Materials and Methods

Seeds of *Cucumis sativus* cv. 'Rapides' were sown in standard fertilised peat (Humus-börsen) in one-litre pots, one seed per pot. After one to two weeks, the plants were placed in a cuvette system for continuous measurement of CO_2 exchange rates (CER). The system consisted of three cuvette units made of 6-mm plexiglass with a volume of 293 litres ($500 \times 480 \times 1220$ mm) placed in a greenhouse compartment. The plant floor (0.24 m^2) was perforated (10 mm holes), and a fan moved the air vertically at a velocity of 0.5 m s^{-1}. The height from the plant floor to the top of the cuvette was 910 mm. At the top of the cuvette unit, the air was circulated through a tube back to a compartment below the plant floor. The air temperature was regulated in this compartment by a water-based cooling unit and an electrical heater, controlled by a Microtherm EFK-13B unit with day and night temperature set points. The CO_2 concentration was controlled by adding pure CO_2 from a container to the cuvette. A scanner switched the air flow from the three cuvette units to an infrared gas analyser (ADC 225 MK3). A Campbell logger (AM25T) controlled the CO_2 concentration and recorded the CO_2 consumption in the different cuvettes. During the night, dark respiration causes an increase in CO_2 concentration. The system was therefore constructed to be able to be ventilated by fresh air through solenoid valves at fixed CO_2 set points. Ventilation stopped when a lower CO_2 limit was reached. Three air temperatures measured by thermocouples, one leaf temperature measured by an infrared thermometer (IRt/c^{TM}, Exergen Corp.) and one air humidity (Vaisala HMP 35A sensor) could be recorded in each cuvette unit. A certain adjustable volume of CO_2 was injected into the cuvettes if the measured CO_2 concentration was below a pre-set value. The injection volume of CO_2 gas was determined by the flow rate and time of application, and it was recorded hourly. Two 400 W and two 600 W high-pressure sodium lamps (Philips SON-T) were mounted above each of the cuvette units, supplying from 0 to 800 µmol m^{-2} s^{-1} PFD at plant level. Up to six PFD levels could be automatically controlled during the day. The light was measured by means of a Lambda LI-185B instrument with a quantum sensor (400–700 nm). All daylight could be eliminated using black curtains if necessary.

Four experiments (Exp.) were carried out in small plant stands, i.e. four cucumber plants in each cuvette.

Exp. 1: The effect of increasing the CO_2 concentration from 380 to 800 µmol mol^{-1} during the daytime

In this experiment, CER was measured at 380 ± 30 and 800 ± 50 µmol mol^{-1} CO_2 in two plant stands during the daytime period from 08.00 until 20.00. During the morning (02.00–08.00) and evening (20.00–22.00), the two plant stands were both exposed to 800 µmol mol^{-1} CO_2. Supplementary light at a level of 300 µmol m^{-2} s^{-1} PFD was provided between 02.00 and 12.00 and again between 17.00 and 22.00. Between 12.00 and 17.00, the plants received only daylight. The temperature was kept constant at 25.0 ± 0.5 °C, except during the dark period when it was 20.0 ± 0.5 °C. On the first day of the experiment, the two cuvettes were given 800 µmol mol^{-1} over the entire photoperiod (02.00–22.00), while different treatments were administered for the four following days. The total leaf area at the end of the experiment was 145 dm^2 (8.8 leaves per plant), corresponding to a leaf area index (LAI) of 6.0 in both treatments.

Exp. 2: The effect of decreasing the CO_2 concentration below the ambient level

In this experiment, the CER was measured in two plant stands at 380 ± 30 µmol mol^{-1} and 210 ± 30 µmol mol^{-1} CO_2, respectively, during a 12-hour period (08.00–20.00). During the morning (02.00–08.00) and evening (20.00–22.00), the two plant stands were both exposed to 800 µmol mol^{-1} CO_2. The light and temperature treatments in this experiment were the same as in Exp. 1. On the first day of the experiment, the two cuvettes were given 380 µmol mol^{-1} of CO_2 throughout the day, and the different treatments were administered over four consecutive days. The total leaf areas at the end of the experiment were 42 and 43 dm^2 in the 380 and 210 µmol mol^{-1} CO_2 treatments, respectively (3.3 leaves per plant). This corresponded to an LAI of 1.75 and 1.79, respectively.

Exp. 3: The effect of increasing the CO_2 concentration from 800 to 1200 µmol mol^{-1}

In this experiment, the CER was measured in two plant stands at 800 ± 50 µmol mol^{-1} and 1200 ± 50 µmol mol^{-1}

CO_2, respectively, during a 12-hour period (08.00–20.00). During the morning (02.00–08.00) and evening (20.00–22.00), the two plant stands were both exposed to 800 μmol mol^{-1} CO_2. The light and temperature treatments in this experiment were the same as in Exp. 1. The different treatments were administered over four consecutive days. The total leaf areas at the end of the experiment were 84 and 87 dm^2 in the 800 and 1200 μmol mol^{-1} CO_2 treatments, respectively (6.5 leaves per plant). This corresponded to an LAI of 3.5 and 3.6, respectively.

Exp. 4: The effect of temperature at different CO_2 concentrations during the photoperiod

In this experiment, supplementary light (300 μmol m^{-2} s^{-1}) was provided during the whole photoperiod (02.00–22.00). From 02.00 until 20.00, the temperatures were 25.0 ± 0.5, 30.0 ± 0.5 and 35.0 ± 0.5 °C, respectively, in the three cuvettes. From 20.00 to 22.00, the temperature was 25.0 ± 0.5 °C, and during the dark period (22.00–02.00 h), 20.0 ± 0.5 °C in all three cuvettes. The CO_2 concentration was 800 ± 50 μmol mol^{-1} during the period 02.00–08.00, 500 ± 30 μmol mol^{-1} during the period 08.00–14.00, 300 ± 30 μmol mol^{-1} during the period 14.00–20.00, and 800 ± 50 μmol mol^{-1} during the period 20.00–22.00. After one day of the same treatment in all three cuvettes, three different treatments were administered during the following four days. The total leaf area at the end of the experiment was 69 dm^2 in the different treatments (5.5 leaves per plant at 25 °C, increasing to 6.0 leaves at 35 °C). This corresponded to an LAI of 2.9.

Relative humidity (RH) varied between 70 and 90 % in the different experiments. At 80 % RH, the vapour pressure deficit (vpd) corresponded to 630, 850 and 1120 Pa at 25, 30 and 35 °C, respectively. Leaf temperature was typically about 1 °C lower than air temperature during the light period, and the maximum soil temperature was 1–2 °C lower than the air temperature in the different experiments.

The experiments were analysed using the SAS-GLM procedure (SAS Institute Inc., Cary, USA). The relative CER values for the different treatments for each day and period were used in the analysis. This was done in order to avoid the variation in CER from day to day obscuring the effect of the treatments. Days were used as replicates.

Results

Exp. 1: The effect of increasing the CO_2 concentration from 380 to 800 μmol mol^{-1}

When the two plant stands were exposed to 800 μmol mol^{-1} CO_2 in the morning (02.00–08.00) and evening (20.00–22.00), the CER was the same (Table 1). During the 12-hour daytime period (08.00–20.00) with different CO_2 concentrations, the CER at 800 μmol mol^{-1} was about 30 % higher than at 380 μmol mol^{-1}, irrespective of PFD, which varied from an average of 391 to 678 μmol m^{-2} s^{-1} in the three different periods. CER increased with PFD in both treatments. The overall daily increase in CER when the CO_2 concentration was kept high throughout the daytime (12 hours) was 23 %. Due to a failure of the cuvette system, dark respiration data were lost in this experiment.

Exp. 2: The effect of decreasing the CO_2 concentration below the ambient level

As long as the two plant stands were exposed to 800 μmol mol^{-1} CO_2 in the morning (02.00–08.00) and evening (20.00–22.00), the CER was the same (Table 1). During the three periods of the day (12 hours in total) with different concentrations, the CER decreased progressively from 20 to 35 % in plants at 210 μmol mol^{-1} CO_2 compared with those at 380 μmol mol^{-1}. The overall daily reduction in CER as a result of the reduced concentration during 12 daytime hours was 12 %. Respiration during the 4-hour dark period was the same in both treatments.

Exp. 3: The effect of increasing the CO_2 concentration from 800 to 1200 μmol mol^{-1}

As long as the two plant stands were exposed to 800 μmol mol^{-1} CO_2 in the morning (02.00–08.00), the CER was the same (Table 1). In the first period (08.00–12.00) with 1200 μmol mol^{-1} CO_2, the CER was increased by 28 % compared to 800 μmol mol^{-1} CO_2. This positive effect decreased to 18 and 7 %, respectively, during the next two periods of the day. When the two plant stands were exposed to the same concentration (800 μmol mol^{-1}) in the evening (20.00–22.00), the CER of the plants exposed to the higher concentration was 12 % lower than it was for the other concentration. The dark respiration was the same in both plant stands.

Exp. 4: Effect of temperature at different CO_2 concentrations during the photoperiod

In moderate light conditions with artificial light mainly in the early morning (02.00–08.00) and at a CO_2 concentration of 800 μmol mol^{-1}, the CER was the same at 25 and 30 °C and decreased by about 15 % at 35 °C (Table 2). As daylight increased during the following hours (08.00–14.00), CER was found to be the same irrespective of temperature as measured at 500 μmol mol^{-1} CO_2. When the CO_2 concentration further decreased to 300 μmol mol^{-1} (14.00–20.00 h), CER decreased as temperature increased above 25 °C. When the three plant stands were exposed to the same temperature (25 °C) in the evening, the CER was the same. Dark respiration as measured at 20 °C was highest in the plant stand treated at 25 °C. The overall daily CER was the same in the 25 and 30 °C treated plants, and decreased by 11 % at 35 °C.

Table 1. The effect on CER of 800 μmol mol^{-1} CO_2 compared with 380 μmol mol^{-1} in Exp. 1, of 380 μmol mol^{-1} CO_2 compared with 210 μmol mol^{-1} in Exp. 2, and on CER of 800 μmol mol^{-1} CO_2 compared with 1200 μmol mol^{-1} in Exp. 3. All experiments (n = 4, ± SD) take part during 12 hours (08.00–20.00) of daytime in one plant stand (CONTR), compared with another plant stand (VAR) For the remaining part of the photoperiod (02.00–08.00 and 20.00–22.00), both stands were exposed to 800 μmol mol^{-1}. In each period, CER is stated at plant stand level or on the basis of leaf area per second. Supplementary light was provided except in the middle of the day (12.00–17.00). Significance levels: ns, P > 0.05; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Period (hrs)	CO_2 conc. (μmol mol^{-1})	PFD (μmol m^{-2} s^{-1})		Total CER (mmol CO_2)		CER (μmol m^{-2} s^{-1})		CER Ratio CONTR/VAR	F-value and sign. level
	CONTR/VAR	Mean daylight	Suppl. light	CONTR	VAR	CONTR	VAR		
Exp. 1									
02–08	800/800	57 ± 25	300	86.4 ± 12.5	83.9 ± 15.7	2.76 ± 0.40	2.68 ± 0.50	1.04 ± 0.07	1.13^{ns}
08–12	800/380	378 ± 106	300	139.7 ± 20.3	106.7 ± 18.5	6.69 ± 0.97	5.11 ± 0.89	1.32 ± 0.06	105***
12–17	800/380	422 ± 59	0	144.6 ± 22.7	112.3 ± 17.2	5.62 ± 0.88	4.30 ± 0.66	1.29 ± 0.01	3249***
17–20	800/380	91 ± 38	300	64.4 ± 10.1	48.0 ± 6.9	4.11 ± 0.64	3.07 ± 0.44	1.34 ± 0.02	1072***
20–22	800/800	0 ± 0	300	24.4 ± 4.3	24.0 ± 4.6	2.34 ± 0.41	2.30 ± 0.44	0.99 ± 0.04	0.22^{ns}
02–22				459.0 ± 67.0	375.0 ± 59.0	4.10 ± 0.60	3.60 ± 0.10	1.23 ± 0.02	487***
Exp. 2									
02–08	800/800	27 ± 25	300	22.3 ± 7.1	23.6 ± 7.9	2.45 ± 0.78	2.52 ± 0.80	1.06 ± 0.07	3.04^{ns}
08–12	380/210	151 ± 130	300	18.3 ± 8.9	14.5 ± 7.0	3.02 ± 1.47	2.32 ± 1.12	0.80 ± 0.08	28.5***
12–17	380/210	115 ± 47	0	6.6 ± 5.6	4.5 ± 3.8	0.87 ± 0.74	0.57 ± 0.48	0.76 ± 0.16	8.93*
17–20	380/210	17 ± 11	300	10.4 ± 2.4	6.9 ± 2.1	2.29 ± 0.53	1.46 ± 0.46	0.65 ± 0.09	55.3***
20–22	800/800	0 ± 0	300	8.8 ± 0.9	9.5 ± 1.8	2.90 ± 0.30	3.04 ± 0.57	1.08 ± 0.13	0.89^{ns}
22–02	800/800	0 ± 0	0	−4.7 ± 1.4	−4.7 ± 1.1	−0.78 ± 0.23	−0.75 ± 0.18	1.02 ± 0.08	0.15^{ns}
02–22				66.3 ± 23.5	58.9 ± 21.5	2.19 ± 0.78	1.88 ± 0.69	0.89 ± 0.03	49.4***
Total 24 hrs				61.7 ± 22.2	54.2 ± 20.4	1.70 ± 0.61	1.22 ± 0.46	0.88 ± 0.03	40.2***
% respir.				7.3 ± 1.3	9.7 ± 1.8				1.02^{ns}
Exp. 3									
02–08	800/800	42 ± 9	300	48.4 ± 8.9	49.9 ± 11.5	2.67 ± 0.49	2.66 ± 0.61	1.02 ± 0.06	0.51^{ns}
08–12	800/1200	295 ± 63	300	68.9 ± 13.7	88.1 ± 17.4	5.70 ± 1.13	7.03 ± 1.39	1.28 ± 0.03	470***
12–17	800/1200	234 ± 42	0	54.2 ± 13.1	64.0 ± 15.5	3.58 ± 0.87	4.09 ± 0.99	1.18 ± 0.13	7.17*
17–20	800/1200	25 ± 6	300	29.5 ± 14.8	31.6 ± 5.9	3.25 ± 0.53	3.36 ± 0.67	1.07 ± 0.05	9.00*
20–22	800/800	0 ± 0	300	16.4 ± 1.7	15.0 ± 2.7	2.71 ± 0.28	2.61 ± 0.47	0.88 ± 0.06	15.0*
22–02	800/800		0	−13.7 ± 2.7	−14.5 ± 4.0	−1.13 ± 0.22	−1.16 ± 0.32	1.05 ± 0.10	0.84^{ns}
02–22				217.4 ± 37.7	248.6 ± 50.3	3.59 ± 0.64	3.97 ± 0.80	1.14 ± 0.06	23.5**
Total 24 hrs				203.7 ± 35.3	234.1 ± 46.5	2.81 ± 0.49	3.11 ± 0.62	1.15 ± 0.06	28.8**
% respir.				6.3 ± 0.6	6.5 ± 0.8				1.07^{ns}

Discussion

The approximately 30 % increase in CER found with a rise in CO_2 concentration from 380 to 800 μmol mol^{-1} is in accordance with yield (Kläring et al. 2007) as well as with previous photosynthetic measurements of cucumber (Nederhoff and Vegter 1994). However, the present results also show that the same percentage effect was maintained throughout the entire 12-hour daytime period at PFD levels ranging between about 400 and 700 μmol m^{-2} s^{-1} obtained by a combination of daylight and supplementary light. Photosynthesis increased with increasing PFD, and no light saturation of CER took place at these light levels, which is in accordance with previous results with cucumber (Hand et al. 1993; Nederhoff and Vegter 1994). Indeed, Janoudi et al. (1993) found a saturation level of 1000 μmol m^{-2} s^{-1} PFD in leaves of this species. No negative acclimation of photosynthesis seemed to take place during the day at the 800 μmol mol^{-1} CO_2 level. However, when the concentration was increased from 800 to 1200 μmol mol^{-1}, a significant positive effect found in the first few hours progressively decreased towards the

Table 2. The effect of temperature on CER (± SD, n = 4) in small stands of cucumber at 25, 30 and 35 °C during different periods of the day with different CO_2 concentrations in Exp. 4. Relative units (± SD) of CER are stated in parenthesis. The temperature during the period 20.00–22.00 was 25 °C and during the dark period (22.00–02.00) 20 °C in all three treatments.

Period (hrs)	CO_2 conc. (µmol mol^{-1})	PFD (µmol m^{-2} s^{-1})		Total CER in each period (mmol CO_2)			CER per leaf area unit and second (µmol m^{-2} s^{-1})			F-value and sign. level
		Mean daylight	Suppl. light	25 °C	30 °C	35 °C	25 °C	30 °C	35 °C	
02–08	800	42 ± 14	300	33.1 ± 6.2 (100 ± 0)	29.6 ± 7.1 (91 ± 6)	27.3 ± 4.1 (83 ± 5)	2.22 ± 0.42	1.99 ± 0.48	1.83 ± 0.27	12.8**
08–14	500	448 ± 62	300	79.7 ± 23.9 (100 ± 0)	80.7 ± 26.9 (99 ± 8)	78.0 ± 22.8 (98 ± 3)	5.35 ± 1.60	5.41 ± 1.80	5.23 ± 1.53	0.14^{ns}
14–20	300	158 ± 53	300	46.5 ± 12.5 (100 ± 0)	41.4 ± 11.4 (90 ± 2)	33.5 ± 7.9 (72 ± 3)	3.12 ± 0.84	2.78 ± 0.77	2.25 ± 0.53	150***
20–22 (25 °C)	800	0 ± 0	300	13.3 ± 3.8 (100 ± 0)	14.6 ± 3.3 (111 ± 10)	14.4 ± 3.5 (109 ± 12)	2.68 ± 0.77	2.94 ± 0.66	2.90 ± 0.70	1.59^{ns}
22–02 (20 °C)	800		0	−12.4 ± 2.6 (100 ± 0)	−9.4 ± 2.5 (76 ± 6)	−8.8 ± 1.8 (72 ± 11)	−1.25 ± 0.26	−0.95 ± 0.25	−0.89 ± 0.18	16.8***
02–22				173 ± 45 (100 ± 0)	166 ± 47 (96 ± 4)	153 ± 36 (89 ± 3)	3.48 ± 0.91	3.34 ± 0.95	3.08 ± 0.72	17.7***
Total 24 hrs				160 ± 44 (100 ± 0)	157 ± 46 (97 ± 4)	143 ± 38 (89 ± 4)	2.68 ± 0.74	2.63 ± 0.77	2.40 ± 0.63	14.9**
% respiration				7.3 ± 1.2	5.9 ± 1.3	5.9 ± 1.3				1.62^{ns}

end of a 12-hour exposure period. The negative acclimation at 1200 compared to 800 µmol mol^{-1} CO_2 was demonstrated by the lower CER of these plants when exposed to the same CO_2 concentration at the end of the photoperiod. Reduced CER in plants grown at high CO_2 concentrations (1000–2000 µmol mol^{-1}) over time has long been known in cucumber (Aoki and Yabuki 1977) as well as in many other species (Reddy et al. 2010). It should be noted that, in spite of the negative acclimation at 1200 µmol mol^{-1} CO_2, this concentration resulted in a higher daily CER than at 800 µmol mol^{-1}. The limited negative acclimation could be related to restored photosynthetic efficiency after the four-hour dark period. The reason for the decrease in the positive effect of 1200 µmol mol^{-1} CO_2 during the day might be an accumulation in the non-structural carbohydrate content, as previously shown for cucumber (Aguera et al. 2006; Kosobryukhov 2008). Other possible reasons for lowered photosynthesis could be a low electron transport rate, RuBP regeneration rate and Pi availability (Kosobryukhov 2008). Also at low CO_2 concentrations (about 200 µmol mol^{-1}), acclimation took place with an increasingly negative effect during the 12-hour daytime period. In a review, Sage and Kubien (2007) concluded that, at < 300 µmol mol^{-1} CO_2, the Rubisco capacity is the predominant limitation on assimilation. Irrespective of the reason for the decline in CER, a dark period seems to be sufficient to restore photosynthetic efficiency. New leaves develop very quickly in cucumber and the assimilate flow to new developing leaves will necessarily be high. Since new leaves develop very quickly (about one per day), the younger leaves will contribute most to photosynthesis by shading the older leaves (Pettersen et al. 2010). Cucumber canopies might therefore be less prone to negative acclimation to high CO_2 concentrations than other crops with a slower leaf development rate. Stomatal conductance and transpiration in cucumber appear to be little affected by CO_2 concentrations in the range 100 to 2000 µmol mol^{-1} (Larios et al. 2001; Aguera et al. 2006), and stomata responses were therefore unlikely to be the reason for reduced CER.

The present results, which show that high temperatures (about 30 °C) can be beneficial as long as the CO_2 concentration is kept high and the light conditions are good, are in accordance with previous results for cut roses (Urban et al. 2001). However, low CO_2 levels when temperature is high greatly reduce photosynthesis, and measures should therefore be taken to keep the CO_2 concentration high under such conditions. Plants grown at elevated CO_2 concentrations are also likely to tolerate higher temperatures with respect to CER than plants grown at ambient concentrations (Taub et al. 2000). It is also important to note that, in many species, the optimal temperature that maximises CER increases with increasing growth temperatures (Hikosaka et al. 2006). It might be surprising that respiration during the four-hour dark period was found to be highest in the 25 °C-exposed plants. However, given that the night temperature was 20 °C in all treatments, this should also be expected. At

high temperatures during the day (30 and 35 °C), respiration will be very high and less amounts of carbohydrates will probably be available for respiration during the short night.

High root temperatures might be critical when plants are grown at high air temperatures. However, CER has been found to be unaffected by root temperatures in the range of 25 to 35 °C in cucumber (CHEN and TACHIBANA 1994). ZHANG et al. (2008) found a slight reduction in CER when increasing the root temperature from 24 to 34 °C, while NADA and TACHIBANA (2003) found a detrimental effect when increasing the temperature from 30 to 38 °C in cucumber. In the present experiments, therefore, the soil temperature, which reached a maximum of around 33 °C, probably did not influence the CER.

The results show that adding moderate amounts of CO_2 gas can be strongly recommended in order to avoid the very negative effect of below-ambient CO_2 concentrations in the greenhouse atmosphere. Because of ventilation, it is difficult to maintain a high CO_2 concentration during daytime at high solar radiation. However, endeavours should be made to keep the concentration as high as possible without using too much CO_2 gas. Maintaining a high CO_2 concentration throughout the day is probably the most efficient means of further improving crop yield in greenhouses. Great effort should therefore be put into developing a closed greenhouse technology that is cheap enough to be used in practice. Since quite high air temperatures are acceptable in a CO_2-enriched atmosphere, less cooling capacity might be needed in closed greenhouses.

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