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The Effect of High CO_2 Concentrations on Diurnal Photosynthesis at High Daytime Temperatures in Small Stands of Cut Roses

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Summary

The aim of this study was to examine the effect of CO_2 concentrations on diurnal carbon dioxide exchange rates (CER) including periods of high daytime temperatures in cut roses. Climatic conditions typical of winter as well as summer production were included. At a photon flux density (PFD) of 225 μmol m^{-2} s^{-1} artificial light supplied 20 hours day^{-1} (winter production) a six-hour increase in temperature from 20 to 32 °C had a minor effect on the CER when the CO_2 concentration was maintained at 800 μmol mol^{-1} CO_2, while the CER decreased by 75 % when the CO_2 concentration dropped to 370 μmol mol^{-1}. Under high light intensity typical of summer conditions (800 μmol m^{-2} s^{-1} PFD), the CER was around 60 % higher at 800 μmol mol^{-1} CO_2/32 °C (simulating a closed greenhouse) as compared to 370 μmol mol^{-1} CO_2/22 °C (simulating a ventilated greenhouse). In an experiment in summer daylight, the night temperature was 15 °C and increased by 2.8 °C per 100 μmol m^{-2} s^{-1} PFD to a maximum of around 32 °C. The CER was measured in two plant stands, one at 370 and the other at 800 μmol mol^{-1} CO_2. The overall effect over 17 days showed a significant correlation between the CER and the PFD (r^2 = 0.74). Increasing the CO_2 concentration from 370 to 800 μmol mol^{-1} CO_2 increased the CER by around 50 % during a six-hour period when the temperature reached 32 °C. Due to the lack of any CO_2 effect during morning and evening (lower temperatures), the overall diurnal CO_2 effect was only 15 %. The results are discussed in relation to controlling the greenhouse climate in traditional greenhouses in winter as well as in closed greenhouses with internal cooling systems in summer.

Key words. Artificial light – closed greenhouses – CO_2 concentration – daylight – photon flux density – photosynthesis – temperature

Introduction

High CO_2 concentrations (800–1000 μmol mol^{-1}) in the greenhouse atmosphere are necessary for optimal growth and the yield of many crops, including roses (Mortensen and Moe 1983; Jiao et al. 1991; Urban et al. 2001; Kim and Lieth 2003). The effect of CO_2 enrichment is greatest at high irradiance levels. However, at such levels, greenhouses are normally ventilated in order to keep the temperature low. In traditional ventilated greenhouses, it is difficult to maintain high CO_2 concentrations during periods of high radiation even with huge amounts of CO_2 gas (Qian et al. 2011). In closed and semi-closed greenhouses where there is an active cooling system and energy-saving measures have been implemented, it is possible to maintain high CO_2 concentrations even at high light levels (Campen and Kempkes 2011; Qian et al. 2011). Closed greenhouse technology is still very expensive and is therefore of limited practical interest at present. In future, however, such greenhouses might be necessary to achieve maximum light utilisation.

It is generally accepted that the optimal temperature for photosynthesis is increased by CO_2 enrichment as well as by increased irradiance levels, as also shown for roses (Jiao et al. 1991; Kim and Lieth 2003). The main part of photosynthesis in roses takes place during the middle of the day when the irradiance levels in the greenhouse are highest, as photosynthesis of roses increases to a photon flux density (PFD) of around 1000 μmol m^{-2} s^{-1} (Jiao et al. 1988; Mortensen 1995; Kim and Lieth 2003). Unfortunately, it is difficult to maintain a high CO_2 concentration at this time of the day as the temperature has to be kept low by ventilation.

The shoot length of roses decreases with increasing mean air temperature, but it is little affected by variation during the day (Moe 1972; Rijsdijk and Vogelezang 2000). Artificial lighting (200–250 μmol m^{-2} s^{-1} PFD) is necessary for efficient rose production at high latitudes during winter due to low solar radiation (Mortensen and Gislerød 1994). In well-insulated greenhouses, the heat from the lamps can increase the temperature by 20–30 °C, and ventilation is therefore often required at this time of year.

The aim of the experiment was to study the extent to which daily photosynthesis of roses could be increased by allowing the air temperature to rise rather than using ventilation and losing CO_2 control. In the present study, we studied the effect of CO_2 enrichment during a period of high temperature with artificial light simulating winter rose production. In addition, the effect of CO_2 was studied under summer daylight conditions where the temperature increased progressively with the irradiance level. In both cases, the mean air temperature was kept low enough to ensure acceptable shoot quality.

Materials and Methods

Plants of *Rosa hybrida* 'Red Champ' were propagated from cuttings in a mixture of limed fertilised peat (Humus-börsen), sand (5 % by volume) and perlite (33 % by volume). After rooting, the plants were placed in the same substrate in 3-l pots, one plant per pot, and grown under supplementary light. They were kept small by regular pinching. One-year-old plants were pinched above 20 cm and new shoots were allowed to develop.

When buds became visible, two pots were placed in two separate cuvette units, as previously described by Mortensen and Gislerød (2012). The CO_2 exchange rate (CER) was recorded continuously. The cuvette units had a volume of 293 litres (500 × 480 × 1220 mm) and were placed in a greenhouse compartment. The plant floor in each cuvette was 0.24 m^2. The carbon dioxide concentration was controlled by adding pure CO_2 from a container to each cuvette. Two 400 W and two 600 W high-pressure sodium lamps (Philips SON-T) supplying from 0 to 800 μmol m^{-2} s^{-1} photon flux densities (PFD) at plant level were mounted above each of the cuvette units. Light was measured by means of a Lambda LI-185B with quantum sensor (400–700 nm). Daylight could be eliminated using black curtains.

Experiments in artificial light

Two experiments were carried out in small plant stands, i.e. two rose plants with a total of six flowering shoots in Experiment 1 and four shoots in Experiment 2. All daylight was eliminated using black curtains.

Experiment 1. CER was measured in two plant stands growing at 225 μmol m^{-2} s^{-1} PFD for 20 hours day^{-1} (16.2 mol m^{-2} day^{-1}), an air temperature of 20.0 ± 0.5 °C (constant) and a CO_2 concentration of 800 ± 30 μmol mol^{-1} on Day 1. During Days 2–4, one plant stand (total leaf area 46.4 dm^2) was exposed to six hours (in the middle of the light period) of 32.0 ± 0.5 °C/800 μmol mol^{-1} CO_2 and the other (total leaf area 45.6 dm^2) to six hours of 32 °C/370 ± 30 μmol mol^{-1} CO_2. The mean temperature in this period was 23.0 °C. Over the next two days (Days 5–6), the treatment was the same as on Day 1. Air and leaf temperatures were the same and correlated with each other, while the soil temperature change was delayed one to two hours compared with the air temperature and reached a maximum of 30 °C. Air humidity was generally 80 ± 5 % RH, increasing to around 90 % during the four-hour dark period.

Experiment 2. CER was measured in two plant stands at 225 μmol m^{-2} s^{-1} PFD for 20 hours day^{-1} (16.2 mol m^{-2} day^{-1}), with an air temperature of 20.0 ± 0.5 °C and a CO_2 concentration of 800 ± 30 μmol mol^{-1} on Day 1. During Days 2–4, both stands were exposed to 225 μmol m^{-2} s^{-1} PFD for 14 hours day^{-1} and 800 μmol m^{-2} s^{-1} PFD for six hours day^{-1}. During the six hours with high PFD one stand was exposed to 32 °C/800 μmol mol^{-1} CO_2 (total leaf area 26.0 dm^2) and the other stand (total leaf area 25.9 dm^2) to 22 °C/370 ± 30 μmol mol^{-1} CO_2. The total photosynthetic active radiation was 28.6 mol m^{-2} day^{-1}. The treatment administered on Day 5 was the same as on Day 1. Air and leaf temperatures were generally the same and correlated with each other, except during the six-hour period with 22 °C/800 μmol m^{-2} s^{-1} PFD, when leaf temperature was 1.0–1.5 °K higher than the air temperature. The soil temperature was 20 °C, increasing to a maximum of 30 °C in the period with 32 °C air temperature and to 22 °C with 20 °C air temperature. The soil temperature change was delayed one to two hours compared with the air temperature. Air humidity was generally 75 ± 5 % at 225 μmol m^{-2} s^{-1} PFD and 70 ± 5 % at 800 μmol m^{-2} s^{-1}, increasing to around 90 % RH during the dark period.

Experiment in daylight

Experiment 3 was carried out using daylight only from 20 June until 6 July (17 days) on three rose plants in two separate cuvettes. On Days 1–2 and 15–17, the temperature was constant at 20.0 ± 0.5 °C. From Days 3 to 14, the night temperature was 15.0 °C, and the temperature in the cuvettes was set to increase by 2.5 °K per 100 W m^{-2} increase in outdoor global radiation. This corresponded to a 2.8 °K increase per 100 μmol m^{-2} s^{-1} PFD inside the cuvettes (at plant level). Air temperature and PFD level were measured every half-hour during the experimental period of 17 days. The daily mean air temperature varied from 18 °C to 23 °C depending on the daily radiation. The CO_2 concentration on Days 1–3 and 15–17 was 370 ± 30 μmol mol^{-1} in both cuvettes. During Days 4–14, two treatments were administered, 370 ± 30 μmol mol^{-1} in one cuvette and 800 ± 30 μmol mol^{-1} in the other. Daily radiation was similar on Days 9–17 (15.0 ± 0.6 mol m^{-2} day^{-1}), and this time period (6 days) was therefore used to compare the effect of the different treatments (Days 9–14), and as a control given the same climate (20 °C/370 ± 30 μmol mol^{-1} during Days 15–17). The total leaf area of the plant stand at 370 and 800 μmol mol^{-1} CO_2 was 68.4 and 67.5 dm^2, respectively. In general, the leaf temperature correlated with the air temperature, and the soil

temperature correlated with the air temperature, with a delay of one to two hours. The CER was recorded every half-hour and summarised each day. The reason why CER was measured each half-hour in this experiment and only each hour in the experiments with artificial light, is explained by the variable light and temperature conditions in daylight. The data were analysed using the SAS-GLM procedure (SAS Institute Inc., Cary, USA) based on the relative CER values for each day. Days were used as replicates.

Results

In Experiment 1, the CERs of the two plant stands growing in two different cuvette units were similar as long as the treatment was the same, 20 °C and 800 µmol mol^{-1} CO_2 (Fig. 1A). At the start of the light period, photosynthesis increased rapidly to around 80 % of the maximum within one to two hours, thereafter slowly to the maximum within around ten hours. This was followed by a gradual decrease to around 70 % of maximum at the end of the light period.

When the temperature was raised from 20 °C to 32 °C for six hours at the same time as the CO_2 concentration was lowered from 800 to 370 µmol mol^{-1}, the CER decreased by around 75 % (Fig. 1B). On reversing this treatment, the CER recovered relatively quickly. When a high CO_2 concentration was maintained, the CER decreased by 25 % during the first hour at 32 °C, and thereafter recovered quickly to the rate at 20 °C.

In Experiment 2, the CERs of the two plant stands were similar when grown in the same climate conditions at 20 °C, 800 µmol mol^{-1} CO_2 and 225 µmol m^{-2} s^{-1} PFD for 20 hours day^{-1} (Fig. 2A). When the PFD was increased

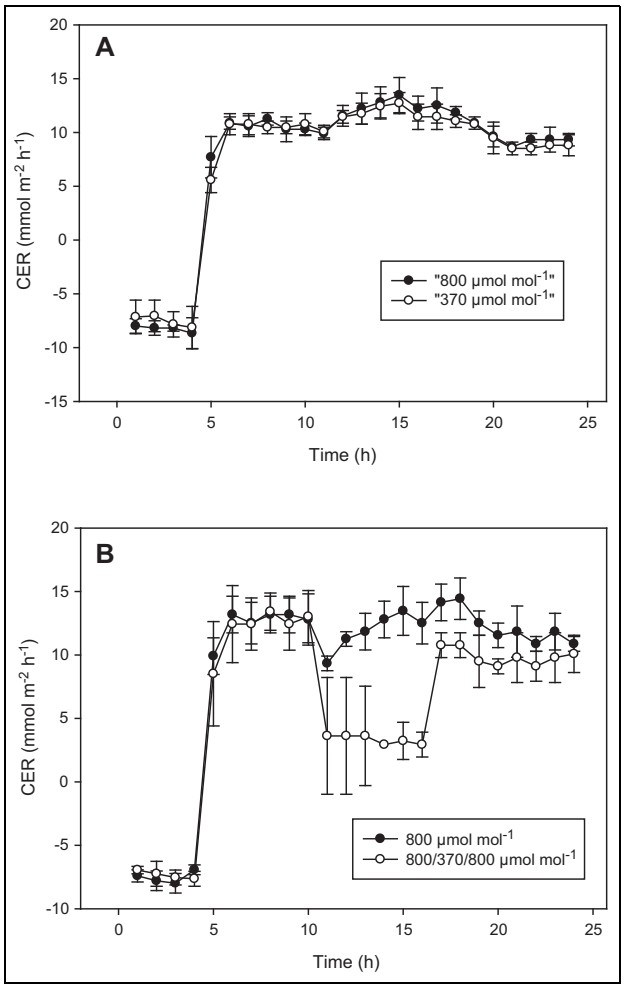


Fig. 1. The CER (n = 3, ± SD) in roses in Experiment 1 as measured under the same constant climate conditions (A) and on days when the temperature was increased from 20 to 32 °C during a six-hour period (10.00–16.00) while keeping the CO_2 concentration at 800 µmol mol^{-1} or decreasing it to 370 µmol mol^{-1} (B).

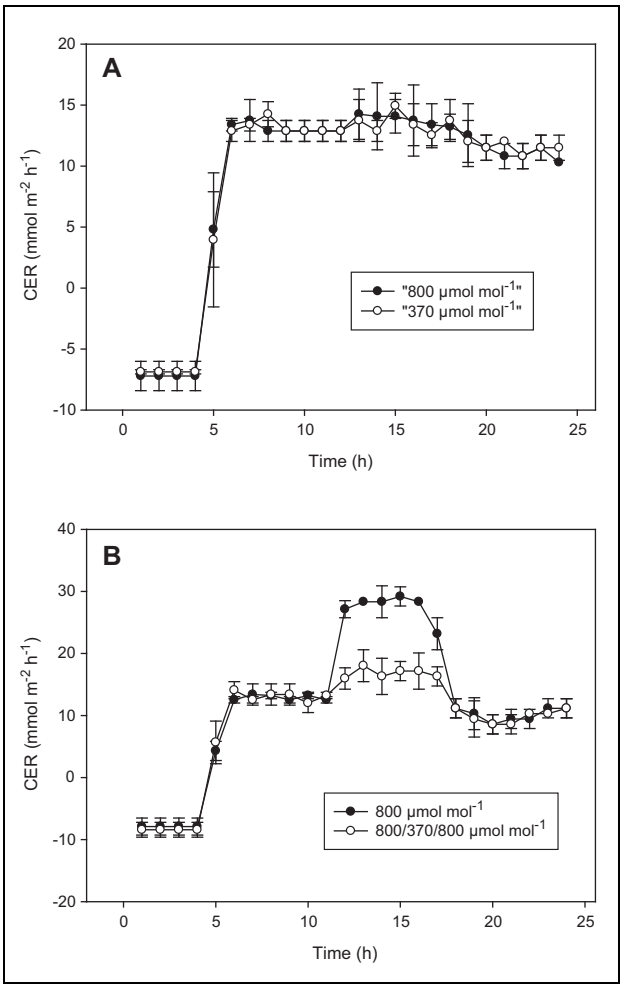


Fig. 2. The CER in roses in Experiment 2A as measured under the same constant climate conditions (n = 2, ± SD) at 225 µmol m^{-2} s^{-1} PFD and 20 °C (A). In Experiment 2B, the PFD was increased from 225 to 800 µmol m^{-2} s^{-1} during a six-hour period (11.00–17.00). During this period, one plant stand was exposed to 800 µmol mol^{-1} CO_2 combined with 32 °C air temperature, and the other to 370 µmol mol^{-1} CO_2 and 22 °C (n = 3, ± SD).

from 225 to 800 μmol m^{-2} s^{-1} for six hours at the same time as the temperature was raised from 20 °C to 32 °C and the CO_2 concentration maintained at a high level, the CER increased by around 125 % (Fig. 2B). In the other plant stand, which was also exposed to the same increase in PFD but where the temperature was raised to 22 °C combined with a drop in CO_2 concentration from 800 to 370 μmol mol^{-1} (simulated ventilation), the CER only increased by 25 %. During this six-hour period, the CER at high CO_2/32 °C was 64 % higher than at low CO_2/22 °C.

A significant correlation ($r^2 = 0.74$, $P < 0.001$, $n = 17$) was found between the CER and the PFD in the experiment that only used daylight, which varied in the range of 0–650 μmol m^{-2} s^{-1} (Fig. 3A, 3B)). In the experimental period (Day 3–14), the temperature varied with the PFD. During Days 9–14, the weather was sunny and the PFD similar, and the mean diurnal CER values are presented for these six days (Fig. 4A, 4B). During the hours in the middle of the day, the PFD reached around 650 μmol m^{-2} s^{-1} with a corresponding air temperature of around 32 °C (Fig. 4B, 4C). Under these climate conditions, the CER of the plants at 800 μmol mol^{-1} CO_2 was around 50 % higher than the plants at a concentration of 370 μmol mol^{-1} (Table 1). As a percentage of the CER during the light period, respiration during the dark period (from about 20.30 h until about 04.30 h) was unaffected by the CO_2 concentration (Table 1). When the two plant stands were exposed to the same climate (20 °C/370 μmol mol^{-1} CO_2) on Days 15–17, the CER was the same (Fig. 5). During this period, the mean total CER was 186 ± 17 and 185 ± 6 mmol m^{-2} day^{-1} in the 370 and 800 μmol mol^{-1} CO_2 stands, respectively (data not presented).

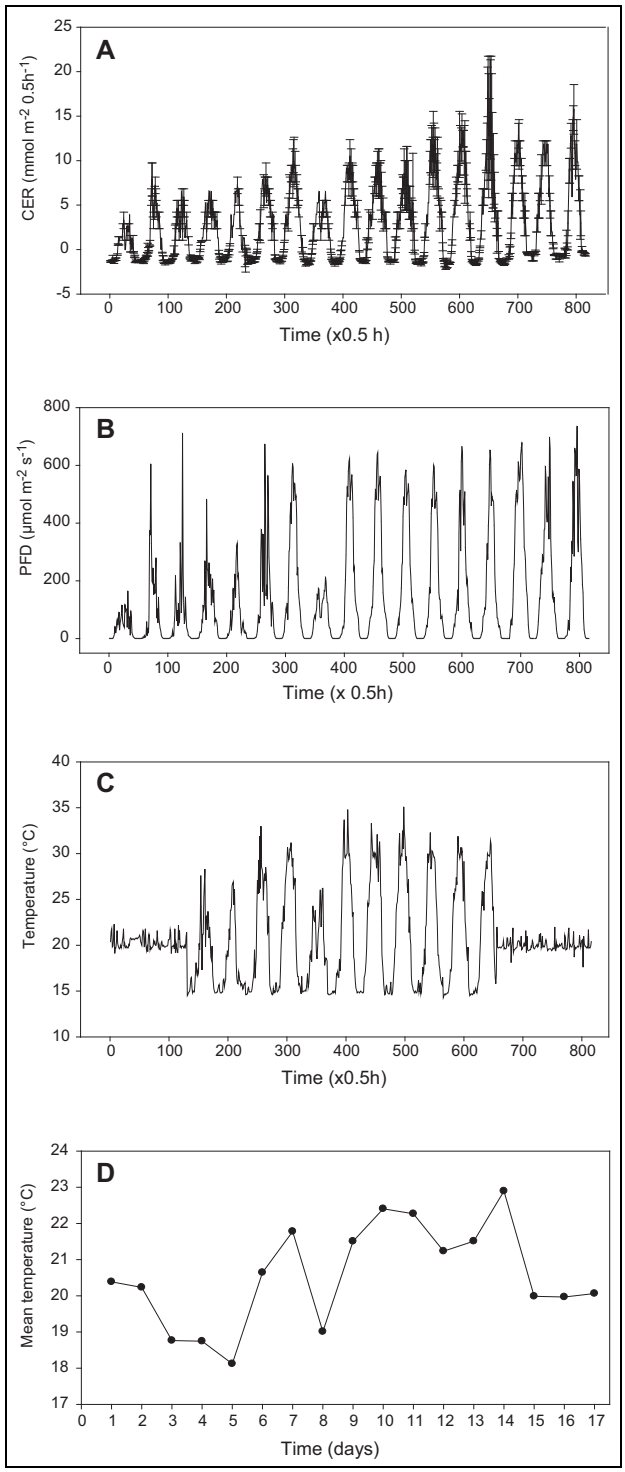


Fig. 3. Diurnal CER (n = 2, ± SD) in roses as measured per half-hour (A) during 17 days in daylight in Experiment 3. The accompanying diurnal PFD (B) and temperature (C) as well as mean daytime temperature (D) are provided.

Discussion

The diurnal photosynthesis found in the present experiment was very similar to that previously found in roses under constant climate conditions (Mortensen 1995). Using artificial lighting typical of that used in the winter production of roses at high latitudes, photosynthesis was more or less unchanged during a period with a temperature increase from 20 to 32 °C as long as the CO_2 concentration was maintained at a high level. Due to the heat from lamps used for artificial lighting, the greenhouse temperature can often increase to this level without ventilation. In practical rose production, ventilation will usually lower the temperature to around 22 °C with an accompanying drop in the CO_2 concentration. However, such a drop will immediately lead to a 30–40 % decrease in photosynthesis (Mortensen and Moe 1983; Jiao et al. 1988; Urban et al. 2001). These results show that delayed ventilation would therefore be beneficial. Experience of practical rose production also supports such a conclusion (Krohn, personal communication). However, high temperatures will adversely affect photosynthesis under low to moderate light conditions at ambient CO_2 concentrations and should be avoided. If photosynthesis in roses is to benefit from an increasing irradiance level, this increase should not result in ventilation (due to the heat load) and a drop in the CO_2 concentration. As the present results show, a three-fold increase in the PFD caused a two-fold increase

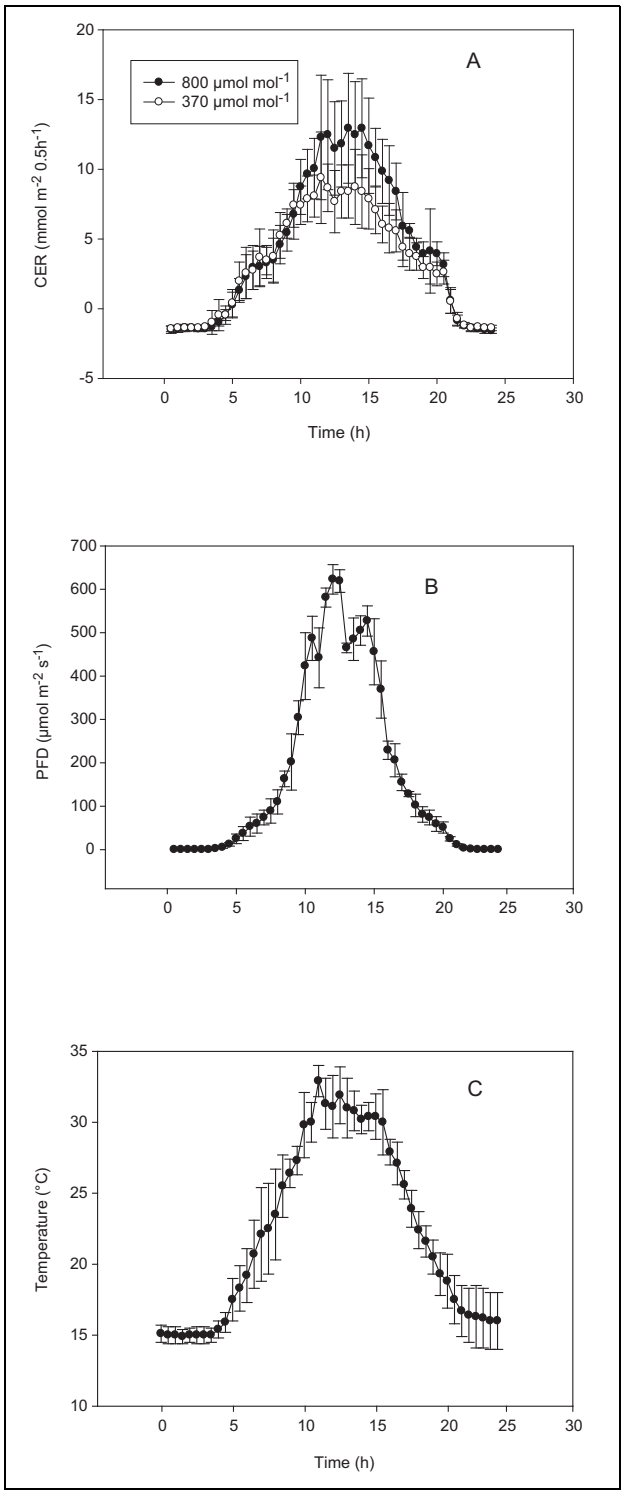


Fig. 4. Diurnal CER (A) in roses as a mean of six days (n = 6, ± SD) as measured at 370 and 800 µmol mol^{-1} CO_2 in Experiment 3. The accompanying diurnal PFD (B) and temperature (C) are provided.

in the CER if the temperature was allowed to increase and the CO_2 concentration was kept high. The increase caused by the PFD in the CER only had a minor effect, with a simultaneous drop in the CO_2 level. For optimal CER, temperatures of up to around 30 °C would probably be beneficial if this is required to avoid ventilation. A positive byproduct of a daily period of high temperature may be a reduction in powdery mildew in roses (Xu 1999; Mortensen et al. 2006).

In the experiment using daylight, the CER was found to be positively correlated with the PFD, which is in line with previous results showing that the photosynthesis of cut roses increases by around 1000 µmol m^{-2} s^{-1} PFD (Jiao et al. 1988; Mortensen 1995). It was also evident from the experiment using daylight that a high CO_2 concentration is a prerequisite for rose plants to efficiently utilise a high PFD level when the temperature increases. While a very strong CO_2 effect (around 50 %) was found in temperatures of above 30 °C during the middle of the day, the overall effect during a 24-hour period was much lower (around 15 %). The diurnal variation in temperature was from 15 to 32 °C, and it may be that the low temperature explains the absence of a CO_2 effect during large parts of the day. The positive effect of high CO_2 concentrations on photosynthesis is known to be related to a reduction in photorespiration in plants, a process that increases with rising temperatures (Joliffe and Tregunna 1968; Brooks and Farquhar 1985; Urban et al. 2001). The effect of CO_2 enrichment is therefore also likely to increase with rising temperatures. In chrysanthemum, photorespiration expressed by O_2 inhibition of photosynthesis at ambient CO_2 concentrations increased from 15 % at around 15 °C to 50 % at 30 °C (Mortensen 1983). This was reflected in a CO_2 enrichment effect of an increase of around 25 % at 15 °C to 50 % at 30 °C. In the present experiment, however, the total daily effect of CO_2 on the CER was lower than expected given the very strong effect during the middle of the day.

In order to control plant quality and the time until flowering, the high daytime temperatures at high irradiances should be compensated by lower temperatures during the night or when the irradiance is low (Rijsdijk and Vogelezang 2000; Dieleman et al. 2005). In the case of roses, an increase in daily average air temperature is known to reduce the shoot length of roses, and the temperature should therefore be kept sufficiently low for quality reasons (Moe 1972). Very high temperatures during the middle of the day with high solar radiation must therefore be balanced with relatively low temperatures during the remaining part of the day.

The present results, however, raise the question of whether strong diurnal temperature variation including a low minimum temperature will decrease the overall effect of CO_2 enrichment compared with less temperature variation. In practice, high CO_2 concentrations can be maintained in the winter production of roses (with artificial light) if the temperature is allowed to increase to around 30 °C without ventilation. However, during large parts of the year, high CO_2 levels can only be maintained in closed greenhouses with a cooling system. The potential of such greenhouses, however, will depend on the magnitude of

Table 1. Mean CER per m² leaf area (± SD, n = 6) as measured as a total per day (respiration during night-time included) or during a six-hour period (CER-6 h) from 11.00 to 17.00 at two CO_2 concentrations in Experiment 3. Respiration is given for the night period (from 20.30 until 04.30). F-values and significance levels are given: ns, $p > 0.05$; *$p < 0.001$.

CO_2 conc.	Total CER (mmol m^{-2} day^{-1})	CER 6-h (mmol m^{-2})	Respiration (mmol m^{-2})	% resp. of CER in the light period
370	182 ± 37	82 ± 20	18.3 ± 3.0	9.3 ± 1.8
800	210 ± 45	123 ± 30	20.4 ± 3.7	8.9 ± 1.4
Ratio 370/800	0.87 ± 0.04	0.68 ± 0.11	0.90 ± 0.05	
Sign. level	59.8*	48.9*	27.1*	0.16^{ns}

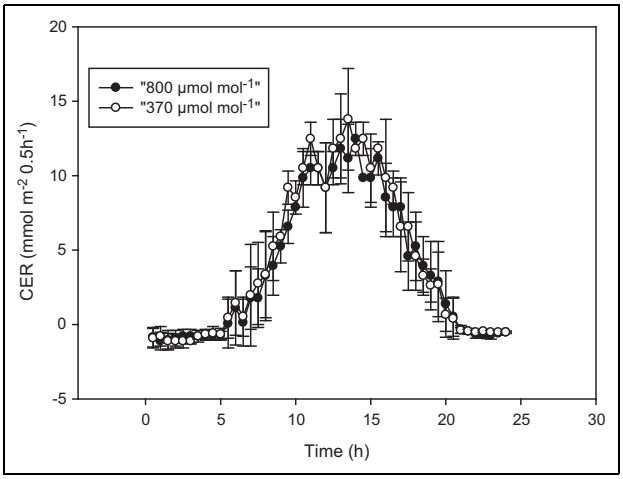


Fig. 5. Diurnal CER in roses as a mean of three days (n = 3, ± SD) measured at 370 µmol mol^{-1} CO_2 and 20 °C in plant stand previously grown at 370 and 800 µmol mol^{-1} CO_2 and variable temperature in Experiment 3.

the CO_2 effect achieved compared with traditional greenhouses. In this respect, it is important to know the maximum acceptable temperature in such greenhouses, since this will significantly influence the investment costs. More studies should therefore be conducted where the CO_2 effect is monitored under diurnal temperature and PFD variations.

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