

EJHS 2017-1**The effect of low night temperature and CO₂ concentration on diurnal photosynthesis of a small canopy of *Argyranthemum frutescens* at high-light conditions**

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Abstract

The main objective of this work was to investigate if a temperature drop during the night would influence the effect of CO₂ enrichment on photosynthesis. The diurnal carbon exchange rate (CER) was continuously measured on a small canopy of *Argyranthemum frutescens* at different day/night temperature fluctuations in ambient (250-415 $\mu\text{mol mol}^{-1}$) and CO₂ enriched environments (900-1250 $\mu\text{mol mol}^{-1}$). The diurnal light conditions of clear late spring days inside a greenhouse were simulated by means of LED lamps (0-800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density, PFD). The daily photosynthetic active radiation (PAR) was 26.3 $\text{mol m}^{-2} \text{day}^{-1}$ during the 16 h photoperiod. In the first experiment, a drop from a day temperature of 20°C to 7°C during the night (8 h) had no effect on CER during the following light period as compared with maintaining a constant temperature. This result was independent of the CO₂ level. Enriching the air with CO₂ roughly doubled the daily CER irrespective of the night temperature. A night temperature drop decreased the dark respiration by 32% at low and 63% at high CO₂ levels. A combination of high CO₂ level and temperature drop gave the maximal CER per day. In the second experiment, the effect of a temperature fluctuation from a minimum of 11°C in the night to a maximum of 31°C in the middle of the day, was compared with a night minimum of 7°C combined with constant 21°C during the day at the two CO₂ levels. The high temperature treatment decreased the daily CER by 34% at low and 27% at high CO₂ level, as compared with the low temperature treatment. The CER during a 6-h period in the middle of the day at 31°C/high CO₂ was 80-100% higher than at 21°C/low CO₂. The higher night temperature had little effect on the respiration at low CO₂ but increased by 139% at high CO₂. While CER increased progressively with PFD up to 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at high CO₂ level, CER started to level off at 500-600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD at low CO₂ in both

experiments. It was concluded that low night temperatures had a positive effect on the total net CER per day irrespective of CO₂ concentration. The results are discussed in relation to climate control and new greenhouse technology.

Keywords

Carbon dioxide exchange rate, photon flux density, respiration, temperature

Significance of this study

What is already known on this subject?

It is already known that CO₂ enrichment increases photosynthesis of plants.

What are the new findings?

This study shows that the effect of CO₂ enrichment on photosynthesis during the day is not negatively affected by a night temperature drop to 5-10°C.

What is the expected impact on horticulture?

The use of dynamic temperature control including low night temperatures/high day temperatures will not decrease the positive effect of CO₂ enrichment on plant growth.

Introduction

It is important for the greenhouse industry to be recognised as environmental friendly. The focus on energy consumption and emissions of CO₂ to the atmosphere are therefore very important (IPCC, 2013). Reducing energy consumption can also be financially beneficial if it has no negative effect on plant production. Minimum energy consumption is achieved when solar radiation is used to heat the greenhouse and energy screens are used to reduce energy loss from the greenhouse. The concept of dynamic temperature control of the greenhouse, where the temperature is allowed to fluctuate between low night and high day temperatures, has been developed over several years (Körner and Challa, 2003; Dieleman and Meinen, 2007). The growth and development of many greenhouse plants respond primarily to the average temperature and less to the diurnal fluctuation (De Koning, 1988; Rijdsick and Vogelesang, 2000; Blanchard and Runkle, 2011). Combining a low night temperature with a

high day temperature can result in significant energy savings (Lund et al., 2006; Blanchard and Runkle, 2011). Although several studies have been performed combining low night with high day temperatures, the extent to which this will influence the effect of CO₂ enrichment is uncertain (Mortensen and Gislerød, 2012). While day temperature affects photosynthesis, night temperature affects the use of carbon accumulated during the light period. High levels of photosynthetic active radiation (PAR) during the day results in high rates of photosynthesis. In combination with low night temperatures that decrease carbon turnover, this may cause starch accumulation and feedback inhibition of photosynthesis (Bunce and Sicher, 2003; Dieleman and Meinen, 2007). The results of studies on the importance of carbohydrates in regulating photosynthetic rates, however, are very contradictory, varying from no effect (Mauney et al., 1979; Potter and Breen, 1980) to a strong negative correlation between carbohydrate concentration and photosynthetic rate (Garrard and Carter, 1976; Thorne and Koller, 1974). Goldschmidt and Huber (1992) concluded that starch accumulation alone did not necessarily account for an observed decrease in photosynthesis, and Gibson et al. (2011) even suggested that starch serves as a transient sink to elevate photosynthesis. Nevertheless, the possibility of low night temperatures interfering with the effect of CO₂ enrichment should be investigated whatever the reason. If a low night temperature was shown to negatively influence the CO₂ effect, this would significantly reduce the value of dynamic temperature control in greenhouses. The present work therefore studied how low night temperatures influenced the effect of CO₂ enrichment in a small canopy of *Argyranthemum frutescens*. This was carried out by continuously measuring the diurnal rate of photosynthesis at fluctuating temperatures. The study was conducted under light conditions simulating clear days and high PAR in late spring at a latitude of about 60°N.

Material and methods

Argyranthemum frutescens cv. Dana was grown from cuttings in 10-cm pots filled with fertilized peat (Jiffy, TPS D Medium course, pH 5.5). The plants were grown during March-April in a commercial greenhouse (J. Kristiansen Gartneri, Grimstad, Norway) with high pressure sodium lamps providing 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density (PFD) supplementary light 20 h day⁻¹. The pots were watered with a nutrient solution (a 50/50 mixture of Pioner yellow NPK 10-4-25 (Azelis) and calcinite (N/Ca 15.5/19, YaraLiva) starting at an electrical conductivity of 2.0 and reduced to 1.0 as the plants grew. The set temperature was 17°C and the ventilation temperature was 19°C. The plants were treated once with 0.8% cycocel to

reduce shoot elongation. The plants were transferred from the greenhouse to the experimental conditions at the visible flower bud stage (1-5 mm diameter).

Chambers for measuring carbon exchange rates (CER)

Plants with visible flower buds were placed in two transparent photosynthesis chambers with a volume of 190 litres (800 mm length x 400 mm width x 600 mm height) as shown in Fig. 1. A Resun ACO-004 pump (China) supplied air to the chambers through a plastic tube at a flow rate of 2200 l h⁻¹ as measured by a flowmeter. The CO₂ concentration was measured by an infrared gas analyzer (PP systems, WMA-4 CO₂ analyzer, Amesbury, MA, USA). A separate chamber was used to mix fresh air and pure CO₂ in order to obtain the desired CO₂ concentration. This was precisely controlled by a constant airflow from the air pumps and a capillary system for control of the flow rate of pure CO₂ from a bottle. By this means, the CO₂ concentration was controlled within $\pm 10 \mu\text{mol mol}^{-1}$. Air sampling was regulated by a solenoid valve relay controller switching between three different channels every minute (AM416 Relay multiplexer, Campbell Scientific Inc., Logan, UT, USA). The CO₂ concentration was measured in the inlet and the outlet air from the two chambers. The CO₂ exchange rate (CER) was calculated using the following formula: $(C_{\text{in}} - C_{\text{out}}) \times F$ where C_{in} and C_{out} were the CO₂ concentrations in and out of the chamber, respectively, and F the flow rate per 0.5 h (1100 l). The temperature in the chambers was controlled by a Jumo dTron 316 unit programmed to give a specific diurnal temperature pattern by switching a 200 W electrical heater on and off in each of the two chambers. The chambers were placed outdoors, and natural low temperatures ensured adequate cooling. The temperature was measured by copper-constantan thermocouples, and the air humidity by Vaisala HMP 35A sensors. The chambers were shaded from daylight and a 180 W LED lamp (Type E21, Evolys, Norway, www.evolys.no) that produces white light was installed at the top of each of the chambers (Gislerød and Mortensen, 2015). The light level was controlled by a homemade unit continuously supporting the LED lamps with a defined voltage that controlled the PFD level during the day. By this means, a typical diurnal variation of daylight in a greenhouse during clear days in spring at 60°N was supplied to the chambers (0-800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD, Fig. 2). The light was measured by a Delta-T Devices PAR sensor (cosine corrected within $\pm 5\%$ up to 70° incidence). The CO₂ concentration, temperature, relative air humidity and light level were stored as 0.5 h means by a Campbell CR10X logger with an AM25T thermocouple multiplexer (Campbell Scientific Ltd, England, UK).

Experiment 1:

Twelve plants, covering an area of 24 dm², were placed in each of the two chambers. The pots were placed in a tray to ensure adequate watering. During the experiment, the plants were given a complete nutrient solution consisting of 1.0 g l⁻¹ Kristalon indigo (Yara) and 1.0 g l⁻¹ calcinite (YaraLiva calcinit). Experiment 1 lasted 13 days with 5 days at 415±15 µmol mol⁻¹ CO₂ followed by 8 days at 1250±50 µmol mol⁻¹ CO₂ in the inlet air. Due to the high photosynthetic rates, the CO₂ concentration decreased to a minimum of 250 µmol mol⁻¹ and 950 µmol mol⁻¹ at the two concentrations, respectively, at the highest light level. In Experiment 1, the same day temperature of 20±1°C (16 h day⁻¹) was maintained in the two chambers. The night temperature was maintained at 20±1°C in one chamber while the temperature in the other chamber gradually decreased to 8±1°C (Fig. 2). The diurnal PFD varied from 0 to 800 µmol m⁻² s⁻¹ simulating the light conditions (16-h photoperiod) in a greenhouse on clear days in late spring (Fig. 2). The mean daily temperature was 20.7±0.1 and 18.5±0.9°C without and with a temperature drop, respectively, during the 5 days at a low CO₂ concentration. During the 8 days at a high CO₂ concentration, the mean temperature was 20.4±0.2 and 17.8±0.5°C without and with a temperature drop, respectively. The relative air humidity varied from 80% in the light period to 95% in the dark period.

At the start of the experiment, the total dry weight of the plant canopy (excluding roots) consisting of 12 plants was 38.3 g, of which 6% was flower buds. At the end of the experiment, the total dry weight was 61.8 g and 68.8 g in the two chambers, respectively. The percentage distribution between flowers/flower buds, stems and leaves was 26, 21 and 53% in the first chamber and 21, 21 and 58% in the second chamber. The mean plant height was 12.5±1.1 cm (±SD, n=12) and 13.8±1.0 cm (±SD, n=12) in the two chambers, respectively.

Fifteen leaves were randomly selected and leaf area and dry weight were measured in order to get a rough estimate of the leaf area index (LAI) of the canopy. The mean leaf area was 6.3±1.4 cm² (±SD) and leaf dry weight 19.8±3.4 mg. These values gave a specific leaf area of 318 cm² g⁻¹ dry weight. Leaf dry weight of the canopy was 32.8 and 39.9 g, calculated to give a leaf area of 1.04 and 1.27 m² in the two chambers, respectively. With a 0.24 m² floor area below the canopies this corresponded to LAI of 4.3 and 5.3 m² leaf area/m² in the two chambers.

Experiment 2:

The same experimental procedure was used in Experiment 2 as in Experiment 1. However, in this experiment the two chambers were given the same treatment but the treatment changed over time. The experiment lasted 8 days with day no. 1, 2, 5 and 6 at $415 \pm 10 \mu\text{mol mol}^{-1} \text{CO}_2$ and day no. 3, 4, 7 and 8 at $1250 \pm 50 \mu\text{mol mol}^{-1} \text{CO}_2$ in the inlet air. During the first 4 days of the experiment, the temperature during the light period (16 h) was $21 \pm 1^\circ\text{C}$, decreasing gradually to $7.5 \pm 1.0^\circ\text{C}$ during the 8-h dark period. The mean temperature was $17.5 \pm 0.5^\circ\text{C}$ (Fig. 4). Over the next four days, the temperature followed the diurnal variation in PFD with a maximum temperature of 31°C during a 5-h period in the middle of the day, decreasing to a minimum of $11.5 \pm 1.0^\circ\text{C}$ at the end of the 8-h night period, giving a mean temperature of $22.0 \pm 0.5^\circ\text{C}$ (Fig. 4).

At the start of the experiment, the total dry weight of the plant canopy (excluding roots) was 35.4 g, of which 4% was flower buds. The total dry weight at the end of the experiment was 60.4 g and 59.1 g in the two chambers, respectively. The percentage distribution between flowers/flower buds, stems and leaves was 22, 28 and 50% and 24, 26 and 50% in the two chambers, respectively. The mean plant height was $14.1 \pm 0.8 \text{ cm}$ ($\pm\text{SD}$, $n=12$) and $14.9 \pm 1.1 \text{ cm}$ ($\pm\text{SD}$, $n=12$) in the two chambers. By using the leaf size and weight data presented under Experiment 1, LAI was calculated to be 4.0 and 3.9 in the two chambers at the end of the experiment.

CER were analysed in different periods of the day using the SAS-GLM procedure (SAS institute Inc., USA) with days as replicates in Experiment 1 and chambers as replicates in Experiment 2. SigmaPlot 10.0 (Systat Software Inc.) was used in the regression and correlation analyses as well as in the presentation of graphs.

Results

Experiment 1:

A temperature drop from 20°C to 8°C during the night only had a marginal negative effect on CER (1-10%) during the following light period (Table 1, Fig. 2). The temperature drop resulted in dark respiration decreasing 32% at low and 63% at high CO_2 levels. This resulted in a total daily CER that was 12% higher in the high CO_2 temperature drop treatment. CO_2 enrichment increased total daily CER (24 h) by 82% at a night temperature of 20°C and 114% when the night temperature decreased to 8°C (Table 1). When PFD and photosynthesis were

at the highest level during a 6-h period in the middle of the day, CO₂ enrichment doubled the CER irrespective of the temperature treatment at night (Table 1, Fig. 2). About 60% of the CER during the light period took place during this 6-h period. Respiration during the night amounted to 14-19% of the CER during the light period, except for the treatment at high CO₂/8°C where it decreased to 6% (Table 1). The photosynthesis at low CO₂ level started to level off at a PFD level of 500-600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ while it continued to increase linearly up to the maximum PFD of about 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at a high CO₂ level (Fig. 2). The regression analyses showed that at low CO₂ concentrations, photosynthesis levelled off at the higher PFD levels while photosynthesis at high CO₂ concentrations increased linearly as shown by the regression equations (Fig. 3).

Experiment 2:

Total CER decreased 34 and 27% by increasing the temperature from 21°C to a maximum of 31°C during the light period at low and high CO₂ levels, respectively (Table 2, Fig. 3). CO₂ enrichment increased the total CER by 77 and 95% under the low and high temperature treatment. Photosynthesis was similarly affected by the CO₂ level during the 6-h period in the middle of the day when about 60% of the daily CER took place. Respiration during the night period decreased 47% at low CO₂ and 42% at high CO₂ by decreasing the temperature (Table 2, Fig. 4). CO₂ enrichment increased respiration by 36% at a high temperature and by 6% at a low temperature (Table 2). The daily CER at the high CO₂/high temperature treatment was 29% higher as compared with the low CO₂/low temperature treatment. Photosynthesis at the low CO₂ level was saturated at a PFD level of about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ while it continued to increase up to the maximum PFD of about 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at a high CO₂ level (Fig. 4). The regression analyses also showed that at a low CO₂ concentration, photosynthesis levelled off at higher PFD levels while photosynthesis at a high CO₂ concentration increased linearly as shown by the regression equations (Fig. 5).

Discussion

In the present experiment with a canopy of *Argyranthemum frutescens*, the photosynthetic rate reached 80 mmol CO₂ m⁻² during 0.5 h, corresponding to 44.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD/high CO₂. Short-term measurements of CO₂ uptake on leaf segments of chrysanthemum under similar climate conditions gave a rate of about 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Janka et al., 2016). The maximum gross photosynthesis (net CO₂ uptake plus dark respiration) in a chrysanthemum crop in a 44 m² closed greenhouse as measured over two days was found to

be about $65 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at $1100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PFD/ $950 \mu\text{mol mol}^{-1} \text{ CO}_2$ (Körner et al., 2007). Taking into account that a maximum PFD of $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in the present study resulted in gross photosynthesis of $50 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (including dark respiration), the results are surprisingly similar. In a small chrysanthemum canopy, a maximum CO_2 uptake of $15\text{-}20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was measured at $550\text{-}600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PFD at a CO_2 concentration of $550 \mu\text{mol mol}^{-1}$ (Jensen et al., 2006). The leaf area index of about four in the present plant canopy probably explains the high photosynthetic rate since high plant density is expected to increase the rate at high-light conditions (Bugbee and Salisbury, 1988). Short-term measurements of photosynthesis may give a good picture of the response if no acclimation of photosynthesis takes place over time. The high rate over time was probably due to a strong sink formed by the numerous flower buds developing into flowers. Bunce and Sicher (2003) concluded that the strong sink in *Brassica oleracea* prevented down-regulation of photosynthesis at an elevated CO_2 concentration. In tomato, photosynthetic acclimation at elevated CO_2 in a semi-closed greenhouse as measured on single leaves, occurred only if the fruits were removed (Qian et al., 2012). Nevertheless, upscaling the photosynthetic rate from single leaf to whole-canopy level will always entail uncertainty with respect to interpretation although it can provide valuable information (Long et al., 1996; Rodrigues et al., 2016). The daily photosynthesis at high CO_2 combined with a night temperature drop to 8°C was $1.17 \text{ mol CO}_2 \text{ m}^{-2}$ in both experiments, corresponding to 14.0 g carbon . With a 40% carbon content in the plant dry biomass (Bugbee and Salisbury, 1988) this amounts to a dry weight production of $35 \text{ g m}^{-2} \text{ day}^{-1}$ at the daily light dose of $26.3 \text{ mol m}^{-2} \text{ PAR}$, resulting in 1.33 g mol^{-1} . Monteith (1978) concluded that the maximum short-term crop growth rates in the field was between 34 and $39 \text{ g m}^{-2} \text{ day}^{-1}$ with PAR levels of over $55 \text{ mol m}^{-2} \text{ day}^{-1}$.

In spite of a very high photosynthetic rate during the day, the drop in night temperature to 8°C was found to have no effect on the rate during the following light period. Previous studies have shown a night temperature of 6°C having no effect in sweet pepper plants (Sanchez et al., 2015) or 10°C in tomato (Hückstädt et al., 2013; Kläring et al., 2015). The present results also showed that the low night temperature had no negative effect irrespective of the CO_2 concentration. This conclusion is very important for the application of dynamic temperature control in greenhouses. If a combination of high-light conditions and a high CO_2 concentration caused starch accumulation (not measured) in the plant cells at low night temperatures, this had no negative effect on the photosynthetic rate.

The most conspicuous effect was that CO₂ enrichment almost doubled the daily CER irrespective of night temperature. This CO₂ effect could mainly be attributed to the saturation of photosynthesis at 500-600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD at low CO₂ in contrast to at high CO₂ where photosynthesis continued to increase linearly up to the maximum of 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The saturation level was probably above the maximum measured in greenhouses at high latitudes (about 1100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD) as previously shown with single leaves of chrysanthemum (Janka et al., 2016) as well as with a chrysanthemum canopy at 800-1000 $\mu\text{mol mol}^{-1}$ CO₂ (Mortensen and Moe, 1983). A high CO₂ level in combination with a low night temperature resulted in the highest daily photosynthesis. Increasing the night temperature only increased respiration and did not stimulate photosynthesis during the following light period, causing an overall carbon loss.

In practice, greenhouses have to be ventilated on days with high global radiation, and maintaining a high CO₂ concentration is difficult without adding huge amounts of CO₂. Allowing the temperature to increase to a maximum of 30-35°C without ventilation may, to some extent, prolong the period of high concentration in the greenhouse (Mortensen and Gislerød, 2012; Mortensen et al. 2012). The development of semi-closed and closed greenhouses where cooling by ventilation is replaced in part or in whole by mechanical cooling (De Gelder et al., 2012) will in combination with high ventilation temperatures (30-35°C) make control of the CO₂ concentration possible even under high solar radiation. As the present results have shown, this will increase photosynthesis and light utilisation resulting in a significant increase in biomass and crop yield. The suggestion by De Gelder et al. (2012) that this could result in a 20% yield increase on an annual basis seems realistic. Combining a high day temperature with a low night temperature to give an optimal mean temperature seems to be an excellent solution for new greenhouse technology both with respect to energy consumption and yield. Thus, further innovation in crop production is a matter of understanding crop physiology and combining it with new greenhouse technology (Marcelis et al. 2014).

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References

- Baille, M., Romero-Aranda, R., and Baille, A. (1996). Gas-exchange responses of rose plants to CO₂ enrichment and light. *J. Hort. Sci.* 71, 945-956.
- Baligar, V.C., Bunce, J.A., Elson, M.K., and Fageria, N.K. (2010). Irradiance, external carbon dioxide concentration and temperature influence photosynthesis in tropical cover crop legumes. *Tropic. Grassland* 44, 24-32.
- Blanchard, M.G., and Runkle, E.S. (2011). The influence of day and night temperature fluctuations on growth and flowering of annual bedding plants and greenhouse heating cost predictions. *HortScience* 46, 599-603.
- Bugbee, B.G., Salisbury, F.B. (1988). Exploring the limits of crop productivity. *Plant Physiol.* 88, 869-878.
- De Gelder, A., Dieleman, J.A., Bot, G.P.A., Marcelis, L.F.M. (2012). An overview of climate and crop yield in closed greenhouse. *J. Hort. Sci. and Technol.* 87, 193-202.
- Dieleman, J.E., Meinen, E. Interacting effect of temperature integration and light intensity on growth and development of single-stemmed cut rose plants. *Scientia Hortic.* 113: 182-187.
- Frantz J.M., Cometti N.N., Bugbee B. (2004) Night temperature has a minimal effect on respiration and growth in rapidly growing plants. *Annals of Botany* 94:155-166.
- Garrard, L.A., Carter, J.L. (1976). Leaf assimilate level and photosynthesis of *Digitaria decumbens* Stent. *Soil and Crop Sci. Soc. Fla. Proc.* 35, 6-10.
- Gibson, K., Park, J.-S., Nagai, Y, Hwang, S.-K., Cho, Y.-C., Roh, K.-H., Lee, S.-M., Kim, D.-H., Choi, S.-B., Ito, H., Edwards, G.E., Okita, T.W. (2011). Exploiting leaf starch synthesis as a transient sink to elevate photosynthesis, plant productivity and yields. *Plant Sci.*, 181, 275-281.
- Gislerød, H.R., Mortensen, L.M., Pettersen, H., Sand, A., Hem, M.S. (2015). Forsøk med LED-lys (Experiments with LED). *Gartneryrket* 6/2015: 16-19.
- Goldschmidt, E.E., Huber, S.C. (1991). Accumulation in leaves of plants storing starch, sucrose, and hexose Sugars. *Plant Physiol.* 99, 1443-1448.

Hückstädt, A.B., Suthaparan A., Mortensen, L.M., Gislerød H.R. 2013. The effect of low night and high day temperatures on photosynthesis in tomato. *Amer. J. Plant Sci.* 4, 2323-2331.

IPCC, 2013: Summary for Policymakers. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Janka, E., Körner, O., Roosenqvist, E., and Ottosen, C.-O. (2016). A coupled model of leaf photosynthesis, stomatal conductance, and leaf energy balance for chrysanthemum (*Dendranthema grandiflora*). *Computers and Electronics in Agriculture* 123: 264-274.

Jensen, L.T., Rosenqvist, E., and Aaslyng, J.M. (2006). A daylight climate chamber for testing greenhouse climate control strategies and calculating canopy carbon dioxide exchange. *HortTechnol.* 16, 191-198.

Kaiser, E., Morales, A., Harbinson, J., Kromdijk, J., Heuvelink, E., and Marcelis, L.F.M. (2015). Dynamic photosynthesis in different environmental conditions. *J. Exp. Bot.* 66, 2415-2426.

Körner, O., and Challa, H. (2003). Design and improved temperature integration concept in greenhouse cultivation. *Comp. Electr. Agric.* 39, 39-59.

Körner, O., Van't Ooster, A., and Hulsbos, M. (2007). Design and performance of a measuring system for CO₂ exchange of greenhouse crop at different light levels. *Scientia Hortic.* 97, 219-228.

Long, S.P., Farage, P.K., Garcia, R.L. (1996). Measurements of leaf and canopy photosynthetic CO₂ exchange in field. *J. Exp. Bot.* 47, 1629-1642.

Lund, J.B., Andreassen, A., Ottosen, C.-O., and Aaslyng, J.M. (2006). Effect of dynamic climate on energy consumption and production of *Hibiscus rosa-sinensis* L. in greenhouses. *HortScience* 41, 384-388.

- Marcelis, L.F.M., Buwalda, F., Dieleman, J.A., Dueck, T.A., Elings, A., De Gelder, A., Hemming, S., Kempkes, F.L.K., Li, T., and van Noort, F. (2014). Innovations in crop production: a matter of physiology and technology. *Acta Hortic.* 1037, 39-45.
- Mauney, J.R., Guinn, G., Fry, K.E., Hesketh, J.D. (1979). Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. *Photosynthetica* 13, 260-266.
- Monteith, J.L. (1978). Reassessment of maximum growth rates for C₃ and C₄ crops. *Exp. Agric.* 14, 1-5.
- Mortensen, L.M., and Gislerød, H.R. (2012). The effect of high CO₂ concentrations on diurnal photosynthesis at high daytime temperatures in small stands of cut roses. *Eur. J. Hort. Sci.* 77, 163-169.
- Mortensen, L.M. and Moe, R. (1983). Growth responses of some greenhouse plants to environment. IV. Effects of carbon dioxide on photosynthesis and growth of *Chrysanthemum morifolium* Ramat. in daylight. *Meld. Norg. LandbrHøgsk.* 61(22), 1-11.
- Mortensen, L.M., Ringsevjen, F., and Gislerød, H.R. (2012). The effect of CO₂ concentration on the CO₂ exchange rate in a small stand of cucumber during different periods of the day. *Eur. J. Hort. Sci.* 77, 24-30.
- Ottosen C.O., Rosenqvist E., Aaslyng J.M., and Jakobsen L. (2005). Dynamic climate control in combination with average temperature control saves energy in ornamentals. *Acta Hortic.* 691, 133-139.
- Quian, T., Dieleman, J.A., Elings, A., and Marcelis, L.F.M. (2012). Leaf photosynthetic and morphological responses to elevated CO₂ concentration and altered fruit number in the semi-closed greenhouse. *Scientia Hortic.* 145, 1-9.
- Potter, J.R., Breen, P.J. (1980). Maintenance of high photosynthetic rates during accumulation of high leaf starch levels in sunflower and soybean. *Plant Physiol.* 66, 528-531.
- Rijsdijk, A.A., Vogelesang J.V.M. (2000). Temperature integration on a 24-hour base: a more efficient climate control strategy. *Acta Hortic.* 519, 163-169.
- Rodrigues, W.P., Filho, J.A.M., da Silva, J.R., de Assis Figueiredo, F.A.M.M., Ferraz, T.M., Ferreira, L.S., da Silva Bezerra, L.B., de Abreu, D.P., de Paula Bernado, W., Passos, L.C., de

Sousa, E.F., Glenn, D.M., Ramalho, J.C., and Campostrini, E. (2016). Whole-canopy gas exchange in *Coffea sp.* is affected by supra-optimal temperature and light distribution within the canopy: The insights from improved multichamber system. *Scientia Hort.* 211, 194-202.

Thiagarajan, A., Lada, R., and Joy, P. (2007). Compensatory effects of elevated CO₂ concentration on the inhibitory effects of high temperature and irradiance on photosynthetic gas exchange in carrot. *Photosynthetica* 45, 355-362.

Thorn, J.H., Koller, H.R. (1974). Influence of assimilate demand on photosynthesis, diffusive resistances, translocation, and carbohydrate levels of soybean leaves. *Plant Physiol.* 54, 201-207.

Wang, F.L., Wang, H., and Wang, G. (2007). Photosynthetic responses of apricot (*Prunus armeniaca* L.) to photosynthetic photon flux density, leaf temperature, and CO₂ concentration. *Photosynthetica* 45, 59-64.

Table 1. The effect of a temperature drop from 20°C to 8°C during the night at low (250-415 $\mu\text{mol mol}^{-1}$, Low) and high CO₂ concentrations (900-1250 $\mu\text{mol mol}^{-1}$, High) on CER ($\pm\text{SE}$, n = 4-5) in different periods of the day in Experiment 1. F- values and significance levels are given. Significance levels; ns, $p>0.05$; *, $p<0.05$; **, $p<0.01$ and ***, $p<0.001$.

CO ₂ /night temp.	CER (mmol m^{-2})					
	Total (24 h day ⁻¹)	Light period (16 h day ⁻¹)	From 10.00-16.00 h	Dark period (8 h day ⁻¹)	% CER 10.00-16.00	% dark respiration of CER in the light period
Low/20°C	579 \pm 9	711 \pm 6	409 \pm 7	-132 \pm 12	58 \pm 1	19 \pm 2
Low/8°C	552 \pm 21	642 \pm 21	390 \pm 11	-90 \pm 5	61 \pm 1	14 \pm 1
High/20°C	1055 \pm 30	1268 \pm 20	794 \pm 20	-196 \pm 4	63 \pm 1	15 \pm 1
High/8°C	1179 \pm 19	1251 \pm 17	800 \pm 13	-72 \pm 5	64 \pm 0	6 \pm 1
F-values and sign. levels:						
CO ₂	631***	1117***	751***	11.4**	37.0***	45.2***
Temp.	4.91*	5.47*	0.13 ^{ns}	170***	11.0**	78.0***
CO ₂ x Temp.	11.8**	2.15 ^{ns}	0.68 ^{ns}	36.2***	2.20 ^{ns}	9.22**

Table 2. The effect of CO₂ concentration (Low and High) on CER (\pm SE, n=4-5) at two temperature regimes: 21°C day temperature/7.5°C minimum night temperature (Low) and 31°C maximum day temperature/11.5°C minimum night temperature (High) in Experiment 2. F-values and significance levels as in Table 1.

CO ₂ /temp.	CER (mmol m ⁻²)					
	Total (24 h day ⁻¹)	Light period (16 h day ⁻¹)	From 10.00- 16.00 h	Dark period (8 h day ⁻¹)	% CER 10.00- 16.00 h	% dark respiration of CER in the light period
Low/Low	663±18	759±17	419±11	-96±1	55±1	13±0
Low/High	437±19	616±23	354±15	-180±5	57±1	14±1
High/Low	1173±11	1275±20	768±21	-102±10	60±1	8±1
High/High	854±30	1098±49	705±36	-244±21	64±1	22±1
F-values and sign. levels:						
CO ₂	631***	1117***	306***	11.4**	47.7***	45.2***
Temp.	4.91*	5.47*	9.89**	170***	13.8**	78.0***
CO ₂ x Temp.	11.8**	2.15 ^{ns}	0.00 ^{ns}	36.2***	1.15 ^{ns}	9.22**

Fig. 1. Picture of the chambers for measurement of photosynthesis with 12 plants of *Argyranthemum frutescens*.

Fig. 2. The diurnal photon flux density (PFD), temperature/CO₂ treatments and CO₂ exchange rates (CER) in Experiment 1.

Fig. 3. Regression lines and equations between PFD and CER at different temperature treatments at low CO₂ level (upper graphs) and at high CO₂ level (lower graphs) in Experiment 1.

Fig. 4. The diurnal photon flux density (PFD), temperature/CO₂ treatments and CO₂ exchange rates (CER) in Experiment 2.

Fig. 5. Fig. 3. Regression lines and equations between PFD and CER at different temperature treatments at low CO₂ level (upper graphs) and at high CO₂ level (lower graphs) in Experiment 2.



Fig. 1

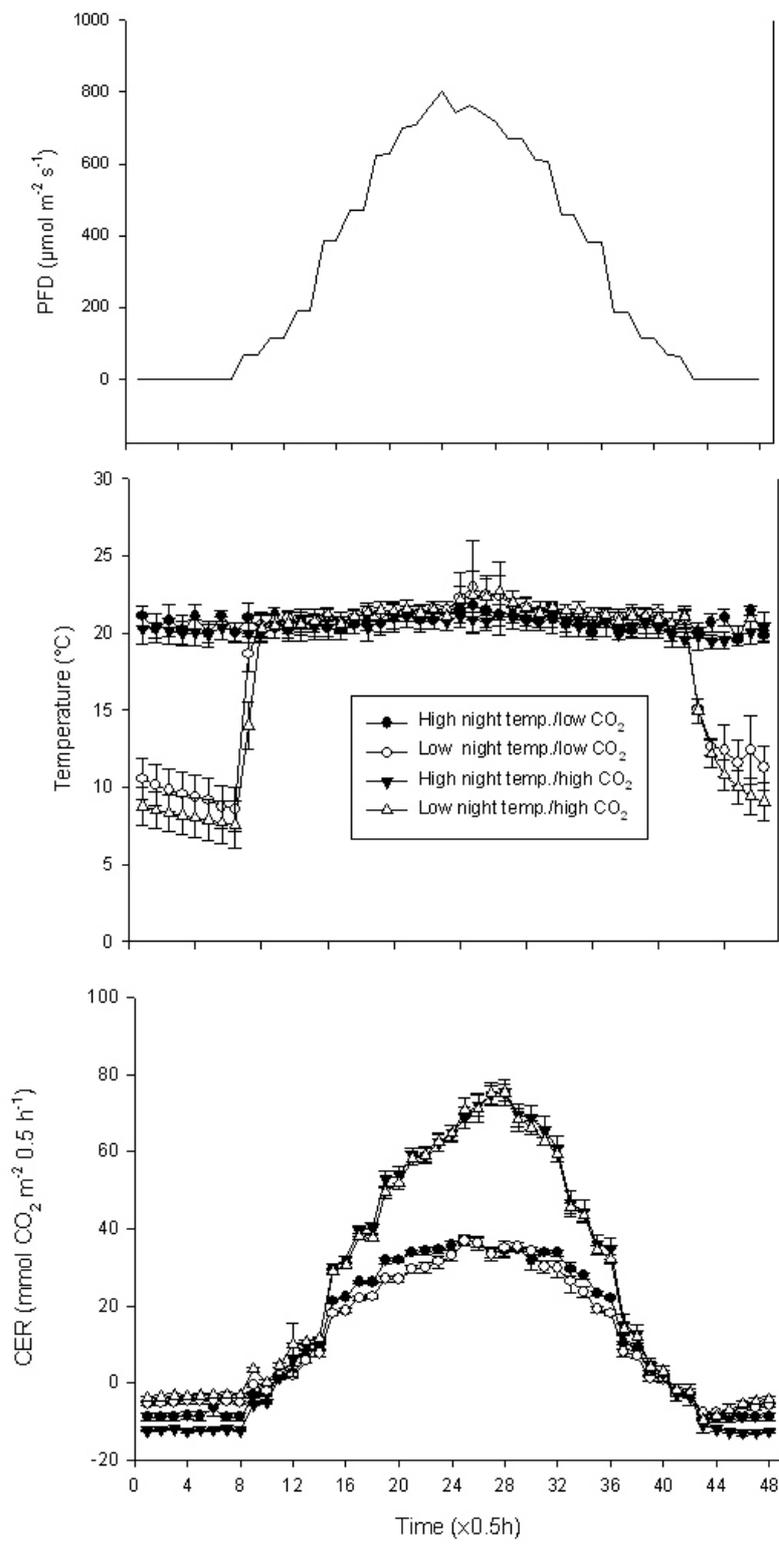


Fig. 2

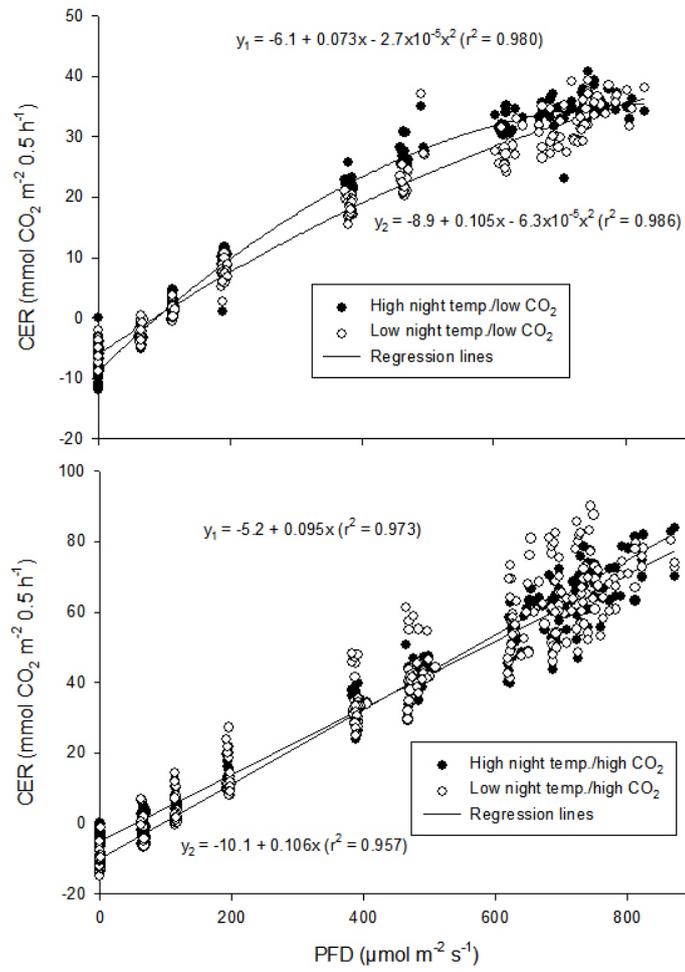


Fig. 3

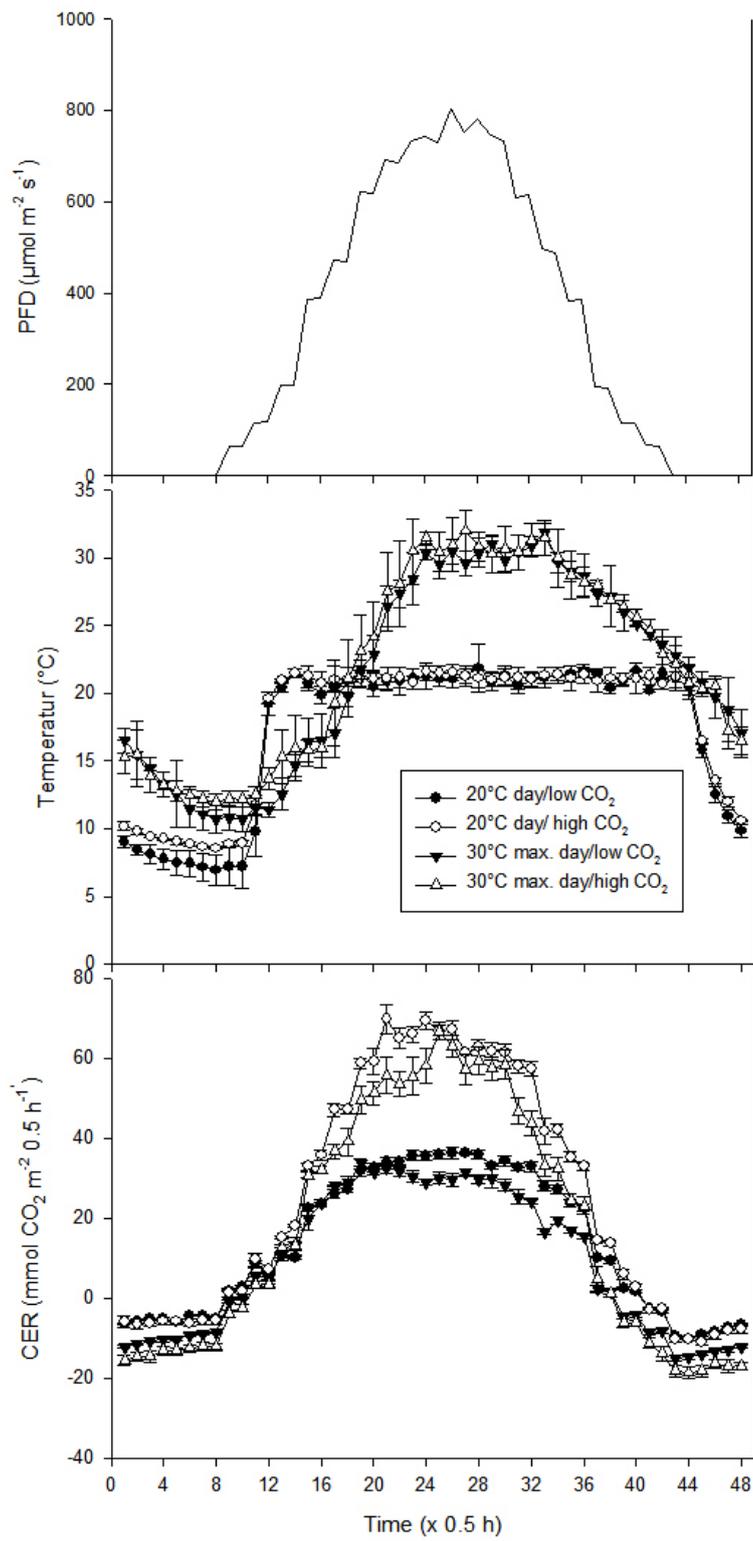


Fig. 4

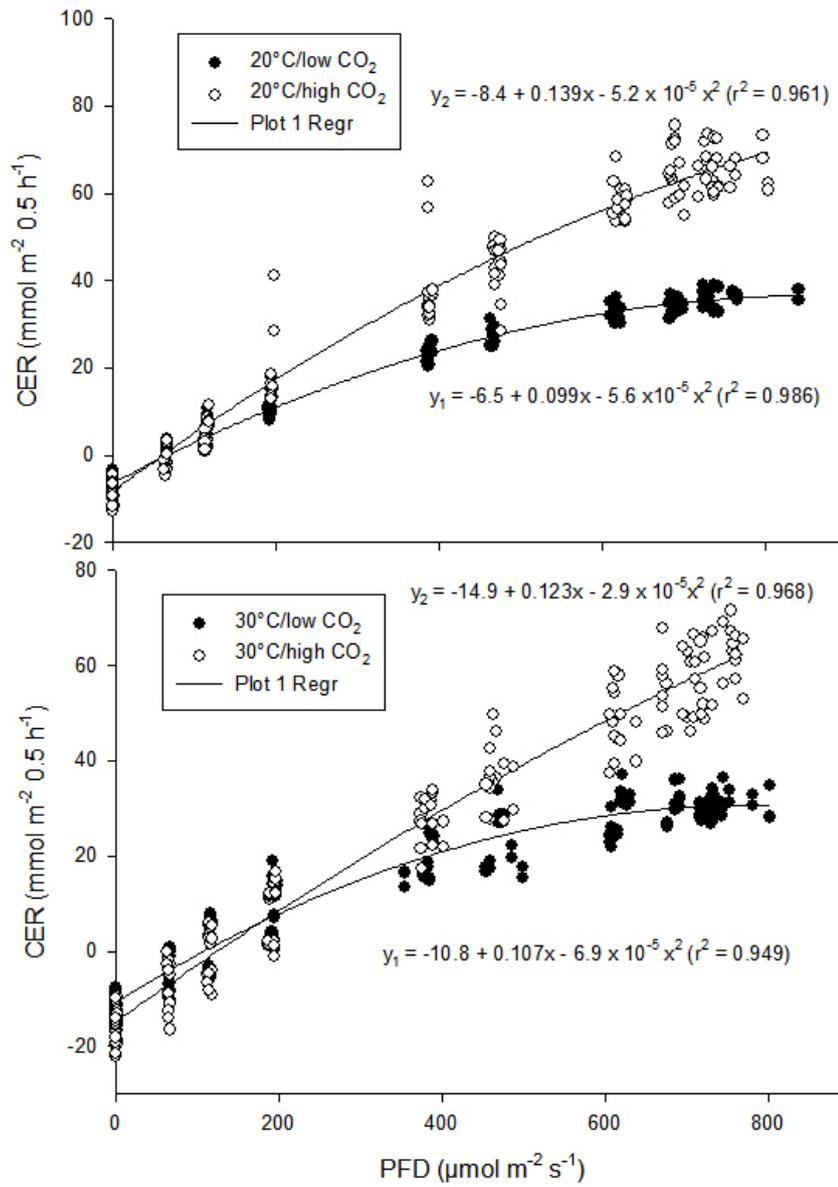


Fig. 5