Night temperature drop affects the diurnal photosynthetic rhythm of *Kalanchoe blossfeldiana*

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Summary

Kalanchoe blossfeldiana is a CAM plant. However, it functions like a C₃ plant under normal greenhouse conditions with net CO₂ uptake during the light period and net CO₂ production during the dark period. Stress conditions such as drought induce a change from C₃ to CAM metabolism. Dynamic temperature control in greenhouses as a means of saving energy entails a drop in night temperature. The question was whether a night temperature drop would be perceived as a stress signal, causing the plants to switch from C₃ to CAM photosynthesis. In the first experiment, the diurnal CO₂ exchange rates (CER) of small plant stands of *K. blossfeldiana* were measured with and without a temperature drop during the dark period from about 20°C to 6–12°C when grown at a photon flux density (PPFD) of 220 μmol m⁻² s⁻¹ during 16 h day⁻¹ (8 h dark period). At a constant temperature, CER was relatively constant throughout the photoperiod. A drop to 12°C during the night caused a strong diurnal rhythm with high CER during the first and last hours of the light period and a 75% decrease in CER in the middle of the day as compared to the first hours of the light period. A drop to 6°C resulted in net photosynthesis reaching zero at midday the following day. Low night temperature caused a change from negative to positive CER values during the night, demonstrating a CAM metabolism. In a second experiment, CER was measured at light conditions simulating clear days in a greenhouse in late spring (0–1100 μmol m⁻² s⁻¹). A drop to 7°C during the night decreased CER by about 50% from morning to midday, before it then started increasing again. By gradually increasing the diurnal minimum night temperature, the midday CER decrease eventually disappeared. Regression analysis showed a close relationship between the temperature drop and the midday decrease as well as increased CAM metabolism. The response illustrated the genetics of *K. blossfeldiana*, originating in dry, arid conditions in Madagascar where low temperature during the night is a signal for the plant to protect itself against a warm, dry day by closing the stomata. Dynamic temperature control involving a night temperature drop is not recommended for this species due to the negative effect on photosynthesis when the plants change from C₃ to the less efficient CAM metabolism under greenhouse conditions.

Keywords

CAM, C₃, carbon dioxide exchange rate, photon flux density, temperature difference

Significance of this study

What is already known on this subject?

- It is known that *Kalanchoe blossfeldiana* functions like C₃ plants under normal greenhouse cultivation.

What are the new findings?

- A temperature drop during the night to save energy causes the plants to switch from C₃ to CAM photosynthesis, resulting in much lower total photosynthesis.

What is the expected impact on horticulture?

- For this species low night temperature to save energy is not recommended.

Introduction

Kalanchoe blossfeldiana is a popular ornamental species with a crassulacean acid metabolism (CAM) photosynthetic pathway, deviating from most greenhouse plants that are C₃ species (Taybi et al., 1995). CAM plants can be divided into obligate (full CAM plants) and facultative (switch between CAM and C₃ photosynthesis) plants, and ornamental CAM species have been shown to belong to both groups (Lee et al., 2006). In facultative plants, drought stress typically induces CAM photosynthesis which rapidly reverts to C₃ photosynthesis by watering (Winter and Holtum, 2014). In several experiments with *K. blossfeldiana*, we have always found that the diurnal photosynthesis as well as growth responses to different environmental factors were similar to that of C₃ greenhouse plants (Mortensen, 1983, 1994, 2000, 2014). Under non-stress conditions, facultative CAM plants are unlikely to perform CAM photosynthesis. However, stress factors other than drought may cause a switch from C₃ to CAM metabolism (Lüttge, 2004; Lee et al., 2006). Today, reducing energy consumption in greenhouses is a major focus. If the industry is to be recognised as environmentally friendly, it must reduce the CO₂ emissions that potentially cause global climate change (IPCC, 2013). One means of saving energy is through dynamic temperature control of the greenhouse environment (Körner and Challa, 2003; Lund et al., 2006; Dieleman and Meinen, 2007). In this concept, the greenhouse air is heated by solar radiation/supplementary lighting during the day while the temperature is allowed to decrease without heating during the night. Since greenhouse plants react primarily to the average temperature, diurnal fluctuations can be applied without negatively affecting plant growth and development (De Koning, 1988; Rijdsdijk and Vogelesang, 2000; Blanchard and Runkle, 2011). As an important greenhouse crop, energy saving is important in the production of *K. blossfeldiana*. However, the question is if dynamic temperature

control that allows low night temperature causes a stress inducing CAM metabolism in this species? In such case, reduced light utilisation may be the result. In order to answer this question, the diurnal photosynthesis was followed when small plant stands were exposed to low temperatures during the night.

Materials and methods

Rooted cuttings of *Kalanchoe blossfeldiana* 'Alicia' were planted in fertilised peat (Kekkilä, Estonia) in 10-cm pots. The plants were grown for six weeks at 18–20°C under short-day conditions (10 h day⁻¹) with 100 µmol m⁻² s⁻¹ supplementary high pressure sodium light in October–November in a greenhouse at 59°N. After six weeks (at the stage of visible flower initiation), the plants were moved to the experimental conditions in four chambers to measure carbon dioxide exchange rates (CER).

Chambers for measuring carbon dioxide exchange rates (CER)

Four chambers with a diameter of 24 cm and a height of 50 cm (22.6 dm³ volume, floor area 4.52 dm²) were made of 6-mm acrylic tubes. A removable lid was placed on top of each chamber. A Resun ACO-001 pump (China) supplied air to the chambers through a plastic tube at a flow rate of 1300 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). Air sampling was regulated by a solenoid valve relay controller switching between three different channels each minute (AM416 Relay multiplexer, Campbell Scientific Inc., Logan, UT, USA). The CO₂ concentration was measured in the inlet and the outlet air from two chambers. Two chambers at a time were measured every other hour. The CO₂ exchange rate (CER) was calculated using the following formula: $(C_{in} - C_{out}) \times F$ where C_{in} and C_{out} were the CO₂ concentrations in and out of the chamber, respectively, and F the flow rate per hour (1300 dm³). The chambers were placed in 10 cm deep water baths. 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 aquarium heater on and off in each water bath. 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) that produces white light was installed at the top of each of the chambers. 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 (0–1100 µmol m⁻² s⁻¹ PFD, Figure 1). The light was measured by a Delta-T Devices PAR sensor (cosine corrected within ±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: Night temperature drop under constant artificial lighting

Three plants were placed in each of the four chambers. A PFD of 225 µmol m⁻² s⁻¹ was given 16 h day⁻¹ (correspond-

FIGURE 2. The mean diurnal temperature for plant stand 1 and 3 ($\pm$ SD, $n=2$) and for plant stand 2 and 4 ($\pm$ SD, $n=2$), in different time periods in Experiment 1. The 8-h dark period is indicated with a black line.

ing to 13.0 mol m⁻² day⁻¹ PAR) in all chambers (Figure 1). A black curtain was used to block out daylight. Chamber 1 and 3 (plant stand 1 and 3) were given the same treatment and Chamber 2 and 4 (plant stand 2 and 4) a second treatment. Air with a CO₂ concentration of 415±15 µmol mol⁻¹ was supplied to the chambers. During day 1–2 of the experiment, the temperature was 20–22°C during the day and night (Figure 2). During day 5–6, plant stand 2 and 4 were exposed to a night temperature drop to about 12°C, and, over the following days, the night temperature dropped to a minimum of 6.5°C (Figure 2). The night temperature in plant stand 1 and 3 also decreased to some extent, however, to a significantly lesser extent than in the low temperature treatment. The temperature during days 3–4 and 7–8 was used to adjust the plants to a new temperature regime.

Experiment 2: Temperature drop under simulated daylight conditions

Three plants were placed in each of the four chambers. A diurnal PFD was established simulating the natural light (16 h) conditions during clear days in late spring in a greenhouse of up to about $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 1). During the normal dark period of eight hours, a constant $34 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD was supplied to eliminate any photoperiodic effect on the photosynthetic rhythm. During day 1–2 of the experiment, the temperature followed the diurnal rhythm of the light level with a minimum temperature of 6°C at night and a maximum day temperature of $21\text{--}22^\circ\text{C}$ (Figure 3). During day 5–6, the temperature dropped to a minimum of 10°C in Chamber 2 and 4 (plant stand 2 and 4) while Chamber 1 and 3 (plant stand 1 and 3) were heated to 21°C during the night (Figure 3). During day 7–8, all the chambers were heated during the night. The temperature during day 3–4 was used to adjust the plants to a new temperature regime.

At the end of the experiments, the total leaf dry weight per plant and dry weight and area of five leaves per plant were measured. Since our leaf area meter was broken the leaf area was estimated by taking the outlines of the leaves on paper sheets. The outlines were cut and weighed. The leaf area was then calculated based on the paper sheet weight per dm^2 . The values were used to calculate total leaf area per plant, and then the total leaf area per chamber (three plants). Regression and correlation analyses were carried out between the temperature drop during the night and the percentage drop in CER from morning until midday, as well as the CER during the night. In addition, the correlation between night CER and percent midday decrease was carried out. 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: Night temperature drop under constant artificial lighting

During the first days of the experiment with small diurnal variation in the temperature between day and night, the CER was relatively constant during the day period after a peak during the first two hours of the light period (Figure 4). A negative CER (respiration) dominated during the night.

FIGURE 1. The diurnal photon flux density (PFD) in Experiment 1 and 2 by means of LED-lamps.

During day 5–6, the night temperature dropped to 12°C in plant stand 2 and 4, causing a 75% decrease in CER from morning until midday. A further drop in night temperature to 6.5°C caused midday CER to be close to zero, while CER during the night changed from negative to positive (Figure 4). A drop in night temperature to a minimum of $14\text{--}15^\circ\text{C}$ also significantly decreased the CER during the middle of the day in plant stand 1 and 3. The CER during the middle of the day (CER_{min}) relative to the maximum in the morning (CER_{max}) was calculated and correlated with the difference between maximum and minimum temperature during the day and night (temperature drop) (Figure 5). When the day/night temperature difference increased from $1\text{--}2^\circ\text{C}$ to 13°C , the CER in the middle of the day, compared with the morning CER, changed from about 80% to 2% (Figure 5). At

FIGURE 3. The mean diurnal temperature for plant stand 1 and 3 ($\pm \text{SD}$, $n=2$) and for plant stand 2 and 4 ($\pm \text{SD}$, $n=2$), in different time periods in Experiment 2. The 8-h time period of $34 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD is indicated with a black line.

the same time, the CER proportionally increased during the night from a negative to a positive value (Figure 5). Thus, the CER in darkness increased proportionally with a decrease in the CER in the middle of the day (Figure 5). At the end of the experiment, the mean leaf area of the plant stands in the four chambers was $18.5 \pm 2.3 \text{ dm}^2$ ($\pm \text{SD}$, $n = 4$).

Experiment 2: Temperature drop under simulated daylight conditions

The temperature fluctuated from 6°C to $21\text{--}22^\circ\text{C}$ during the first two days in Experiment 2. The maximum CER was about $30 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in the morning, with a 50% decrease at midday before it increased again somewhat (Figure 6). At a minimum temperature of 10°C (day 5–6), the CER increased to a maximum of about $50 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, still with a drop in CER at midday in spite of increasing PFD up to $1100 \mu\text{mol m}^{-2} \text{ s}^{-1}$. By maintaining the night temperature at between 15 and 20°C (day 7–8), the CER more or less followed the diurnal PFD level, reaching a maximum of about $90 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$. The CER at night changed from positive to negative as the night temperature increased. It should be noted that the low-level light of $34 \mu\text{mol m}^{-2} \text{ s}^{-1}$ during the

FIGURE 4. The mean CO_2 exchange rate (CER) for plant stand 1 and 3 ($\pm \text{SD}$, $n = 2$) and for plant stand 2 and 4 ($\pm \text{SD}$, $n = 2$), in different time periods in Experiment 1. The 8-h dark period is indicated with a dark line.

night increased the CER to some extent. At the end of the experiment, the mean leaf area of the plant stands in the four chambers was $15.4 \pm 1.4 \text{ dm}^2$ ($\pm \text{SD}$, $n = 4$).

Discussion

As long as the temperature during the day and night remained relatively constant, the diurnal CER was quite similar to that previously measured in *K. blossfeldiana* as well as in roses (Mortensen, 1995, 2014). This reflected a typical C_3 photosynthesis pattern with negative rates (respiration) during the dark period and a positive CER depending on the light level during the day. This was found in spite of the recent transferral of the plants from a six-week, short-day treatment to long-day conditions. Based on literature, this species was expected to retain CAM metabolism after

FIGURE 5. Correlations between temperature drop ($^\circ\text{C}$) and % decrease in CER from morning until midday (A), between temperature drop and CER in darkness (B) and between % decrease in CER from morning until midday and CER in darkness (C) in Experiment 1.

FIGURE 6. The diurnal CO_2 exchange rate (CER) as a mean for plant stand 1 and 3 ($\pm \text{SD}$, $n=2$) and as a mean for plant stand 2 and 4 ($\pm \text{SD}$, $n=2$), in different time periods in Experiment 2. The 8-h time period of $34 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD is indicated with a black line.

short-day treatment (Queiroz and Brulfert, 1982; Winter and Høltum, 2014). However, a temperature drop during the night adversely changed the typical C_3 pattern of photosynthesis. Unlike other greenhouse species such as *Argyranthemum frutescens*, a temperature drop immediately induced a midday decrease in photosynthesis even at a constant light level (Mortensen and Gislerød, 2016). The midday CER decreased proportionally with the drop in temperature the previous night, reaching close to zero at a night temperature of 6°C . At the same time, net respiration switched to a significant positive CO_2 uptake during the night. CAM can be divided into four distinct phases during a day (Yamori et al., 2014): CO_2 uptake via stomata during the night and accumulation of malic acid (phase I), a transition phase with CO_2 uptake at

down when the stomata are open (phase II), decarboxylation of malic acid and re-fixation of CO_2 behind closed stomata at midday (phase III) and a transition phase when stomata are open at dusk (phase IV). Thus, we can conclude that typical CAM photosynthesis was a result of the temperature drop at night. According to Yamori et al. (2014), the diurnal photosynthetic pattern in CAM plants as a response to day/night temperature variation has yet to be clarified, although day and night temperature vary considerably in deserts where many CAM plants are found. A temperature drop during the night thus appears to immediately induce a change from C_3 to CAM photosynthesis in *K. blossfeldiana*. This may reflect a natural response to the environment of a species that originates in arid regions of Madagascar ($15\text{--}25^\circ$ southern latitude) with large diurnal temperature fluctuations. The surface temperature in a desert at low latitudes may vary $20\text{--}30^\circ\text{C}$ during the 24-h cycle, including hot days and cool nights close to zero degrees (Pinker et al., 2007). For CAM plants, a low night temperature therefore signals a hot, dry day when the stomata should be kept closed to avoid water loss. Since this temperature effect is genetically based, the response persists even when it is not necessary under the well-watered conditions of *K. blossfeldiana* in greenhouses.

Rascher et al. (1998) found that a rapid, rather than a slow, temperature change (0.5°C h^{-1}) induced a change in the photosynthetic rhythm in *Kalanchoe daigremontiana*. In the present experiment, the temperature drop was $2\text{--}3^\circ\text{C h}^{-1}$ so this may have caused the very strong effect on the diurnal photosynthetic rhythm. If dynamic temperature control is applied for this species, a slow temperature drop may reduce the negative effect on photosynthesis. In practice, this will entail some heating during the night. However, it would be interesting to investigate whether the speed of the drop is more important than the temperature level itself.

In the present study, the CER of about $40 \text{ mmol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ at constant $225 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD was similar to that measured by Pagter et al. (2013) on single leaves at about $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the same species. They also found that two days chilling at 4°C decreased the photosynthesis by about 50%, a finding similar to that in the present experiment by abruptly decreasing the temperature from 20°C to below 10°C during the night. Generally, it can be concluded from the present results that *K. blossfeldiana* is a species that can easily switch from C_3 to CAM photosynthesis with a night temperature drop. This will likely result in a considerable decrease in overall photosynthesis and growth, and dynamic temperature control of the greenhouse atmosphere to save energy cannot therefore be recommended.

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