Effect of CO₂ Enrichment on Growth and Flowering of *Phalaenopsis*

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To increase the photosynthesis of crop and improve plant quality, we evaluated the effect of elevated CO₂ on vegetative growth and flowering in *Phalaenopsis* 'Fuller's Pink Swallow'. Plants were exposed to 450 (control), 800, 1600, and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ for 31 weeks. The number of leaves, leaf length, and leaf width displayed greater increases in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ than in plants grown under 450 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. The times to leaf initiation were reduced to 90.7 and 85.8 days in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂, respectively, compared with that of the control, 177.1 days. The leaf elongation rate was significantly increased in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ compared to plants grown under 450 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Plants grown under 1600 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ had the highest total number of flower buds among all plants grown under the four tested CO₂ concentrations. Leaf injuries were not observed in any plants regardless of CO₂ concentration, but flower bud abortion and bud withering were observed in CO₂-enriched plants, especially in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂. Plants subjected to long-term CO₂ elevation of over 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ displayed increased biomass production despite a concomitant reduction in the number of buds. These results showed that 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO₂ significantly enhanced the vegetative growth of *Phalaenopsis*. However, long-term exposure to high CO₂ concentrations can adversely affect the flowering of *Phalaenopsis*, and result in reduced flower production and increased flower bud abortion.

Key Words: CAM plants, CO₂ concentration, flowering quality, long-term CO₂ treatment, withered flower buds.

Introduction

Atmospheric CO₂ is rising at an unprecedented rate, and the upward trend is mostly linked to anthropogenic emissions. To reduce CO₂ emissions, stabilization of the atmospheric CO₂ concentration a combination of limiting fossil fuel use and creation of carbon sinks, especially crassulacean acid metabolism (CAM) plants, could be exploited for terrestrial sequestration of atmospheric CO₂ (Reddy et al., 2010). This has promoted considerable interest in the potential impact of elevated CO₂ on plant production systems. CO₂ enrichment ben-

efits ornamental plant production by stimulating plant growth, which in turn improves flower yield and quality (Liu et al., 2000). A CO₂ concentration from 700 to 900 ppm is generally recommended in greenhouses (Mortensen, 1987). However, the amount of CO₂ a plant requires for optimum growth varies from plant to plant (Gouk et al., 1997; Mortensen, 1987). For example, an early report on the effect of CO₂ concentrations on the growth of the 'Hark' soybean reported that higher seed yield was obtained by treatment with 1350 ppm CO₂ (Cooper and Brun, 1967). Without visible morphological damage, the stem and leaf growth rate were increased in *Pharbitis nil* Choisy grown under 5000 ppm CO₂ (Hicklenton and Jolliffe, 1980). Optimal CO₂ concentrations for plant growth and flower production were 900 ppm in *Alstroemeria* 'Fiona', whereas the flower quality in *Alstroemeria* 'Helios' decreased significantly at 900 ppm CO₂ (Van Labeke and Dambre, 1998). Therefore, optimizing the CO₂ concentration is required to improve plant growth and quality based on plant species and genotypes.

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Phalaenopsis holds a leading position in the number of potted plants sold internationally. *Phalaenopsis* plants with multiple spikes and more flowers yield higher prices; therefore, *Phalaenopsis* growers look for ways to increase the number of spikes and flowers. *Phalaenopsis* is a CAM plant, which fixes CO₂ during the daily scotoperiod (Guo and Lee, 2006). Unlike C₃ and C₄ plants, studies investigating the effects of CO₂ enrichment on the vegetative and reproductive growth of CAM plants have reported inconsistent outcomes, including decreases in vegetative growth, no change in either vegetative growth or CO₂ uptake (Croonenborghs et al., 2009), and large increases in both vegetative growth and CO₂ uptake (Monteiro et al., 2009; Weiss et al., 2010).

A previous study reported that up to 1000 ppm CO₂ may have a positive effect on photosynthesis and flowering in *Phalaenopsis* (Kromwijk et al., 2014). Endo and Ikushima (1997) observed increases in the number of spikes and flowers, and higher spike fresh weight in cut flower *Phalaenopsis* when the CO₂ concentration was increased to 700 and 1000 ppm. Hwang and Jeong (2009) suggested that the vegetative growth of *Phalaenopsis* cultivars grown under 2000 ppm CO₂ was greater than that of plants grown under 1000 ppm CO₂. Previous studies were unable to evaluate the effects of long-term CO₂ enrichment on both vegetative and flowering response in *Phalaenopsis*. CO₂ concentration is a key environmental factor influencing the metabolism and development of CAM plants; therefore, further improvement in *Phalaenopsis* production demands a better understanding of plant responses to CO₂. The objective of this study was to determine the optimum CO₂ concentration to improve the growth and flowering quality of *Phalaenopsis* 'Fuller's Pink Swallow'.

Materials and Methods

Plant growth conditions

Phalaenopsis 'Fuller's Pink Swallow' was propagated by tissue culture, and 15-month-old clones were purchased from Gobong Orchid Nursery, Goyang, Korea (latitude 37°43'38.2"N, longitude 126°49'49.6"E). Plants with six leaves (5.3 cm in diameter and 11.5 cm in length) were transplanted into 12 cm pots filled with 65% peat moss (Klasmann-Dellmann GmbH, Geeste, Germany), 30% sphagnum moss (Lonquen Ltd., Puerto Montt, Chile), and 5% Indonesian medium-grade Douglas fir bark. Twenty plants each were cultured in four different growth chambers (HB-301MP; Hanbaek Scientific Co., Ansan, Korea; 1.4 m × 1.1 m × 2.1 m) with different CO₂ concentrations. The air temperatures of the cultivation periods for vegetative growth, flower spike induction, and flower spike development were 29/29, 23/18, and 25/20°C (12 h light/12 h dark), respectively. The daytime photosynthetic photon flux density of the cultivation periods for vegetative growth, flower spike

induction, and flower spike development were 120, 160, and 160 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from 12:00 to 24:00, respectively. Photosynthetic photon flux was provided at the plant canopy with three-wave cool white fluorescent lamps (Triband phosphor fluorescent lamp, Dulux L 36 W; Osram Korea Co., Korea). The relative humidity in the growth chamber was 50% during the experimental period. The plants were fertigated once every 10 days by hand with a solution of water-soluble fertilizer (EC $0.8 \pm 0.1 \text{ dS}\cdot\text{cm}^{-1}$ and pH 6.0–6.5; Newgold 20N-8.7P-16.7K; Neufarm Corp., Ltd., Munster, Germany).

CO₂ enrichment

Twenty plants each were cultured in four different growth chambers with different CO₂ concentrations (daily mean of ambient atmosphere $450 \mu\text{mol}\cdot\text{mol}^{-1}$), 800, 1600, and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$. The CO₂ concentration was maintained by automated continuous injection of pure CO₂. Pure CO₂ (cylinders of compressed CO₂; Seoul Gases Co., Ltd., Seoul, Korea) was supplied through a flow meter that controlled the flow rate at approximately $50 \text{ mL}\cdot\text{min}^{-1}$. In all four chambers, the CO₂ concentrations were monitored by using a CO₂ analyzer (AM-21A; WISE Sensing Inc., Gyeonggi, Korea). CO₂ treatments were applied to the plants for 6 hours during the nighttime (18:00–24:00) in a controlled growth chamber for 31 weeks.

Growth and flowering parameters

The total number of leaves with lengths of ≥ 0.5 cm was measured for each plant every 2 weeks for 31 weeks. Leaf length and width were measured every 2 weeks for each plant, starting with the first leaf that was produced after the start of CO₂ treatment. The leaf elongation rate (LER) was calculated from the equation: $\text{LER} = dL/dt$ (L , leaf length; t , days after treatment). The time to leaf initiation from the start of CO₂ treatment was measured when the first visible leaf was 0.5 cm long. The leaf chlorophyll content was measured in the uppermost mature leaf using a chlorophyll meter (SPAD 502; Konica Minolta Sensing, Inc., Sakai, Japan) at 31 weeks after the start of the treatment. The fresh and dry weight of shoots and roots were measured at 31 weeks after the start of CO₂ treatment. Dry weight was measured after drying the shoots and roots in an oven at 80°C for 10 days.

Flowering was defined as full expansion of the labelum of the first flower. Days to flowering were recorded. The flowering percentage was calculated as the percentage of flowering plants out of twelve plants. The number of flower spikes and flowers was counted for each plant once a week. At flowering, the flower spike length was measured for the first flower spike. Lateral branch length, total number of buds, and total number of withered buds was measured for each plant every 2 weeks. The fresh weight of flower spikes was measured

first, then the flower spikes were dried in an oven at 80°C for 10 days and dry weight was measured.

Statistical analysis

The experimental design was a completely randomized block with twelve replicates of one plant each. Statistical analyses were performed using the SAS system (version 9.3; SAS Institute Inc., Cary, NC, USA). Mean separation was performed on all other data with Tukey's honestly significant difference test at $P < 0.05$. Graph module analysis was performed using Sigma Plot software (version 10.0; Systat Software Inc., Chicago, IL, USA).

Results

Leaf growth and development

Phalaenopsis plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 produced more leaves than those grown under 450 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 at 17 weeks after the start of treatment (Fig. 1A). Leaf length and width were significantly greater in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 than in plants grown under 450 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 at 16 weeks after the start of the treatment (Fig. 1B and C). The time to leaf initiation was reduced to 90.7 and 85.8 days in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 , respectively, compared with that of the control's 177.1 days (Table 1). The leaf elongation rate was significantly increased in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 compared to plants grown under 450 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 . The fresh weight of roots was higher for plants grown under 800, 1600, and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 than for plants grown under 450 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 , but there were no significant differences in the leaf chlorophyll content, and the fresh and dry weight of shoots for plants grown under the four tested CO_2 concentrations (Table 1).

Flowering/inflorescence characteristics

Days to flowering of plants grown under 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 was delayed for about 33 days compared to the 170 days of plants grown under 450 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 (Table 2). Approximately 92% and 67% of plants grown under 450 and 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 flowered, respectively. In contrast,

Fig. 1. Changes in total number of leaves (A), leaf length (B), and leaf width (C) of *Phalaenopsis* 'Fuller's Pink Swallow' under different CO_2 concentrations. Error bars represent means $\pm$ SE, $n = 12$.

Table 1. Effects of CO_2 concentration on time to leaf initiation, leaf elongation rate, leaf chlorophyll content, and fresh and dry weight of shoots and roots in *Phalaenopsis* 'Fuller's Pink Swallow' after 31 weeks.

CO_2 concentration ($\mu\text{mol}\cdot\text{mol}^{-1}$)	Time to leaf initiation (days)	Leaf elongation rate ($\text{cm}\cdot\text{day}^{-1}$)	Leaf chlorophyll content (SPAD)	Fresh weight (g)		Dry weight (g)	
				Shoots	Roots	Shoots	Roots
450 (control)	177.1 a ^z	0.019 c	73.93 a	55.05 a	17.0 b	3.636 a	1.92 b
800	163.4 ab	0.030 bc	73.67 a	55.02 a	21.5 a	3.555 a	1.96 a
1600	86.4 c	0.053 ab	71.39 a	56.93 a	21.2 a	3.482 a	2.05 a
2400	91.3 bc	0.061 a	73.95 a	54.90 a	22.3 a	3.470 a	2.22 a

^z Mean separation within columns by Tukey's honestly significant difference test at $P < 0.05$ ($n = 12$).

none of the plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 flowered during the experiment due to aberrant flower development and bud drop (Table 2; Fig. 2D). The number of flower spikes was not significantly affected by different CO_2 concentrations. The number of flowers was significantly higher in plants grown under 450 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 than in plants grown under 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 . The fresh and dry weights of flower spikes were highest in plants grown under 450 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 compared with those under the other CO_2 concentrations. Plants grown under 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 produced longer flower spikes than plants grown under the other tested CO_2 concentra-

tions at 26 weeks after the start of treatment (Fig. 2A). All plants produced lateral branches at 18 weeks after the start of the treatment. The lateral branch length was significantly longer in plants grown under 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 than under the other CO_2 concentrations at 23 weeks after the start of treatment (Fig. 2B). Floral buds appeared at 17 weeks after the start of treatment regardless of CO_2 concentration (Fig. 2C). Plants grown under 1600 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 had the highest total number of flower buds compared with plants grown under the other CO_2 concentrations. However, flower buds became withered in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 at 20 weeks after

Table 2. Effects of CO_2 concentration on days to flowering, flowering percentage, number of flower spikes and flowers, and fresh and dry weight of flower spikes in *Phalaenopsis* 'Fuller's Pink Swallow' after 31 weeks.

CO_2 concentration ($\mu\text{mol}\cdot\text{mol}^{-1}$)	Days to flowering	Flowering Percentage	Number of flower spikes	Number of flowers	Fresh weight ^z (g)	Dry weight ^z (g)
450 (control)	170 b ^y	92	1.87 a	9.1 a	22.4 a	2.09 a
800	203 a	67	1.50 a	5.5 b	15.3 b	1.38 b
1600	— ^x	0	2.25 a	0.0 c	11.7 bc	1.39 b
2400	—	0	1.67 a	0.0 c	10.8 c	1.23 b

^z Fresh and dry weight of flower spikes includes flowers and buds.

^y Mean separation within columns by Tukey's honestly significant difference test at $P < 0.05$ ($n = 12$).

^x The dash symbol (—) indicates that no information was available at 31 weeks.

Fig. 2. Changes in the flower spike length (A), lateral branch length (B), total number of flower buds (C), and total number of withered buds (D) of *Phalaenopsis* 'Fuller's Pink Swallow' under different CO_2 concentrations. Error bars represent means $\pm$ SE, $n = 12$.

the start of treatment, and the total number of withered buds sharply increased at 23 weeks (Fig. 2D). The flower buds in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 finally dropped after the experiment ended (data not shown).

Discussion

This study showed that CO_2 enrichment significantly increased leaf development, which was measured as the number of leaves, leaf length, and leaf width (Fig. 1). Leaf growth rates are frequently modulated by differences in plant water potential (Taylor et al., 1994). Leaf growth under elevated CO_2 concentration enhances the efficiency of water use, which increases cell turgor pressure, promotes cell wall relaxation and/or cell division (Pritchard et al., 1999), and thereby increases the leaf elongation rate (Table 1). Lateral branch length and flower spike length of *Phalaenopsis* 'Fuller's Pink Swallow' increased especially in plants grown under 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 . Numerous studies have reported increased stem or branch elongation in plants grown under elevated CO_2 . For example, Rogers et al. (1992) reported a 15% increase in plant height for *Glycine max* grown under elevated CO_2 . Similarly, the height of *Triticum aestivum* plants grown under elevated CO_2 increased by 17% due to increased internode length rather than increases in the numbers of nodes (Slafer and Rawson, 1997). Increases in the numbers of branches with elevated CO_2 can be due to effects on overall developmental rate rather than changes in the pattern of branch initiation (Ackerly et al., 1992). In the present study, the flower spike number did not significantly differ among the treatments. These results suggest that CO_2 enrichment stimulates the growth and development of cells and tissues below the site of lateral organ formation to a greater extent than it stimulates organ primordia formation at the shoot tip (Pritchard et al., 1999).

Plant quality, expressed by the growth habit and the number of flowers, is often enhanced by CO_2 enrichment (Endo and Ikushima, 1997). CO_2 application can increase growth rates and reduce production time, but leaf senescence or visible leaf injuries such as chlorosis, necrosis, and leaf curling is observed at higher CO_2 levels in some annual plants (Mortensen, 1987). In ornamental bromeliads, CO_2 enrichment induced aberrant plant shapes with long and slender leaves (Croonenborghs et al., 2009). In the present study, visible leaf injuries were not observed in any plants regardless of CO_2 concentration, but withered flower buds and bud abortion were observed in CO_2 -enriched plants, especially in plants grown under ≥ 1600 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 , resulting in non-flowering (Fig. 2D; Table 2). The ability of plants to respond to elevated CO_2 levels depends on physiological characteristics such as sink strength, efficiency of nitrogen and water use, and photosynthetic pathway and capacity (Diaz, 1995; Pritchard et al.,

1999). If plants are unable to use fixed carbon for growth, the result is typically an increase in total non-structural carbohydrates and possibly increased levels of carbon-based secondary compounds (Poorter et al., 1997). However, limitations on carbon assimilation may be imposed by mechanical and biochemical processes within source leaves resulting from weak sink activity (Pritchard et al., 1999). Other structural functional attributes may limit the capacity to exploit the extra carbon available under higher CO_2 concentrations. Temporal competition for carbohydrates appeared between vegetative and reproductive organs. The sucrose synthesis in the developing shoot tips of peaches reached the maximum when growth in fruits was lowest (Lo Bianco et al., 1999). In maize, ovary abortion under stress conditions is often a consequence of carbon starvation rather than a direct effect of these stresses (Mäkelä et al., 2005). In this study, the leaf elongation rate increased by CO_2 enrichment (Table 1), whereas flower buds dropped in plants grown under over 1600 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 (Fig. 2D). This may be related to the changed sink strength or carbon limitation between leaves and flower buds under higher CO_2 concentrations.

In many cases, plant growth responses to elevated CO_2 may be modulated by nutrient availability (Conroy et al., 1990; Prior et al., 1997) or supplemental light. For example, restricting the nutrient concentration to a low level of 1.0 $\text{mS}\cdot\text{cm}^{-1}$ blocked the effect of CO_2 enrichment on growth due to nutrient deficiency, whereas CO_2 enrichment with a high nutrient concentration of 4.0 $\text{mS}\cdot\text{cm}^{-1}$ increased growth and enhanced plant quality (Meier and Fuhrer, 1997). In *Alstroemeria*, the combined effect of CO_2 enrichment and supplemental lighting enhanced flower stem growth and prevented flower abortion more significantly than that of either factor alone (Van Labeke and Dambre, 1993). These results suggest that complex environmental conditions should be considered when plants are grown under CO_2 -enriched air in order to maintain high plant quality. Further study on the effects of CO_2 interaction with other environmental factors is required for *Phalaenopsis* cultivation.

In conclusion, this study showed that 1600 and 2400 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 significantly enhanced vegetative growth of *Phalaenopsis*. However, long-term exposure to high CO_2 concentrations can adversely affect the flowering of *Phalaenopsis*, and result in reduced flower production and increased flower bud abortion. *Phalaenopsis* subjected to CO_2 -enriched conditions of over 800 $\mu\text{mol}\cdot\text{mol}^{-1}$ CO_2 before flower spike induction displayed increased biomass production.

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