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THE GROWTH AND DEVELOPMENT OF HIPPEASTRUM IN RESPONSE TO TEMPERATURE AND CO_2.

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EPHRATH, J. E., BEN–ASHER, J., ALEKPEROV, CH., SILBERBUSH, M. and DAYAN E. *The growth and development of Hippeastrum in response to temperature and CO_2.* BIOTRONICS **30**, 63–73, 2001. Flowering time of Hippeastrum can be controlled by applying specific thermal regime to large sized bulbs. Due to high–energy costs, the aim of this study was to examine the possibility to reduce soil heating and keep high bulb growth rate by increasing the CO_2 concentration. Two sets of experiments were carried out in a controlled greenhouse at the North–Western Israeli Negev Desert. In both experiments, bulbs of different initial sizes were grown under two levels of CO_2 concentrations (ambient, 350 ppm and elevated, 1000 ppm) combined with different minimum soil temperature regimes. In the first experiment three temperature regimes (16℃, 22℃ and 24℃) were tested, while in the second experiment only one minimum soil temperature regime (22℃) was investigated. In both experiments, raising CO_2 concentration from the ambient level to elevated one, or increasing soil temperature resulted in a higher bulb growth rate. Temperatures, CO_2 concentration and initial bulb size significantly influenced the final diameter of the bulbs. A significant difference in final bulb diameter was obtained only between the 16℃ treatment and the 22℃ and 24℃ treatments, but not between the two high temperatures tested. The area of the largest leaf was significantly affected only by the soil temperature treatments. No effect of CO_2 concentration on leaf area development was detected. The number of leaves, however, was affected by the CO_2 but not by the temperatures. Bulbs grown under elevated CO_2 had a higher flowering rate compared to ambient CO_2. This was effective both in shortening the period of time from re–planting until flowering and by the significant high number of flowers compared to the ambient CO_2 conditions.

Key words: Leaf area; bulb size; number of leaves; flowering

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INTRODUCTION

The highest demand for Hippeastrum bulbs is during the Christmas holiday at the end of December. Previous studies (*10, 12*) have shown that during the winter, when soil temperature is reduced below 15℃, bulb growth would cease. Hippeastrum naturally flowers in the spring, from the middle of March until the beginning of May. The main factor that affects the flowering time is the size of the bulb (*3, 17*) with no effects of day-length or other external factors. Spring flower development would cause a reduction in the bulb size due to the use of stored carbohydrates, which results in a delay in flowering. In order to meet the market demand and to shorten the growing season, farmers in Israel and the Netherlands grow Hippeastrum bulbs in greenhouses and usually heat the soil in order to keep soil temperature above a threshold (15℃) and to have a continuous growth throughout the year. Several heating practices are used: Pipes buried in the soil or on the surface with hot water running through them whenever soil temperatures reduced or heating of the entire greenhouse which increases the production costs tremendously.

The rise in global atmospheric CO_2 has been well documented. Carbon dioxide enrichment has been shown to increase growth of rice (*2*) and other crops (*4, 7, 13*). Several studies examined the combined effects of elevated CO_2 concentration and temperature on the growth and development of the above and below the soil surface parts of crops. Idso et al. (*11*) reported that the proportional yield increases due to elevated CO_2 concentration are often much larger under warmer temperatures. Similar results also were reported by Long (*14*). On the other hand, no such interaction was obtained in carrot (*18*), cauliflower (*19*) or wheat (*15, 20*).

Yield increases of root crops grown at elevated CO_2 are often larger than the average, probably because the harvestable portion of the plant is a larger sink for photosynthetic assimilates (*6*). It is not known if CO_2 concentration affects bulb formation in onion (*5*). However, the time for bulbing was found to be more rapid at high temperatures (*5*).

There is no doubt that a possible interaction between high temperatures and elevated CO_2 on the development of Hippeastrum bulbs is a complex response. Improved understanding of crop responses to these two factors is of great importance. The overall objective of the study presented here was to examine the combination of several temperature regimes and elevated CO_2 concentration on the bulb development of Hippeastrum. More specifically this study examines the possibility of compensating the reduction in soil heating due to high-energy costs by increasing the CO_2 concentration, and maintain high bulb growth rate

MATERIALS AND METHODS

The results presented here are from a study conducted from 1994–1999 in the Northern Negev Desert of Israel. Hippeastrum bulbs (*Hippeastrum hybridum,* Var. Red Lion) were planted in a controlled greenhouse. Thermometers were installed in the soil at the depth of bulbs placement (5 cm) and minimum soil temperature was thermostatically controlled by circulating hot water in a set of pipes placed on the soil surface.

The greenhouse was divided into two sections in which two levels of CO_2 concentrations were tested: 1000 ppm (enriched) in one section and 350–360 ppm (ambient) in the other. CO_2 enrichment was achieved by a Priva CO_2 heater and controlled by an analyzer (*PRIVA 0292 model 07, Serial No. DK 2290* Priva, the Netherlands). The CO_2 enrichment system started daily at one hour after sunrise and turned off one hour before sunset.

As air temperature inside the greenhouse exceeded 32℃, the sidewalls of the greenhouse would open allowing the exchange of air to ventilate and reduce the temperature inside the greenhouse. At this point, the CO_2 enrichment system was turned off automatically. When air temperature decreased below 28℃, the sidewalls were closed again and the CO_2 enrichment system resumed operation.

Two studies, which examined the effects of CO_2 enrichment and an increase in soil temperature, were carried out. The first experiment was planted in November 15, 1994. Two hundreds bulbs of four initial sizes (50 of each of the following diameters: 3.5 cm, 4.14 cm, 4.78 cm and 5.4 cm) were grown for 255 days at three levels (treatments) of minimum soil temperature: 16℃, 22℃ and 24℃ and two levels of CO_2 concentrations. In the second experiment 200 bulbs were planted in January 12, 1998 and harvested 220 days later. In this experiment only one minimal soil temperature (22℃) was tested with two CO_2 concentrations and four initial size categories (50 bulbs with te following initial diameters: 3.5 cm, 4.14 cm, 4.78 cm and 6.1 cm). In the two experiments, all measurements were replicated five times and averaged. At the end of the second experiment, 18 bulbs at the size (diameter) of eight cm grown in the two CO_2 concentrations were stored in 8℃ for six weeks and then were re-planted in November 4, 1998 in 4 l pots and grown in a greenhouse in order to follow the flowering rate.

Bulb growth rate was expressed as a change of diameter with time. The diameter was measured every two weeks by carefully removing soil surrounding the bulbs to allow measurement of the diameter. The bulbs were re-covered after measurements.

Leaf area was estimated from the product of its length and width. A correction factor due to the shape of the leaf (*9*) was introduced to obtain the actual leaf area. Actual leaf area was measured with a leaf area meter (model LI-3000 Li-Cor Inc., Logan Utah, USA) and the correlation between leaf length and maximum width and leaf area is described in Eq. [1].

$$LA = (W * L) * 0.66 + 15.45 \qquad R^2 = 0.985 \quad [1]$$

Where LA is the leaf area (cm^2), W and L are leaf blade width and length (cm) respectively and 0.66 is a shape correction factor. At $LA = 15.45\ cm^2$ the first term on the right hand side of the equal sign is negligible.

RESULTS

The final size of bulb grown in three temperature regimes and two CO_2 concentrations as a function of initial bulb size is presented in Fig. 1. Raising CO_2 concentration from the ambient level to 1000 ppm or increasing soil temperature resulted in a higher bulb growth rate. The final bulb size at the end of the measuring period (255 days after planting, DAP) at all three temperature regimes was not significantly different when bulbs were grown under elevated CO_2 concentration. The analysis of variance (ANOVA), presented in Table 1, shows that temperatures, CO_2 concentration and initial bulb size significantly influenced ($P>0.001$) the final size of the bulbs. Analysis of the data revealed that a significant difference in bulb final size was found only between the 16℃ treatment and the 22℃ and 24℃ treatments (Table 1). No significant difference in bulb final size was found between the two high temperatures tested. There was also no significant difference in final size of bulbs developed from the two small initial diameters (3.5 and 4.2 cm, Table 1)

The effect of CO_2 concentration on bulb size for bulbs with different initial diameters grown at a constant soil temperature of 22℃ is presented in Fig. 2 (A–D). In three out of the four initial size categories that were examined, higher CO_2 concentration resulted in a larger bulb diameter at the end of the growing season. In the small size category (a diameter of 3.5 cm., Fig 2–A) there was no effect of the elevated CO_2 concentration on bulb size. Only bulbs of the initial large size category (diameter of 6.1 cm), which were grown under the elevated CO_2 concentration reached marketing size (a diameter of 8 cm) at the end of the growing season. When examining the effect of initial bulb size on the difference

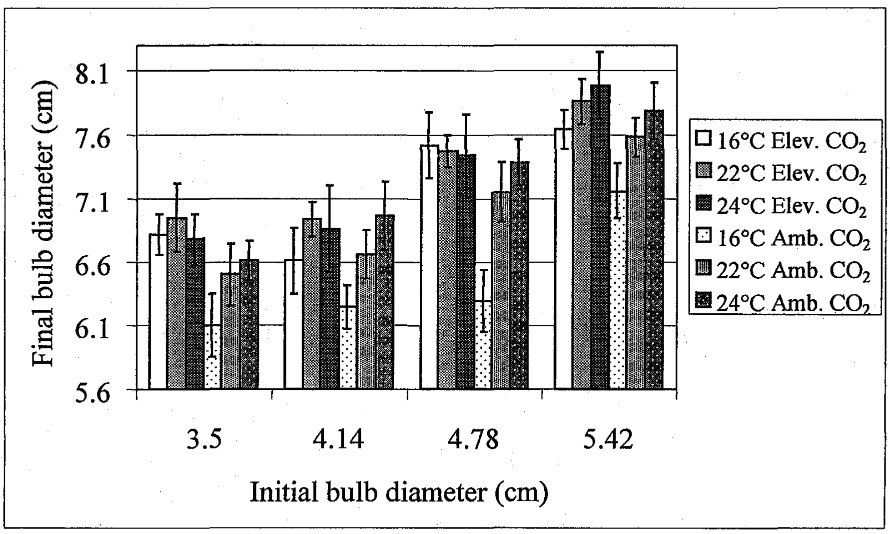

Fig. 1. Final bulb diameter as a function of three levels of minimum soil temperature, two CO_2 concentrations and initial bulb diameter (controlled greenhouse, 1994–95). Error bars represent ± standard error of the mean, $n=5$. Temperature levels are presented in the graph. CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated).

in diameter values between the beginning and the end of the growing season at the two CO_2 concentrations (Fig. 3), we can see that as the initial bulb size increased, the differences between the initial and final diameter decreased. This slope reduction was more than two times larger under the ambient CO_2 concentration compared to the elevated CO_2 concentration.

The effect of CO_2 concentration on bulb fresh biomass is presented in Fig. 4. A significant effect of the elevated CO_2 concentration on biomass was found in bulbs with initial size larger than 3.5 cm in diameter (Fig. 4 B–D compared to Fig. 4–A). Except for the bulbs of the large initial size category (Fig. 4–D, a diameter of 6.1 cm), bulb biomass increased throughout the growing period.

The area of the largest leaf was significantly affected only by the soil temperature treatments (Table 2). The effect of CO_2 concentrations on leaf area development was not significant (Table 2). The number of leaves per plant, however, was significantly affected by the CO_2 concentrations but not by temperatures (Table 3).

The effect of the CO_2 concentration on the flowering percentage of bulbs

Table 1. Analysis of variance for the final bulb diameter, 255 days after planting, in the 1994–95 experiment. Temperatures were 16℃, 22℃ and 24℃. CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated). Initials diameter sizes were 3.5, 4.2, 4.7 and 5.4 cm (n=5). Means with different letters are significantly difference at $p<0.05$.

SOURCE	DF	SS	MS	F	P
Temperature	2	0.81295	0.40647	9.93	0.0010
CO_2	1	0.81918	0.81918	20.01	0.0003
Initial size	3	4.22431	1.40810	34.39	0.0000

LSD (T–test) comparison of means of final diameter by: Temperature

Temperature	Mean (cm)
22℃	7.2260 a
24℃	7.1400 a
16℃	6.7997 b

LSD (T–test) comparison of means of final diameter by: CO_2

CO_2 (ppm)	Mean (cm)
1000	7.2400 a
350	6.8705 b

LSD (T–test) comparison of means of final diameter by: Initial size

Initial size (cm)	Mean (cm)
3.5	7.6713 a
4.2	7.2097 b
4.7	6.7137 c
5.4	6.6263 c

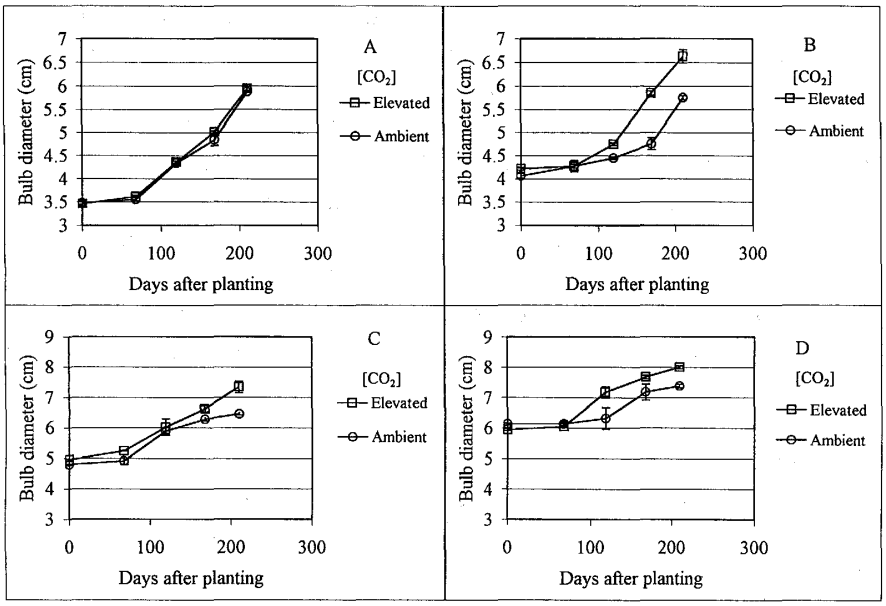

Fig. 2. The effects of two CO_2 concentrations at a minimum soil temperature of 22℃ and different initial bulb size categories (A–3.5 cm.; B–4.14 cm.; C–4.78 cm.; D–6.1 cm.) on the development of bulb diameter (controlled greenhouse, 1998–99). Error bars represent±standard error of the mean, *n*=5. CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated).

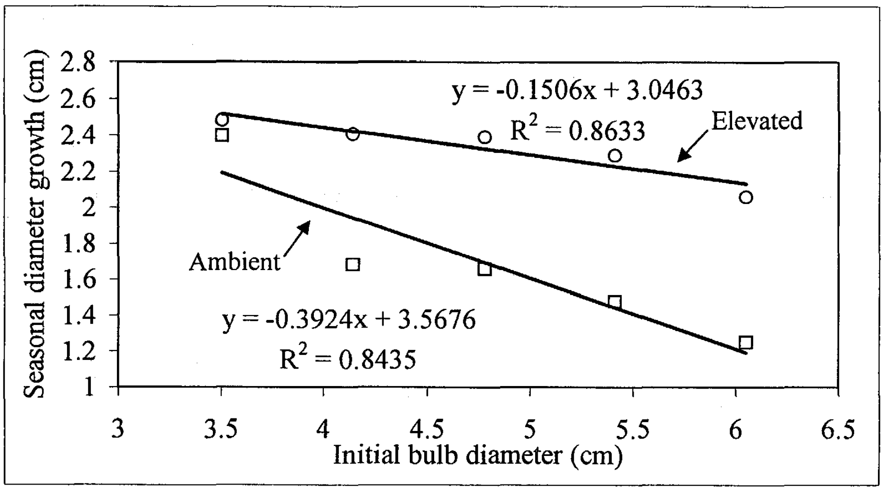

Fig. 3. The seasonal diameter growth of bulbs planted in different sizes and grown in elevated and ambient CO_2 concentrations (controlled greenhouse, 1998–99). Regression equations are presented in the graph. CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated).

replanted after storage is presented in Fig. 5. About 80% of the bulbs grown in elevated CO_2 concentration flowered compared to only 40% of the bulbs grown under ambient CO_2 concentration (Fig. 5-A). Furthermore, the elevated CO_2 grown bulbs flourished sooner: 88% of the flowered bulbs bloomed after 88 days and the rest after 95 days compared the ambient CO_2 concentration where only 30% bloomed after 88 days and the remaining 70% flowered after 102 days (Fig. 5-B).

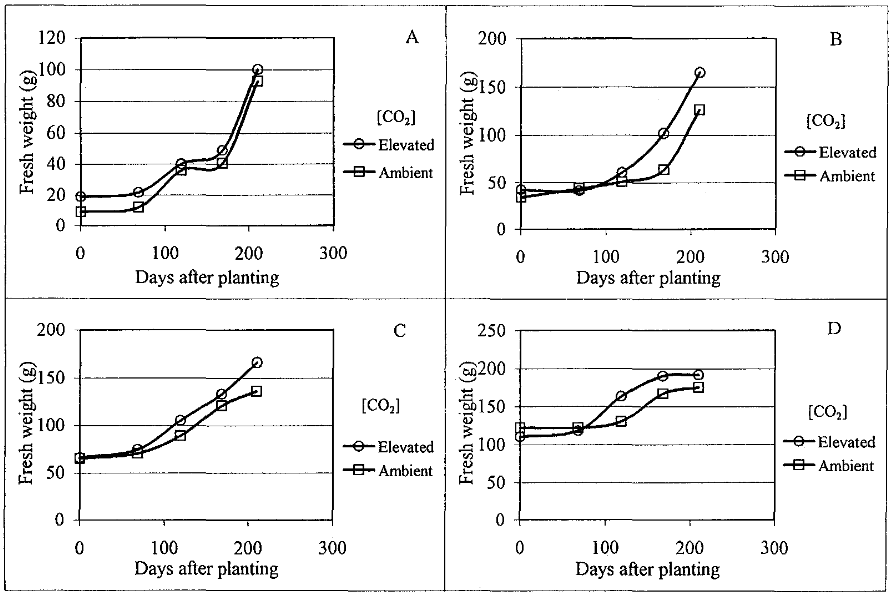

Fig. 4. The effects of two CO_2 concentrations at a minimum soil temperature of 22℃ and different initial bulb size categories (A-3.5 cm.; B-4.14 cm.; C-4.78 cm.; D-6.1 cm.) on the development of bulb fresh weight (Controlled greenhouse, 1998-99). CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated).

Table 2. Analysis of variance for the area of the largest leaf in the 1994-95 experiment. Temperatures were 16℃, 22℃ and 24℃; CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated). (n=5). Means with different letters are significantly difference at $p<0.05$.

SOURCE	DF	SS	MS	F-value	P
Temperature	2	4640.62	2320.31	7.76	0.0032
CO_2	1	0.02927	0.02927	0.00	0.9922

LSD (T-test) comparison of means of leaf area by: temperatures

Temperature	MEAN (cm^2)	GROUPS
24℃	179.04	a
22℃	170.78	a
16℃	146.30	b

Table 3. Analysis of variance for the number of leaves (per plant) in the controlled greenhouse experiment, 1994–95. Temperatures were 16℃, 22℃ and 24℃; CO_2 concentrations were 350 ppm (ambient) and 1000 ppm (elevated). (n=5). Means with different letters are significantly difference at $p<0.05$.

SOURCE	DF	SS	MS	F	P
Temperature	2	0.49000	0.24500	1.44	0.2602
CO_2	1	2.53500	2.53500	14.91	0.0010

LSD (T-test) comparison of means of leaf number by: CO_2

CO_2	MEAN (number of leaves)	GROUPS
Elevated	8.6167	a
Ambient	8.0333	b

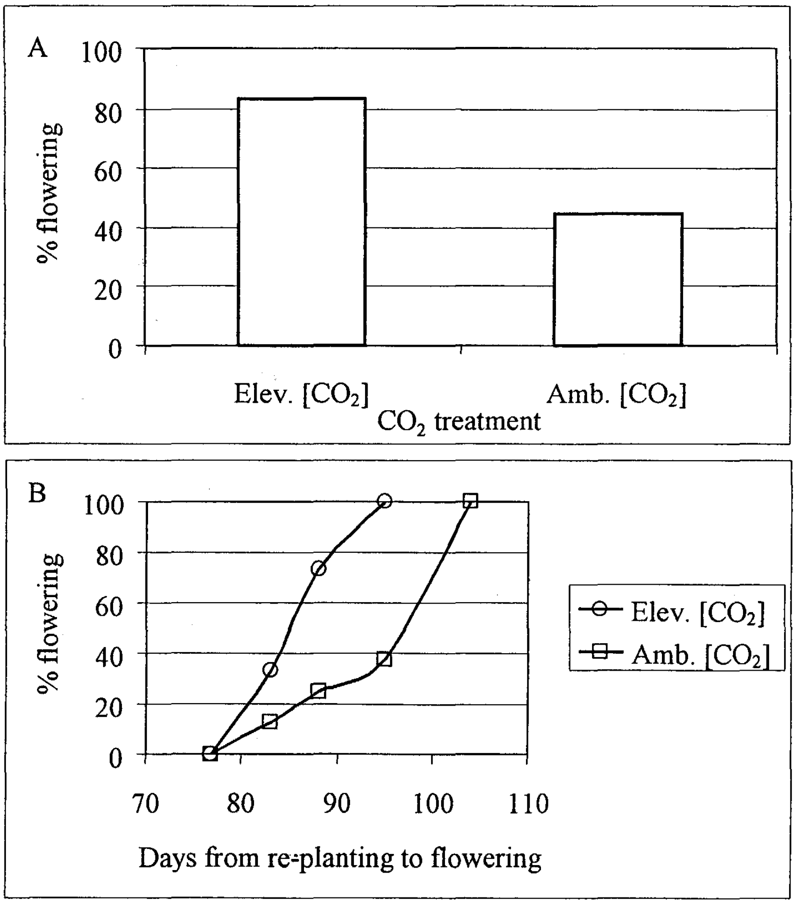

Fig. 5. Percentage (A) of flowering of bulbs and flowering rate of the flowered bulbs (B) grown under ambient (350 ppm) and elevated (1000 ppm) CO_2 concentrations flowering rate of the flowered bulbs (controlled greenhouse, 1998–99).

DISCUSSION

The aim of this study was to investigate if elevated CO_2 in a greenhouse could compensate for the reduction in temperature needed for high bulb growth rate of Hippeastrum plant. To answer this question a series of experiments were carried out in a controlled greenhouse in which several soil temperatures treatments and two CO_2 concentrations were imposed on the plants.

Several indices were tested to study the effects of temperatures, CO_2 and the combine effects of the two. The indices were bulb diameter, bulb weight, number of leaves and leaf area and the potential flowering capacity of bulbs grown either in elevated or ambient CO_2 concentration after storage in 8℃ for eight weeks.

Increasing the soil temperatures from 16℃ to 22℃ and above resulted in a larger bulb but no effect was observed when soil temperature increased from 22℃ to 24℃. This response is similar to what was reported in previous studies with onion (*5, 8*). The results of this study confirm our hypothesis that reduced soil temperature can be compensated by increasing the CO_2 concentration: When comparing the final size of bulbs grown in the three temperature regimes (Fig. 1) we can see that, under elevated CO_2 concentration no significant differences in bulb size were observed. These results were obtained for all the initial size categories tested. We found a similar pattern in bulbs of different initial size grown at a minimal soil temperature of 22℃ (Fig 3, A–D): Elevated CO_2 concentration increased bulb growth rate. Except for the small size bulbs (initial diameter of 3.5 cm, Fig 2–A) a significant difference in bulb size and biomass was observed between bulbs grown under the ambient and the elevated CO_2 concentration. The minimal marketing size of amaryllis bulb, which will ensure flowering, is 8 cm. in diameter (*3, 17*). In our study we found that bulbs grown at a minimum soil temperature of 22℃ and under elevated CO_2 concentration reached the marketing size within 210 days. In all other initial sizes and CO_2 treatments bulbs attained smaller final diameter. This result indicates that the elevated CO_2 concentration treatment shortened the time for maturity. The effect of elevated CO_2 concentration on bulb fresh weight (Fig. 4 A–D) was similar to that of bulb size increase throughout the season. Since we found that under the elevated CO_2 concentration bulbs were larger, with no effect on the area of the largest leaf (Table 2) but with a significant effect on the number of leaves per plant (Table 3), we can assume that the enhanced bulbs development under these conditions was associated with an increase in the total photosynthesizing area, as was found in other crops (*1, 16*).

The commercial product of the amaryllis is a bulb, which is supposed to flower within a short and pre-determined period of time after harvest. One of the most significant effects of the elevated CO_2 concentration appeared to be the flowering rate after storage (Fig. 5). Bulbs grown under elevated CO_2 concentration had better flowering characteristics compared to those grown under ambient CO_2 concentration. The improvement was both in shortening the period of time from planting to flowering and in the significantly higher number of flowers in bulbs grown under elevated CO_2 compared to those grown under ambient CO_2 conditions.

CONCLUSIONS

The results presented in this study show that reducing the soil temperature from 24℃ to 16℃ did not affect bulb growth rate when grown under elevated CO_2 concentration of 1000 ppm. Elevated CO_2 concentration significantly increased the number of leaves developed while higher temperature increased the area of the largest leaf. We also found that elevated CO_2 concentration significantly improved the flowering characteristics of Hippeastrum and shortened the period from re-planting to flowering after common storage conditions.

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