

Genotypic Variation of Cut Chrysanthemum Response to High CO₂ Concentration: Growth, Time to Flowering and Visual Quality

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Abstract

In this study sixteen cut chrysanthemum cultivars were used to evaluate the effects of high CO₂ concentration (1500 µmol mol⁻¹) on growth, time to flowering and visual quality as compared to the concentration used in commercial greenhouses (600 µmol mol⁻¹). CO₂ enrichment increased light use efficiency (11-41%) and total plant dry mass (TDM) (5-40%) in a cultivar dependent manner. This TDM increase was a result of: (i) higher relative growth rate during the long day period (i.e., 0 to 2 weeks; LD); and (ii) higher absolute growth rate both during the period between 2 to 6 weeks (SD₁), and 6 weeks to final harvest (SD₂). Cultivar differences in TDM at flowering between the two CO₂ concentrations could be explained by differences in growth rate during the LD and SD₂ periods. Furthermore, growing at high CO₂ regime enhanced the number of flowers and flower buds per plant (NoF, 4-48%). Interestingly, the cultivars that showed the highest percentage of TDM increase, with CO₂ enrichment, were not the ones that had the highest increase in the percentage of NoF. In contrast, high CO₂ concentration had only a minor or no effect on the number of internodes on the main stem and on the reaction time in all the cultivars examined. From this research it is concluded that there is a large variation in the response of cut chrysanthemum cultivars to CO₂ enrichment, in terms of TDM and NoF, which gives possibilities for breeding.

INTRODUCTION

The development of closed greenhouses (closed ventilation windows) is one of the major innovations in Dutch horticulture in the last years (Gelder et al., 2005). This new greenhouse concept is described in Opdam et al. (2005) and leads to a strong decrease in the energy and water consumption, a reduction in chemical crop protection as well as a yield increase, mainly because of the continuously high CO₂ concentration (Heuvelink et al., 2008). To assure the return of the investment and high profitability in such a production system the selection of efficient cultivars, namely in their responsiveness to CO₂ enrichment, is of utmost importance. However, besides vegetable crops (tomato, Gelder et al., 2005; cucumber, Luomala et al., 2008) there is no experience of growing ornamentals in such a system and the only comparable situation is to grow plants in climate chambers. Therefore, the impact of the new climate (i.e., high CO₂ concentration and high light level) on plant growth and development is not yet fully understood.

In chrysanthemum most studies on the effect of CO₂ concentration have been focused on one cultivar. To the best of our knowledge only one in-depth systematic comparison between three cultivars ('Refour', 'Dark Flamengo' and 'Cassa') was performed, where an interaction between cultivar and CO₂ concentration in biomass production, stem length and number of flowers was observed, when ambient CO₂ was compared to 900 µmol mol⁻¹ (Mortensen, 1986). To breed for cultivars more responsive

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to higher rates of CO₂ enrichment, it is important to know the variation of the CO₂ response existing in modern (recently introduced) cultivars. In this experiment our aim was to evaluate cultivar responses to long term high CO₂ enrichment (from 600 to 1500 $\mu\text{mol mol}^{-1}$) in terms of plant growth, time to flowering and visual quality aspects.

MATERIALS AND METHODS

Experimental Setup and Greenhouse Climate

The experiment was carried out in two conventional compartments (15×9.6 m; open ventilation windows) from a multispans Venlo-type glasshouse (52°N, Bleiswijk, The Netherlands), from 1 February to 14 April 2007. Block-rooted cuttings of sixteen *Chrysanthemum morifolium* cultivars ('Reagan Elite White', 'Calabria', 'Tobago', 'Paintbal' and 'Vyking' (Royal van Zanten, Valkenburg, The Netherlands); 'Anastasia', 'Zembla', 'Biarritz' and 'Noa' (Deliflor, Maasdijk, The Netherlands); 'Euro', 'Timman', 'MonaLisa' and 'Snowflake' (Dekker, Hensbroek, The Netherlands); 'Arctic Queen', 'Feeling Green' and 'Ibis' (Fides, De Lier, The Netherlands)) were planted in soil beds at a density of 64 plants m⁻². Each compartment contained six parallel soil beds (1×9 m per bed), where the two outer beds acted as borders. Plants were initially submitted to long-day (LD) (20 hours/day) conditions during 12 days followed by a short-day (SD) (10 hours/day) period up to the final harvest. Supplementary light, provided by high-pressure sodium lamps (50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ Photosynthetic Active Radiation, PAR), was applied to the crop to extend the natural photoperiod, and to supplement natural sunlight. The lamps were switched on when outside global radiation was lower than 150 W m⁻², and switched off when higher than 250 W m⁻². Irrigation was provided as required. In the cultivars 'Anastasia', 'Paintbal' and 'Noa' no growth regulators were applied, whereas for the remaining cultivars different types, concentrations and frequencies of growth regulators were applied following the breeding companies' indications. The terminal flower bud was pinched as soon as it was separated from the other crown buds (<5 mm).

Day temperature was set at 18°C and night temperature at 19°C, as is common practice for commercial chrysanthemum production in The Netherlands. The ventilation temperature set point was adjusted to the outside global radiation level to guarantee the high CO₂ concentration. This resulted in 20.2±0.1°C (low CO₂) and 20.1±0.1°C (high CO₂). Pure CO₂ was supplied to the crop during daytime (from 0700 to 1700 hours). In the low CO₂ treatment, enrichment started when the greenhouse level was lower than 400 $\mu\text{mol mol}^{-1}$ and dosing was stopped at 600 $\mu\text{mol mol}^{-1}$ (leading to a realized concentration of 580±10 $\mu\text{mol mol}^{-1}$; comparable to commercial practice). In the high CO₂ treatment, CO₂ was supplied when lower than 1400 $\mu\text{mol mol}^{-1}$ and was stopped at 1600 $\mu\text{mol mol}^{-1}$ (realized concentration of 1430±20 $\mu\text{mol mol}^{-1}$).

Destructive Measurements

Plants were destructively harvested on days 0, 14, 42 after planting and at final harvest stage (i.e., when the outer row of disc florets had reached anthesis in at least three inflorescences (flowers) per plant). Six (day 42), eight (day 14) or 12 (day 0 and final harvest) plants were measured in each of the two experimental units per treatment, resulting in 12-24 plants per treatment. Within a given cultivar, final harvest data were collected on all plants at the same time. If within the same cultivar, in one CO₂ concentration flower was induced earlier, the flowering date was registered, and the harvest date was postponed until the flowering was induced in the other CO₂ concentration too. Between cultivars, harvest dates were spread between day 59 and 71 after planting, because of the different rates of flower development. Total fresh mass per plant, number of internodes on the main stem (≥ 10 mm), stem length and leaf area (LI-COR, Model 3100 Area Meter; Lincoln, NE, USA) were recorded in time. At final harvest some additional measurements were performed, including: total dry mass of each experimental unit (ventilated oven, 105°C for at least 15 h), number of flowers including flower buds (>5 mm; NoF), and reaction time (i.e., time from start of SD period to

harvest). To examine the effect of high CO₂ on flower size, individual flower area and flower fresh mass were determined in the cultivars ‘Noa’ (‘spray’ type) and ‘Tobago’ (‘santini’ type). Relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) were calculated over the LD period according to the ‘classic approach’ (Hunt, 1990), using the measurements at planting (leaf area index (LAI) >0.31) and at the end of the LD period (LAI <1.9). Furthermore, the absolute growth rate (AGR) was calculated as the slope of total dry mass per m² (TDM_a) against time during the two parts of the SD period. A time course of LAI, based on linear extrapolations between destructive leaf area measurements, was calculated for each treatment. Daily intercepted PAR was based on measured daily global radiation, assuming 47% PAR in global radiation, a greenhouse transmissivity of 70% and a light extinction coefficient for a chrysanthemum crop of 0.72 (Lee et al., 2002). Light use efficiency (LUE) was defined as the slope of accumulated dry mass production during the SD (i.e., dry mass at final harvest minus dry mass at the start of the SD period) and accumulated intercepted PAR over the SD period.

Photosynthesis Measurements

Light-saturated rate of photosynthesis (P_{\max}) was measured weekly on both CO₂ treatments using three leaves (1 leaf/plant) of two cultivars: ‘Reagan Elite White’ (reference cultivar; week 4 to 8 after planting) and ‘Feeling Green’ (highly responsive cultivar to CO₂ enrichment; week 5 to 8 after planting). P_{\max} was determined from a light response curve at six light levels (100, 300, 600, 900, 1200, 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$; step of 5 min; temperature: 22-25°C, RH of about 70% during the measurement) at the same CO₂ concentration as during crop growth. Subsequently, P_{\max} was also recorded in two time steps (light level of 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in the CO₂ concentration of the other compartment. Every week the same leaf/plant was used. The CO₂ exchange was measured by a portable photosynthesis measurement system LI-6400 (LI-COR Biosciences, Nebraska, USA).

Statistical Analysis

The experimental set up was a split plot design (two blocks per cultivar in the same glasshouse compartment) where the main factor was the CO₂ concentration and cultivar the split factor. Data were subjected to analysis of variance (ANOVA). Treatment effects were tested at 5% probability level using F-test. The statistical software Genstat 10 was used (VSN International Ltd., Herts, UK).

RESULTS

Total Dry Mass, Photosynthesis and Growth Characteristics

Reaction time was cultivar dependent ($P < 0.001$), and in general CO₂ enrichment had no effect on this characteristic (Table 1). Cultivars ‘Tobago’ and ‘Noa’ showed the shortest reaction time (47 days) while ‘Vyking’ showed the longest one (59 days). Among the 16 studied cultivars reaction time was only significantly influenced by CO₂ enrichment in three cultivars, but the magnitude of this effect was rather small (<4%; Table 1). Ten cultivars had a significantly higher TDM at final harvest when grown at 1500 compared with 600 $\mu\text{mol mol}^{-1}$ CO₂ (Table 1). For instance, ‘FeelingGreen’ and ‘MonaLiza’ were very sensitive to CO₂ enrichment showing an increase of 36 and 40% in TDM, respectively. For the other six cultivars (e.g., ‘Biarritz’ and ‘Calabria’) there were no significant differences between the two CO₂ regimes. Based on their contrasting behavior in response to CO₂ in biomass production these four cultivars were selected for a more detailed analysis (Tables 2 and 3). In general, ‘FeelingGreen’, which reacted similarly to ‘MonaLiza’, was more responsive to CO₂ in all characters examined. On the other hand, in ‘Biarritz’ only NoF was significantly increased when plants were grown at 1500 $\mu\text{mol mol}^{-1}$ CO₂ (Table 2). Furthermore, the CO₂ effect on TDM differed with the phase of the cultivation period (Table 2). During the first part of SD period (SD₁) plants

were most sensitive to CO₂ (i.e., highest increase in TDM at the end of that period), and the four cultivars responded in a similar way to CO₂. In contrast, cultivar differences were observed in response to CO₂ during LD period and 2nd part of the SD period. These cultivar differences arise from a differential increase in the RGR during LD and the AGR during the 2nd part of the SD period. Both CO₂ concentration and cultivar had a strong influence on RGR ($P < .001$) (Fig. 1), but there was no interaction ($P = 0.589$) between these two factors. Net assimilation rate was significantly higher at high CO₂, whereas LAR was decreased by CO₂ enrichment (Table 3). Relative growth rate during the LD period was not affected in ‘Biarritz’ and ‘Calabria’. Furthermore ‘Biarritz’ and ‘Calabria’ had a lower increase in NAR. To the contrary, ‘FeelingGreen’ and ‘Monalisa’ had a significantly higher RGR at high CO₂ concentration due to a higher increase in NAR, though a higher decrease in LAR. Moreover, cultivars ‘FeelingGreen’ and ‘Monalisa’ acquired higher AGR in the second part of the SD period (SD₂) when grown at high CO₂, while cultivars ‘Biarritz’ and ‘Calabria’ showed a lower AGR in the same period as compared to the low CO₂ concentration. ‘MonaLiza’ was the most responsive cultivar showing an increase of 41% in LUE during the SD period in the high CO₂ compartment, while cultivar ‘FeelingGreen’ responded similarly (35%). Cultivars ‘Calabria’ and ‘Biarritz’ were the least responsive, showing an increase of 11 and 16%, though not statistically significant, in LUE at the higher CO₂ concentration.

The light saturated rate of photosynthesis (P_{\max}) of plants grown at high CO₂ was on average 44 and 59% higher in ‘Reagan’ and ‘FeelingGreen’ respectively, compared to low CO₂ grown plants, when the CO₂ level during the measurement was that of growth (Fig. 2). A negative slope in P_{\max} was present, independently of growth CO₂ concentration. High CO₂ did not affect P_{\max} until week 7 for ‘Reagan’, and week 8 for ‘FeelingGreen’, when the measurement CO₂ level was high. A different pattern was found in both cultivars when the measurement took place at low CO₂ concentration, where the plants grown at high CO₂ concentration had on average 34 and 25% lower P_{\max} for ‘Reagan’ and ‘FeelingGreen’ respectively, compared with plants grown in low CO₂.

Quality Aspects

Stem length was significantly longer at 1500 as compared with 600 $\mu\text{mol mol}^{-1}$ CO₂, in 14 out of 16 cultivars, but the magnitude of this effect varied between 3% (‘Reagan Elite White’) and 12% (‘MonaLiza’) (Table 1). This increase in stem length occurred mostly during the 1st part of SD period (Table 2), which was likely due to a higher internode elongation rate as number of internodes (NoI) was only significantly affected in one cultivar (‘Paintbal’, reduced by 6% at high CO₂; Table 1). For NoF a large variation in CO₂ response was observed (Table 1). Eight cultivars had a significantly higher NoF at harvest (up to 49% more) when cultivated at high CO₂ concentration, whereas, for instance, in ‘Anastasia’ (Table 1) and ‘Calabria’ (Table 2) no significant effect of CO₂ on NoF was found. Moreover, significant increase in TDM after growth at high CO₂ was not always reflected in a significant increase in NoF. Three cultivars acquired higher NoF at 1500 compared with 600 $\mu\text{mol mol}^{-1}$ CO₂, while their TDM was not significantly affected. Individual flower size (Table 2) and flower fresh mass (data not shown) were not affected by CO₂ increase in none of the two cultivars examined.

DISCUSSION

This study clearly demonstrates a large variation in growth related traits and quality aspects between cut chrysanthemum genotypes in their response to CO₂ enrichment, when comparing 600 with 1500 $\mu\text{mol mol}^{-1}$. In general CO₂ enrichment had no effect on the reaction time and only a minor variation between cultivars was observed on the CO₂ effect on this characteristic. Similar results were reported when ambient CO₂ was compared with 900 $\mu\text{mol mol}^{-1}$ (Mortensen, 1986). In contrast, CO₂ enrichment increased TDM in a cultivar dependent manner (from 5 to 40%). Mortensen (1986) reported an increase in TDM of at least 15% on TDM at 900 $\mu\text{mol mol}^{-1}$, when the control situation was ambient CO₂ concentration. In our case, apparently the CO₂

concentration of $600 \mu\text{mol mol}^{-1}$ was enough to saturate the potential of certain examined cultivars, which showed no difference in TDM when the CO_2 level reached $1500 \mu\text{mol mol}^{-1}$. Higher CO_2 during the LD period increased RGR, as a result of an increase in the assimilatory component (NAR), despite a decline in the morphological component (LAR) (Fig. 1), which is supported by direct photosynthesis measurements (Fig. 2). In addition to this, AGR was increased in both first and second part of the SD period in response to higher CO_2 concentration, though the increase during the 1st phase of SD period was much more prominent (Table 3). This observation is in agreement with Figure 2, where a decrease in P_{max} takes place, probably due to aging. At later stages of crop growth an acclimation to high CO_2 is shown, which leads to a further decrease in P_{max} , also reported by Mortensen (1982). Figure 2 also shows that plants grown for at least 4 weeks under high CO_2 have lower photosynthetic efficiency in $600 \mu\text{mol mol}^{-1} \text{CO}_2$ than plants grown under $600 \mu\text{mol mol}^{-1} \text{CO}_2$, and that a decrease of CO_2 concentration after that period will negatively affect growth. Mortensen (1982) showed that this adaptation in the high CO_2 concentration takes place after two weeks in high CO_2 . Our result is in contradiction with his work, where leaves grown and measured at high CO_2 are as efficient as low CO_2 leaves till the late stages of cultivation (week 7 or 8, depending on the cultivar). The higher LUE at $1500 \mu\text{mol mol}^{-1}$ during the SD period confirms that plants convert light more efficiently into biomass under higher CO_2 concentration (Table 3).

Although detailed partitioning data were not obtained in this study it is clear that under higher CO_2 dosages additional assimilates were partly diverted to the vegetative organs (higher stem length (3-12%), due to increased internode length) and/or to the generative organs (Table 2). When these extra assimilates are preferentially partitioned to the flowers these are invested in increasing NoF rather than increasing flower size (Table 2). Similar results were obtained when the increased assimilate availability came from diverse growing conditions, including higher light intensity, higher CO_2 concentration (up to $625 \mu\text{mol mol}^{-1}$) and lower plant density (Carvalho and Heuvelink, 2003). These authors also found a linear relationship between NoF and TDM within a given cultivar. However, in this study for the cultivars that CO_2 enrichment did significantly increase both NoF and TDM, the cultivars that showed the highest percentage of TDM increase ('Monalisa' and 'FeelingGreen') were not the ones that had the highest increase in the percentage of NoF (Fig. 3). This was probably due to different flower sizes (e.g., cultivars from 'santini' type have much smaller flowers than 'spray type' and therefore can produce more flowers with the same increase in TDM), since within a given cultivar such a relation does exist (Carvalho and Heuvelink, 2003).

CONCLUSION

There is a great genetic variation in cut chrysanthemum for CO_2 response in characters such as TDM and NoF, which are highly relevant when determining the selling price (Carvalho and Heuvelink, 2001). Furthermore, the cultivars that had a high biomass increase, when grown at a high CO_2 level, could be planted at higher densities which would lead to higher energy efficiency. These results present breeding opportunities for more responsive cultivars to higher CO_2 doses than the ones currently used in conventional greenhouses, assuring a higher return of the investment. However, to better understand this genotypic variation in CO_2 response more detailed studies using contrasting cultivars are needed, focusing on the partitioning of the higher biomass and photosynthetic efficiency over time.

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Tables

Table 1. Range of variation for CO₂ response among 16 cut chrysanthemum cultivars grown at low CO₂ (600 μmol mol⁻¹) and high CO₂ (1500 μmol mol⁻¹) for reaction time, total dry mass (TDM), number of internodes (NoI), stem length, and number of flowers (NoF).

	Difference (high CO ₂ -low CO ₂) ^x				
	Median	Maximum		Minimum	
Reaction time (d) ^y	0	FeelingGreen	1 (NS)	Paintbal	-2 (-3.7)
TDM (g/plant)	1.96	MonaLiza	3.23 (39.5)	Calabria	0.54 (NS)
NoI (no./plant)	0.17	Tobago	1.33 (NS)	Paintbal	-2.09 (-5.6)
Stem length (cm) ^y	3.65	MonaLiza	10 (12.0)	Calabria	-1.54 (NS)
NoF (no./plant) ^y	2.94	Snowflake	5.91 (48.6)	Anastasia	-0.21 (NS)

^x Numbers in parentheses are the relative increase at high CO₂ (as a percentage) when the differences were found to be significant.

^y F probability of cultivar × CO₂ interaction <0.05.

^{NS} No significant difference between low and high CO₂.

Table 2. Effect of CO₂ increase from low CO₂ (600 μmol mol⁻¹) to high CO₂ (1500 μmol mol⁻¹) during three phases of the cultivation period on total dry mass (TDM), stem length, number of internodes (NoI), number of flowers (NoF) and individual flower area (FA) measured at final harvest in two or four cut chrysanthemum cultivars.

	CO ₂ effect (high CO ₂ -low CO ₂)					
	LD period ^x		SD ₁ period ^x		SD ₂ period ^x	
TDM (g/plant)	NS	Biarritz	+33.8	Biarritz	NS	Biarritz
	NS	Calabria	+33.5	Calabria	NS	Calabria
	+16.5	FeelingGreen	+28.3	FeelingGreen	+35.9	FeelingGreen
	NS	MonaLiza	+47.2	MonaLiza	+39.5	MonaLiza
NoI (no./plant)	NS	Biarritz	NS		NS	
	NS	Calabria				
	NS	FeelingGreen				
	+5.2	MonaLiza				
Stem length (cm)	-7.8	Biarritz	NS	Biarritz	NS	Biarritz
	NS	Calabria	+7.5	Calabria	NS	Calabria
	NS	FeelingGreen	+5.3	FeelingGreen	+4.9	FeelingGreen
	+8.3	MonaLiza	+20.9	MonaLiza	+12.0	MonaLiza
NoF (no./plant)					+23.8	Biarritz
					NS	Calabria
					+31.2	FeelingGreen
					+22.6	MonaLiza
FA (cm ² /flower) ^y				NS		

^x LD period: 0-2 weeks; SD₁ period: 2-6 weeks; SD₂ period: 6 weeks to final harvest.

^y Examined in cultivars 'Tobago' and 'Noa'.

^{NS} No significant difference between low and high CO₂.

Table 3. Effect of CO₂ concentration and cultivar on relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) during the long-day (LD) period, absolute growth rate during the first (AGR SD₁) and second (AGR SD₂) part of the short-day period (SD) and light use efficiency (LUE) during the whole SD period of cut chrysanthemum.

	RGR (g g ⁻¹ d ⁻¹)	NAR (g m ⁻² d ⁻¹)	LAR (cm ² g ⁻¹)	AGR SD ₁ (g m ⁻² d ⁻¹)	AGR SD ₂ (g m ⁻² d ⁻¹)	LUE (g MJ ⁻¹)
CO ₂ (μmol mol ⁻¹)						
600	0.129 a	2.91 a	232 b	7.46 a	11.1 a	3.09 a
1500	0.135 b	3.17 b	214 a	9.95 b	13.2 b	3.91 b
F _{pr} ^x	<0.001	0.026	0.048	<0.001	0.002	<0.001
Cultivar						
Biarritz	0.131 bc	3.04	218	9.78	10.6	3.35 a
Calabria	0.123 a	3.18	227	8.78	13.3	3.66 b
FeelingGreen	0.129 b	3.15	221	8.55	12.9	3.59 ab
MonaLiza	0.134 c	2.70	251	8.88	12.9	3.63 b
F _{pr} ^x	<0.001	0.373	0.129	0.103	0.107	0.007

^x F probability; significant levels less than 0.05 presented in bold type. Different letters within a column indicate significant differences between treatments based on Student's *t*-test (P=0.05).

Figures

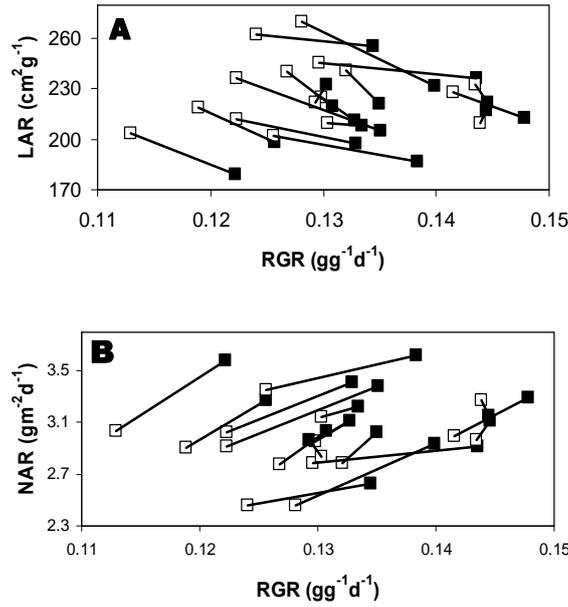


Fig. 1. Relationship between leaf area ratio (LAR) and relative growth rate (RGR) (A) and between net assimilation rate (NAR) and RGR (B) of 16 cultivars grown at low CO₂ (open symbols) and high CO₂ (closed symbols).

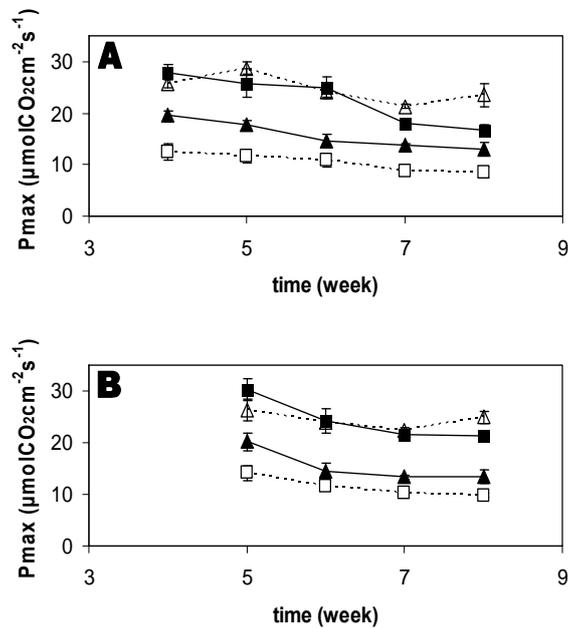


Fig. 2. Light saturated rate of photosynthesis (P_{max}) as a function of time after planting in chrysanthemum 'Reagan Elite White' (A) and 'FeelingGreen' (B). \blacktriangle : low/low CO₂; \triangle : low/high CO₂; \blacksquare : high/high CO₂; \square : high/low CO₂ plants (i.e., CO₂ concentration during crop growth/ during photosynthesis measurements). Vertical bars indicate s.e.m. when larger than symbols (n=3).

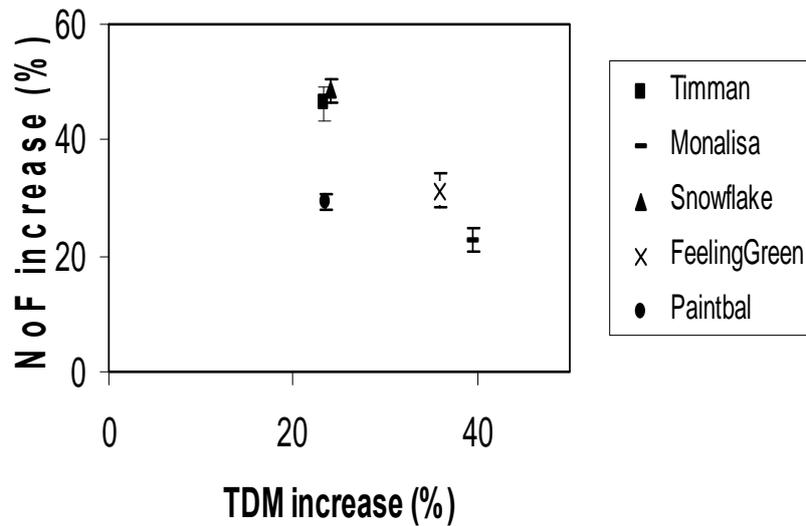


Fig. 3. Relationship between the relative increase on the number of flowers (NoF) and on the total dry mass per plant (TDM) at final harvest in response to CO₂ enrichment (from 600 to 1500 $\mu\text{mol mol}^{-1}$). In the cultivars included, a significant CO₂ effect was found in both characteristics based on Student's *t*-test ($P=0.05$). Vertical bars indicate s.e.m. when larger than symbols (n=24).