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Effect of elevated CO_2 on photosynthesis and chlorophyll fluorescence of rose plants grown at high temperature and high photosynthetic photon flux density

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Abstract

Gas exchange and chlorophyll (Chl) fluorescence were measured on young mature leaves of rose plants (*Rosa hybrida* cvs. First Red and Twingo) grown in two near-to-tight greenhouses, one under control ambient CO_2 concentration, AC (355 μmol mol^{-1}) and one under CO_2 enrichment, EC (700 μmol mol^{-1}), during four flushes from late June to early November. Supply of water and mineral elements was non-limiting while temperature was allowed to rise freely during daytime. Leaf diffusive conductance was not significantly reduced at EC but net photosynthetic rate increased by more than 100 %. Although the concentration of total non-structural saccharides was substantially higher in the leaves from the greenhouse with EC, Φ_{PS2} (quantum efficiency of radiation use) around noon was not significantly reduced at EC indicating that there was no down-regulation of electron transport. Moreover, CO_2 enrichment did not cause any increase in the risk of photo-damage, as estimated by the $1 - q_P$ parameter. Non-photochemical quenching was even higher in the greenhouse with EC during the two summer flushes, when temperature and photosynthetic photon flux density (PPFD) were the highest. Hence rose photosynthesis benefits strongly from high concentrations of atmospheric CO_2 at both high and moderate temperatures and PPFD.

Additional key words: carotenoids; chlorophyll; cultivar differences; leaf conductance to water vapour; *Rosa hybrida*; saccharides; stomata.

Introduction

Greenhouse rose crops strongly benefit from CO_2 enrichment of the air. No acclimation has been observed to long-term enrichment in CO_2 performed during the cool season (Balazsovits *et al.* 1989, Beeson *et al.* 1991, Jiao *et al.* 1991), probably because plants grown in heated greenhouses in soil-less systems can take advantage of elevated CO_2 (EC) without experiencing any of the usual limiting factors that occur in open field conditions such as sink activity (Arp 1991, Bowes 1991) and mineral and water availability (Bowes 1993). Few questions remain unsolved. To make the all-year round, all day long use of even cheap CO_2 economically viable, injection must be performed in near-to-tight greenhouses. Inside such greenhouses, temperature (T) tends to become much higher than outside during daytime because of the greenhouse effect, especially during summer.

The response of photosynthesis to EC and high T is not easy to predict. If factors are taken separately, the short-term effect of EC is an increase in net photosynthetic rate (P_N) while rising T may have the opposite effect. CO_2 and O_2 compete for the primary acceptor molecule of C_3 photosynthesis, ribulose-1,5-bisphosphate.

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Abbreviations: AC – ambient CO_2 concentration; Car – carotenoids; Chl – chlorophyll; F_0 – minimal Chl fluorescence level when PS2 centres are open; EC – elevated CO_2 concentration; F_m – maximal Chl fluorescence level when PS2 centres are closed; F_m' – F_m measured after induction of quenching; F_s – steady state Chl fluorescence after induction of quenching; F_v – variable fluorescence level (= $F_m - F_0$); g_s – leaf diffusive conductance to water vapour; NPQ – non photochemical quenching [= $(F_m - F_m')/F_m'$]; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS2 – photosystem 2; Q_A – primary electron acceptor of the quinone pool; q_P – photo-chemical quenching [= $(F_m' - F_s)/(F_m' - F_0)$]; RuBPCO – ribulose-1,5-bisphosphate carboxylase/oxygenase; T – temperature; TNS – total non-structural saccharides; $\Delta F/F_m'$ – quantum efficiency of radiation-use under actinic irradiation [= $(F_m' - F_s)/F_m'$]; Φ_{PS2} – quantum efficiency of radiation use of PS2 (= $\Delta F/F_m'$).

The enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) catalyses both carboxylation and oxygenation. Carboxylation leads to photosynthesis *via* the photosynthetic carbon reduction cycle and oxygena-tion leads to photorespiration *via* the photosynthetic carbon oxidation cycle. The short-term effect of EC is thus a decrease in the ratio of photorespiratory loss of carbon to photosynthetic gain. In the usual T range (up to 35/40 °C), the T dependence of the photorespiration/ photosynthesis ratio in C_3 plants is generally attributed to both a decrease in CO_2 solubility, relative to O_2, and a decline in CO_2/O_2 specificity of RuBPCO with increasing T (Jordan and Ogren 1984, Brooks and Farquhar 1985, Valentini *et al.* 1995). Temperatures greater than 40 °C may have a negative effect on photosynthesis, too, by accelerating photoinhibition or inducing photoinhibition in plants exposed to high photon flux densities (Björkman and Powles 1984, Bongi and Long 1987, Terzaghi *et al.* 1989). The observed reduction in F_v/F_m (the ratio of variable to maximal Chl fluorescence) is associated with an increase in F_0 [the minimal Chl fluorescence level when photosystem 2 (PS2) reaction centres are open] and thermal damage of the PS2 reaction centre. Although there are a few contradictory reports (Kellomäki and Wang 1997), EC may also result in increased photo-inhibition and decreased electron flow rates as the con-sequence of the accumulation of non-structural saccha-rides under non-limiting water supply (Roden and Ball 1996). Interactive effects of EC times high T are not well documented. Simulations by Long (1991) showed a strong $CO_2 \times T$ interaction on irradiance-saturated P_N and maximum quantum yields, but more recent observations suggest that the T dependence of the stimulation of photosynthesis by EC is not universal and may vary with species (Bunce 1998). Guehl (1997) found that EC provides *Quercus robur* with a better tolerance to high T, but Wang and Kellomäki (1997) observed that elevated T counteracts the CO_2 stimulation of P_N.

The aim of this study was to find the effect of EC on photosynthesis of roses grown at high temperatures, such as those prevailing in summer in the south of France, by following gas exchange and Chl fluorescence parameters from the end of spring to mid-autumn.

Materials and methods

Trials were conducted near Nice on the French Riviera. Rose plants (*Rosa hybrida* L.) of two cultivars, First Red (a long-stem, large bud rose) and Twingo (a typically small cultivar), were grown in two 250 m^2 greenhouses: a control one (AC) and one with EC. Cuttings were rooted in rockwool cubes on 28 November 1998 and planted in plastic containers filled with perlite at a density of 7 plants per m^2 on 20 January 1999. Pruning was performed around 20 cm above ground level to minimise the buffering effect of basal shoots. Plants were irrigated and fertilised according to Urban (1997) to avoid any water and salinity stress. pH was set at 5.6 and electrical conductivity at 1.4 mS cm^{-1}.

In the EC greenhouse, CO_2 was injected from 20 April 1999 from a liquid gas tank to maintain 700 µmol mol^{-1} throughout daytime under the control of a gas analyser (*Infrared Gas Monitor 3600*, *Mine Safety Appliance Company*, Pittsburgh, USA). Roof vents had a fixed aperture of 5 % and temperature was allowed to rise freely. In the AC greenhouse, roof vents had a minimal aperture of 5 % to force the CO_2 concentration of the inside air to stay near ambient (355 µmol mol^{-1}), but then their aperture could be adjusted under the control of a climate control system (*Syspil*, *INRA*, Avignon, France) to match the temperatures of both greenhouses. Climatic parameters were continuously recorded in both greenhouses. We checked that average temperatures remained in close range in both greenhouses (Table 1). Four plots of 2 m^2 each were selected within each greenhouse for each cultivar for being homogeneous in terms of initial number of shoots, PPFD, air T, and relative humidity.

Leaves used for fluorescence and gas exchange measurements were chosen according to the selection criteria described by Urban and Langelez (1992). For all measurements we selected the first non-shaded five-leaflet leaves from the base of shoots having a flower bud of 3 mm in diameter at least.

Four periods of measurement corresponded to four successive flushes (Table 1): from 22 to 29 of June (high T and PPFD), from 18 to 25 of August (slightly lower T and PPFD), from 23 to 30 of September (relatively high day T and PPFD), and from October, 26 to November, 2 (moderate day T and PPFD).

P_N and leaf diffusive conductance to water vapour (g_s) were measured around noon on specific clear days (one per flush) with a portable, open system infra-red gas analyser *LCA-2* (*ADC*, Hoddesdon, UK) and a leaf chamber (Parkinson 1983). Eight leaves per treatment and cultivar were taken alternatively. Special care was taken to homogenise the photosynthetic photon flux at the time measurements were performed. About 30 s were required for equilibration of CO_2 depletion in the diffe-rential mode. Calculations were performed according to the models of Caemmerer and Farquhar (1981).

Fluorescence parameters were measured on attached leaves by a portable modulated fluorometer (*FMS*, *Hansatech*, Pentney, UK). F_0 was measured before dawn or after dark adaptation for at least one hour, provided by dark clips. Saturating pulses of 5 200 μmol m^{-2} s^{-1} were applied for 0.8 s to obtain maximal fluorescence before dawn (F_m) and under actinic irradiation (F_m'). The F_v/F_m parameter (Butler 1978) calculated as $(F_m - F_o)/F_m$ was used as an indicator of photoinhibition (Krause 1988). $\Delta F/F_m'$ [$= (F_m' - F_s)/F_m'$] was measured around noon as an estimate of Φ_{PS2} (Genty *et al.* 1989) on leaves exposed to a steady irradiation of 1 800 μmol m^{-2} s^{-1}. F_s was obtained after imposing 3 s of far-red irradiation to fully re-open closed PS2 centres. $1 - q_p$ (which is an estimate of the proportion of closed centres, *i.e.*, of reduced Q_A) was calculated as $1 - (F_m' - F_s)/(F_m' - F_0)$ to estimate the risk of photodamage to PS2 (Osmond *et al.* 1993). Non-photochemical quenching (NPQ) was also calculated as $(F_m - F_m')/F_m'$ after the Stern-Volmer equations (Gilmore and Yamamoto 1991, Krause and Weis 1991). NPQ is directly proportional to the heat dissipation rate constant of PS2 (Demmig-Adams 1990) and is closely correlated to the formation of zeaxanthin (Bilger and Björkman 1991) which is believed to play an essential role in photoprotection.

The same selection criteria of leaves used for gas exchanges and Chl fluorescence measurements were applied to the leaves collected for biochemical analysis. Five leaves were taken per treatment. Starch was determined by enzymatic hydrolysis to glucose (Thievend *et al.* 1972). Glucose and sucrose were assayed by an enzyme-based analyser (*YSI 2007*, *Yellow Springs Instruments Co.*, Yellow Springs, USA) after the procedure described by Barthélémy (1998). Total non-structural saccharides (TNS) were computed as the sum of glucose, sucrose, and starch.

Table 1. Average daily climatic parameters.

Flush	Period of time	Mean daytime T [°C]		Maximal daytime T [°C]		Mean night T [°C]		Maximal PPFD [μmol m^{-2} s^{-1}]
		AC	EC	AC	EC	AC	EC	
One	22 to 29 June	31.9±0.5	31.2±0.8	39.2±0.7	38.9±1.0	19.1±1.2	18.6±1.2	1631±97
Two	18 to 25 August	30.9±1.5	30.3±1.5	36.6±1.9	36.3±2.2	21.8±0.6	21.3±0.6	1598±108
Three	23 to 30 September	28.3±2.3	28.3±2.3	35.5±1.9	36.0±1.7	16.6±1.3	16.5±1.4	1112±140
Four	26 October to 2 November	24.2±2.7	24.0±2.3	28.5±3.7	28.3±3.0	16.4±0.9	16.6±0.8	529±216

Carotenoids (Car) and Chls were extracted from 2 cm diameter leaf discs, then incubated in *N,N*-dimethylformamide (100 %) for 2 to 4 h at 65 °C. Chl *a* and *b* and total Car were measured with a spectrophotometer (*Philips PU 8675*, Eindhoven, The Netherlands) at 664 and 647 nm for Chl and 440 nm for Car (Moran 1982, Wellburn 1994).

Values were analysed by ANOVA followed by Multiple Comparison of Means (*S-Plus 4, MathSoft,* Bagshot, UK). Results are expressed as means ± SE. Treatment differences were assessed as significant at $p < 0.05$.

Results and discussion

Stomata of 'First Red' and 'Twingo' rose plants did not close in response to EC (Table 2) confirming earlier observations by Urban (1994) on cv. Sonia. Stomata of most species close as a short-term response to EC (Murray 1997). On the other hand, Bunce (1992) observed that stomata of *Malus sylvestris*, *Quercus prinus*, and *Quercus robur* were unaffected by EC, as found by Conroy *et al.* (1988) on *Pinus radiata.* Other studies on beech trees (Dufrêne *et al.* 1993), beech seedlings (Heath and Kerstiens 1997), and *Pinus taeda* (Ellsworth *et al.* 1995) showed that reductions in g_s were similarly absent or minimal. Hibbs *et al.* (1995) and Barton *et al.* (1993) observed that EC resulted in an increase in g_s in red alder leaves and *Picea sitchensis* needles, respectively. There are currently no explanations for such discrepancies.

CO_2 enrichment resulted in a substantial increase in TNS in leaves of both cultivars (Table 3). Although there are some contradictory observations (Lindroth *et al.* 1993, Roth and Lindroth 1994), it is generally acknowledged that TNS concentration increases in response to EC (Poorter *et al.* 1997).

Chl and Car concentrations were not significantly reduced as a consequence of EC with the exception of the Car concentration in 'First Red' leaves during flush three (Table 3). Such decreases are sometimes reported in the literature. Decreases in concentration of antenna pigment molecules have been suggested as adaptations reducing the antenna size to avoid over-excitation of the electron transport although they may not affect the electron transport chain itself (Besford *et al.* 1996, quoted by Saxe *et al.* 1998).

Predawn F_v/F_m was very high in our trial (Table 4), but not unrealistic (Björkman and Demmig 1987). Predawn F_v/F_m was not affected by EC. Although there are a few observations of positive effect of EC on F_v/F_m (Ceulemans *et al.* 1995), it is generally believed that EC does not affect F_v/F_m (Saxe *et al.* 1998).

Table 2. Gas exchange characteristics of rose leaves from the control (AC) and the elevated (EC) CO_2 greenhouses (means ± SE, $n = 8$): net photosynthetic rate (P_N) and leaf diffusive conductance (g_s). For each treatment within each line and cultivar, values followed by the same letter are not significantly different at $p < 0.05$.

	Flush	'First Red' AC	EC	'Twingo' AC	EC
P_N [μmol(CO_2) m^{-2} s^{-1}]	one	15.84±0.29 a	33.46±2.64 b	16.14±0.25 a	34.48±1.45 b
	two	15.93±0.41 a	32.10±2.15 b	16.13±0.90 a	28.86±3.28 b
	three	14.55±0.94 a	31.69±1.17 b	15.00±0.44 a	32.10±2.15 b
	four	12.41±1.01 a	25.98±1.72 b	12.91±1.01 a	24.68±2.44 b
g_s [mol(H_2O) m^{-2} s^{-1}]	one	0.273±0.018 a	0.263±0.020 a	0.279±0.020 a	0.268±0.019 a
	two	0.230±0.028 a	0.216±0.029 a	0.218±0.024 a	0.243±0.026 a
	three	0.256±0.015 a	0.240±0.021 a	0.221±0.016 a	0.234±0.016 a
	four	0.220±0.017 a	0.219±0.017 a	0.220±0.021 a	0.224±0.020 a

Table 3. Concentration in leaves of total non-structural saccharides (TNS) and pigments of rose leaves from the control (AC) and the elevated (EC) CO_2 greenhouses (means ± SE, $n = 5$). For each treatment within each line and cultivar, values followed by the same letter are not significantly different at $p < 0.05$.

	Flush	'First Red' AC	EC	'Twingo' AC	EC
TNS [g kg^{-1}(dry matter)]	one	62.72±5.06 a	87.66±5.53 b	70.23±2.67 a	99.44±2.97 b
	two	55.90±2.03 a	92.44±6.55 b	31.64±2.10 a	39.30±1.78 b
	three	38.62±0.93 a	114.80±1.96 b	38.12±0.83 a	85.12±2.77 b
	four	71.78±0.71 a	95.62±2.90 b	75.74±2.50 a	88.34±3.19 b
Chl *a* and *b* [g kg^{-1}(dry matter)]	one	13.87±0.90 a	12.54±0.77 a	11.98±0.47 a	11.76±0.18 a
	two	11.49±1.62 a	13.46±0.42 a	15.32±1.25 a	14.09±0.84 a
	three	16.78±0.80 a	15.08±0.70 a	13.58±0.58 a	14.08±0.68 a
	four	19.96±1.83 a	15.11±0.59 a	17.97±0.23 a	18.78±0.42 a
Carotenoids [g kg^{-1}(dry matter)]	one	2.91±0.16 a	2.61±0.15 a	2.95±0.09 a	2.75±0.06 a
	two	2.61±0.05 a	2.87±0.06 b	2.57±0.29 a	3.55±0.15 a
	three	3.77±0.15 a	3.20±0.11 b	3.19±0.14 a	2.82±0.14 a
	four	3.59±0.11 a	3.33±0.19 a	3.95±0.09 a	4.14±0.09 a

CO_2 injection did not significantly affect Φ_{PS2} at midday (Table 4). There were no differences in leaf absorptance between treatments in our trial (values not shown). Since the amount of radiant energy absorbed by leaves was similar, no difference in Φ_{PS2} at midday means any difference in electron flow rate. Some authors found that EC stimulated Φ_{PS2} (Scarascia-Mugnozza *et al.* 1996) while others reported the opposite effect (Marek *et al.* 1995, Wang 1996). Increased photoinhibition and decreased electron flow rates may be associated with increased TNS concentration and the subsequent down-regulation of electron transport (Pammenter *et al.* 1993). This is what Roden and Ball (1996) observed in leaves of two well-watered *Eucalyptus* species grown at EC. Such down-regulation of the photosynthetic capacity did not occur in our trial, probably because of the strong sink activity. There was even an increase in NPQ in the EC greenhouse in both cultivars during flushes one and two (when T and PPFD were the highest) but in 'First Red' only during flush three (Table 4). This seems consistent with observations of Guehl (1997) on Quercus robur L. A greater tolerance to high T at EC may be related to the stabilisation of heat-susceptible enzymes by the increased amounts of sugars in these plants or by the capacity of certain species to produce photoprotective pigments through the conversion of violaxanthin and zeaxanthin of the xanthophyll pool (Demmig-Adams and Adams 1992). Moreover, CO_2 injection did not result in any increase in reduction of Q_A as estimated by $1 - q_p$ (Table 4), indicating that the risk of photodamage was not increased by EC.

P_N increased in EC conditions by more than 100 % in all four flushes in leaves of both 'First Red' and 'Twingo' (Table 2). Urban (1994) already observed that 900 μmol(CO_2) mol^{-1} may result in an increase of P_N up to 200 % at saturating PPFD and of about 57 % in dry matter production in Sonia rose plants grown soil-less with non-limiting water and mineral supply. Such figures appear high when compared to values from the literature but are not isolated. Idso *et al.* (1995) found that EC could result in an increase in P_{max} of up to 200 % in orange leaves. Assuming a constant ratio of internal to external concentrations of CO_2 and that the ribulose-1,5-bisphosphate regeneration capacity is non-limiting (Long

1991), increases in P_N with CO_2 concentration may be attributed either to an increase in the total photosynthetic electron flow rate (photosynthesis ± photorespiration), with the ratio of photosynthesis to photorespiration remaining constant, or to an effect on the partitioning of the photosynthetic electron flow at RuBPCO level, with CO_2 fixation increasing at the expense of O_2 reduction. During flushes 1, 2, and 3, P_N doubled while Φ_{PS2} was unaffected by EC (Tables 2 and 4) suggesting that only the partitioning of electrons between CO_2 and O_2 was changed (Ghashghaie and Cornic 1994). One may wonder whether a change in the carboxylation to oxygenation ratio, due to a doubling of the CO_2 concentration of the air, may account for a doubling of P_N. According to Bunce (1998), doubling the CO_2 concentration of air results only in a 50 % increase in P_N at T around 20 °C, but at T above 30 °C the increase in P_N can be greater than 100 %. Our observation of a double P_N at 700 μmol(CO_2) mol^{-1} during flushes 1, 2, and 3, when T were clearly above 30 °C (Tables 2 and 4), is consistent with these findings which Bunce (1998) attributes to the temperature dependency of the solubilities of CO_2 and O_2 in water and the temperature dependency of the kinetic characteristics of RuBPCO. But during flush 4, mean daytime T was around 28 °C as a result of reduced radiation (Table 1). Such a T, according to Bunce (1998), cannot lead to a doubling of P_N with a doubling of the CO_2 concentration of the air. The explanation for the doubling of P_N during flush 4 probably lies in the increase in Φ_{PS2} observed at that time in the EC treatment (Table 4). We have no explanation for the temperature or radiation dependency of the effect of EC on Φ_{PS2}.

Table 4. Fluorescence parameters of rose leaves from the control (AC) and the elevated (EC) CO_2 greenhouses (means ± SE, $n = 12$): predawn maximal quantum efficiency of radiation use (F_v/F_m), quantum efficiency of radiation use (Φ_{PS2}) at 1 800 μmol m^{-2} s^{-1}, non-photochemical quenching (NPQ), and the $1 - q_P$ parameter. For each treatment within each line and cultivar, values followed by the same letter are not significantly different at $p < 0.05$.

	Flush	'First Red'		'Twingo'	
		AC	EC	AC	EC
Predawn F_v/F_m	one	0.854±0.001 a	0.857±0.001 a	0.853±0.003 a	0.858±0.002 a
	two	0.852±0.002 a	0.853±0.001 a	0.847±0.003 a	0.848±0.002 a
	three	0.855±0.001 a	0.858±0.001 a	0.857±0.003 a	0.859±0.002 a
	four	0.856±0.003 a	0.860±0.003 a	0.856±0.003 a	0.859±0.002 a
Φ_{PS2}	one	0.335±0.021 a	0.319±0.023 a	0.339±0.022 a	0.326±0.012 a
	two	0.349±0.017 a	0.332±0.022 a	0.316±0.028 a	0.335±0.026 a
	three	0.439±0.015 a	0.410±0.025 a	0.416±0.028 a	0.410±0.033 a
	four	0.346±0.014 a	0.389±0.026 a	0.351±0.019 a	0.414±0.032 a
NPQ	one	2.00±0.06 a	2.35±0.13 b	2.04±0.07 a	2.34±0.12 b
	two	2.04±0.05 a	2.33±0.10 b	1.95±0.14 a	2.39±0.08 b
	three	1.49±0.11 a	2.12±0.21 b	1.87±0.18 a	2.05±0.20 a
	four	2.49±0.09 a	2.19±0.20 a	2.59±0.17 a	2.24±0.18 a
$1 - q_P$	one	0.250±0.032 a	0.257±0.041 a	0.249±0.028 a	0.252±0.015 a
	two	0.246±0.024 a	0.255±0.022 a	0.288±0.025 a	0.277±0.041 a
	three	0.240±0.023 a	0.260±0.017 a	0.250±0.027 a	0.242±0.018 a
	four	0.299±0.006 a	0.282±0.015 a	0.274±0.031 a	0.267±0.021 a

In conclusion, EC did not decrease g_s of rose leaves but increased substantially P_N at high or moderate T and PPFD. The resulting increase in TNS concentration of leaves is probably not associated to any down-regulation of Φ_{PS2} neither in summer nor in autumn. Although we lack information about the effect of EC on carboxylation efficiency, our observations strongly suggest that rose plants probably do not acclimate to high CO_2 concentrations. From a more general standpoint, our observations support the view developed by Saxe *et al.* (1998) that EC results in a more persistent and strong photosynthesis than previously thought.

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