Gas exchange of carrot leaves in response to elevated CO_2 concentration

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Abstract

Short-term responses of four carrot (*Daucus carota*) cultivars: Cascade, Caro Choice (CC), Oranza, and Red Core Chantenay (RCC) to CO_2 concentrations (C_a) were studied in a controlled environment. Leaf net photosynthetic rate (P_N), intercellular CO_2 (C_i), stomatal conductance (g_s), and transpiration rate (E) were measured at C_a from 50 to 1 050 µmol mol^{-1}. The cultivars responded similarly to C_a and did not differ in all the variables measured. The P_N increased with C_a until saturation at 650 µmol mol^{-1} (C_i = 350–400 µmol mol^{-1}), thereafter P_N increased slightly. On average, increasing C_a from 350 to 650 and from 350 to 1 050 µmol mol^{-1} increased P_N by 43 and 52 %, respectively. The P_N *vs.* C_i curves were fitted to a non-rectangular hyperbola model. The cultivars did not differ in the parameters estimated from the model. Carboxylation efficiencies ranged from 68 to 91 µmol m^{-2} s^{-1} and maximum P_N were 15.50, 13.52, 13.31, and 14.96 µmol m^{-2} s^{-1} for Cascade, CC, Oranza, and RCC, respectively. Dark respiration rate varied from 2.80 µmol m^{-2} s^{-1} for Oranza to 3.96 µmol m^{-2} s^{-1} for Cascade and the CO_2 compensation concentration was between 42 and 46 µmol mol^{-1}. The g_s and E increased to a peak at C_a = 350 µmol mol^{-1} and then decreased by 17 and 15 %, respectively when C_a was increased to 650 µmol mol^{-1}. An increase from 350 to 1 050 µmol mol^{-1} reduced g_s and E by 53 and 47 %, respectively. Changes in g_s and P_N maintained the C_i:C_a ratio. The water use efficiency increased linearly with C_a due to increases in P_N in addition to the decline in E at high C_a. Hence CO_2 enrichment increases P_N and decreases g_s, and can improve carrot productivity and water conservation.

Additional key words: CO_2 compensation concentration; cultivar differences; *Daucus carota*; net photosynthetic rate; nonlinear regression model; stomatal conductance; transpiration rate; water use efficiency.

Introduction

The rising atmospheric CO_2 concentration and its effects on crop growth and yield has been a subject of major interest during the past two decades. Several studies have demonstrated that elevated CO_2 concentration usually increases photosynthesis in C_3 plants stimulating various physiological processes, plant growth, and productivity (Bowes 1996, Drake *et al*. 1997). Enhanced assimilate production under elevated CO_2 concentration has been attributed to the increased supply of CO_2 to the Calvin cycle enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO), which is not saturated in the current atmosphere, as well as to decrease in the rate of photorespiration (Stitt 1991, Bowes 1996). However, the extent of this response is not well defined as various responses to increased CO_2 have been reported for different species of plants (Gifford 1992) and even among different cultivars of the same crop (Ramachandra Reddy *et al*. 1993). For example, decreases in net photosynthetic rate (P_N) in cucumber (*Cucumis sativus* L.) (Peet *et al*. 1986) and cotton (*Gossypium hirsutum* L.) (DeLucia *et al*. 1985) after an initial large increase have been reported. Stitt (1991) and Kirschbaum (1994) attributed this decrease to the plant's inability to fully utilize the available assimilates; a process commonly called end-product feedback inhibition. However, Sharkey (1990) associated this process of down regulation with the loss of capacity for sucrose synthesis rather than with the direct effect of end-product inhibition.

In addition to increase in P_N, elevated CO_2 concentration decreases stomatal conductance (g_s) and may reduce

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transpiration rate (E) leading to an increase in plant water use efficiency (WUE) (Radoglou *et al*. 1992, Morison 1998). Mott (1988) and Morison (1998) indicated that stomata respond to intercellular CO_2 concentration (C_i) such that the ratio of C_i to ambient CO_2 (C_i/C_a) remains fairly constant. Thus, as P_N increases with increasing C_a, g_s declines.

Various models have been used to analyze the P_N/C_a response curves. For example, Farquhar *et al*. (1980) and Farquhar and Caemmerer (1982) used biochemical models to describe this response. The general asymptotic, rectangular, and non-rectangular hyperbolic models, which are nonlinear, have also been used to derive the photosynthetic parameters for horticultural crops including cherry (*Prunus cerasus* L.) (Sams and Flore 1982), tomato (*Lycopersicon esculentum* Mill.), cucumber, sweet pepper (*Capsicum annuum* L.) (Nederhoff and Vegter 1994), *Alstroemeria* (Leonardos *et al*. 1994), and other crops and trees (Wheeler *et al*. 1993, Ellsworth *et al*. 1995, Cannell and Thornley 1998).

Such information provides a better understanding of the consequences of changes in C_a on plant productivity. However, information on the photosynthetic responses of carrot leaves to C_a is very limited. Therefore, the objectives of the study were (*a*) to assess the effects of increasing C_a on leaf P_N, g_s, E, and WUE of four carrot cultivars using repeated measure analysis, and (*b*) to model leaf P_N of each cultivar as a function of C_i using the non-rectangular hyperbolic model and to compare the four cultivars in terms of the model parameters.

Materials and methods

The study was conducted in a controlled environment room using carrot (*Daucus carota* var. *sativus* L.) cv. Caro Choice (CC), Cascade, Oranza, and Red Chore Chantenay (RCC). Ten seeds were sown in 15-cm diameter plastic pots containing *Pro-mix* (*Premier Horticulture*, Rivière-du-Loup, Quebec, Canada). Seedlings were thinned to three at the first true leaf stage, approximately seven days following emergence. Plants were watered daily and fertilized weekly with 100 cm^3 nutrient solution containing 1.5 kg m^{-3} of NPK (15 : 15 : 30). A combination of incandescent, cool white fluorescent and high-pressure sodium lamps provided photosynthetic active radiation (PAR) of approximately 450±20 µmol m^{-2} s^{-1} at the top of the plant canopy. Growth room conditions were maintained at a 16-h daylength, and mean temperatures were 20 °C during the day and 10 °C during the night. Relative humidity was maintained at 70±2 % and the CO_2 concentration in the growth room was 370±10 µmol mol^{-1} air, which was monitored through a computerized infrared gas transmitter (*90DM3A, Vulcain Inc*., New Stanton, PA, USA).

Leaf gas exchange measurements: P_N, g_s, C_i, and E were measured at 11 C_a [50, 150, 250, 350, 450, 550, 650, 750, 850, 950, 1 050 µmol mol^{-1}] on the youngest fully expanded intact leaves 30 d after seedling emergence (approximately seven-leaf stage). Measurements were done using a portable open-flow gas analyzer in conjunction with a Portable Leaf Chamber (*LCA-4, Analytical Development Company*, Hoddesdon, UK) and a portable Leaf Microclimate Control System (*Analytical Development Company*, Hoddesdon, UK). The Leaf Microclimate Control System (LMCS) was used to vary the microclimate of the leaf placed within the leaf chamber associated with the *LCA-4*. This photosynthetic system allows the ambient air temperature in the leaf chamber, the ambient irradiance incident on the leaf, and C_a around the leaf to be varied. A CO_2 canister was installed on the LMCS to supply the CO_2 through the analyzer. The analyzer was equipped with a gas-mixing subsystem, which provides an air supply within nearly constant CO_2 and water vapor concentrations within the leaf chamber as set by the user. The analyzer was operated in differential mode at an airflow rate of 400 µmol s^{-1}. Leaf temperature was determined using a leaf temperature sensor attached to the leaf chamber.

Measurement temperature was maintained at 20 °C, PAR at 500 µmol m^{-2} s^{-1}, and relative humidity at 65 %. The C_a was varied in 11 steps from 50 to 1 050 µmol mol^{-1}. At least 5 min was allowed between changes in C_a for a steady-state condition before recording measurement. Five measurements were recorded automatically at 60 s intervals for each C_a level per plant. Measurements were taken on four consecutive days, with one block consisting of four pots measured a day. The effective-time constant in detecting changes in gas concentration for the *LCA-4* was typically 16–20 s. Leaves used for measurements were collected to determine the leaf area using leaf area meter (*LI-3000, LI-COR*, Lincoln, NE, USA). Gas exchange measurements were calculated on leaf area basis.

Repeated measures analysis (RMA): The design for the RMA was a two factor (cultivar with 4 levels, and CO_2 with 11 levels) factorial in four time blocks, and the response variables were P_N, C_i, g_s, and E. Instantaneous WUE was computed as P_N/E. For each cultivar, the five response measurements were taken on each plant at each C_a and were averaged prior to analysis. Since the response measurements for the 11 C_a were measured repeatedly on the same leaflet, the independence assumption on the error terms for the ANOVA was likely violated (Potvin *et al*. 1990, Littell *et al*. 1998). Consequently, the error term was assumed as normally distributed with constant variance, and the dependence expressed with a covariance structure of Σ. Cubic root transformed values of P_N and WUE were analyzed to satisfy the normal distribution of error terms assumption, and the back transformed values reported. The appropriate co-variance structure was determined to be AR(1) for P_N and Compound Symmetry (CS) for C_i, g_s, E, and WUE using the AIC and SBC (Littell *et al*. 1998). The analysis was completed using the Mixed Procedure of SAS (SAS Inst. 1999).

Nonlinear regression model fitting: For each cultivar, plot of P_N against C_i suggested an asymptotic regression model, which is similar to the non-rectangular hyperbola model proposed by Marshall and Biscoe (1980) for modeling leaf photosynthesis as a function of irradiance. Therefore, for each cultivar, P_N(Y) as a function of C_i(X) was modeled using the non-rectangular hyperbola. Following this, a nested nonlinear regression with incremental parameters model (Bates and Watts 1988) was used for comparing pairs of cultivars in terms of the model parameters. The analysis was completed using the *NLIN* procedure of *SAS* (SAS Inst. 1999). The functional form of the non-rectangular hyperbola model proposed by Marshall and Biscoe (1980) is:

$$\theta_1 Y^2 - (\theta_2 + \theta_3 X - \theta_1\theta_4)Y + \theta_3 X[\theta_2 - (1-\theta_1)\theta_4] - \theta_2\theta_4 = 0 \qquad [1]$$

where Y is P_N, θ_1 is the curvature (convexity) of the P_N-C_i relationship, θ_2 is maximum P_N, θ_3 is the initial slope of the C_i response curve at low CO_2, *i.e*., an estimate of carboxylation efficiency, and θ_4 represents respiration rate (R_D).

To facilitate easier nonlinear regression estimation, we fitted the following reparameterization of the non-rectangular hyperbola model:

$$Y = \frac{\theta_2\theta_4 - \theta_3 X[\theta_2 - (1-\theta_1)\theta_4]}{\theta_1 Y - (\theta_2 + \theta_3 X - \theta_1\theta_4)} + \varepsilon \qquad [2]$$

where all the parameters are as defined above, and ε is the error term assumed to be normally distributed with zero mean, constant variance, and independent of one another. The CO_2 compensation concentration (Γ) at C_i where Y is zero was calculated from the fitted model.

Results and discussion

Increasing CO_2 concentration had a significant effect on P_N, C_i, g_s, E, and WUE of all four cultivars. No significant differences in these variables occurred among the cultivars and, similarly, the interaction effects were not significant indicating that the cultivars responded equally to CO_2 enrichment. Therefore, the data were average across cultivars (Table 1) and also across C_a levels (values not shown). The similar P_N in response to C_a among the cultivars is in agreement with the results for potato species (*Solanum* sp.) (Olivo *et al*. 2002). For every 100 µmol mol^{-1} increase in C_a, the increase in P_N was significant until C_a reached 650 µmol mol^{-1}. Thereafter, increases in C_a did not influence P_N significantly. Averaged across cultivars, an increase in C_a from 50 to 350 µmol mol^{-1} produced a 100-fold increase in P_N and the value increased by 43 % when C_a was elevated from 350 to 650 µmol mol^{-1}. Only 7 % increase in P_N was observed when C_a was increased from 650 to 1 050 µmol mol^{-1}. The increase in P_N in response to C_a is within the range of values reported for other C_3 crops when C_a was doubled (Cure and Acock 1986, Radoglou *et al*. 1992, Olivo *et al*. 2002). In an extensive review of short-term responses of many C_3 plants including soybean (*Glycine max* L.), cotton, and potato, Cure and Acock (1986) indicated that doubling CO_2 concentration increased P_N by 41–105 %. Radoglou *et al*. (1992) also found that increasing C_a from 350 to 700 µmol mol^{-1} resulted in 40 % increase in P_N for bean (*Phaseolus vulgaris* L.) plants grown with low nutrient supply and about 30 % increase for plants grown with high nutrient supply.

Table 1. Least squares means of net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and water use efficiency (WUE) averaged over four carrot cultivars at 11 CO_2 concentrations. Least squares means followed by the same letter are not significantly different at the 5 % level.

CO_2 [µmol mol^{-1}]	P_N [µmol m^{-2} s^{-1}]	g_s [mol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	WUE [mmol mol^{-1}]
50	0.08 g	0.058 de	0.401 g	0.24 k
150	2.71 f	0.079 cd	0.764 bc	3.70 j
250	5.70 e	0.097 ab	0.874 ab	6.69 i
350	8.38 d	0.106 a	0.917 a	9.14 h
450	10.21 c	0.106 a	0.916 a	11.24 g
550	11.30 b	0.100 a	0.865 ab	13.56 f
650	11.96 a	0.088 bc	0.777 bc	15.98 e
750	12.42 a	0.073 cd	0.678 cd	18.82 d
850	12.37 a	0.063 de	0.601 de	21.42 c
950	12.56 a	0.055 e	0.527 ef	24.65 b
1050	12.76 a	0.050 e	0.485 fg	27.70 a

Increased P_N after short-term exposure of C_3 plants to elevated C_a is attributed to increased availability of substrate for the primary enzyme ribulose-1,5-bisphosphate (RuBP) carboxylase (Sage 1994) and the suppression of photorespiration (Sharkey 1988). We observed a linear increase in C_i with increasing C_a (Fig. 1*A*) and the increases were proportional to changes in P_N. Presumably, an increase in C_i reduced RuBP oxygenation and at the same time enhanced RuBP carboxylation resulting in increased P_N. No significant differences in C_i occurred

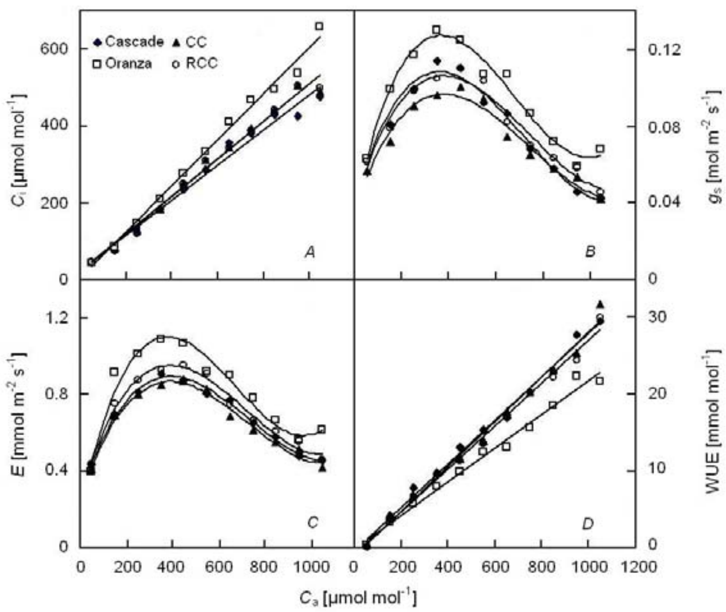

Fig. 1. Responses of intercellular CO_2 concentration (C_i) (*A*), stomatal conductance (g_s) (*B*), transpiration rate (*E*) (*C*), and instantaneous water use efficiency (WUE) (*D*) in four carrot cultivars to various external CO_2 concentrations (C_a) at 20 °C and 500 μmol m^{-2} s^{-1} irradiance. Means of four replications, and each replicate is the average of five measurements.

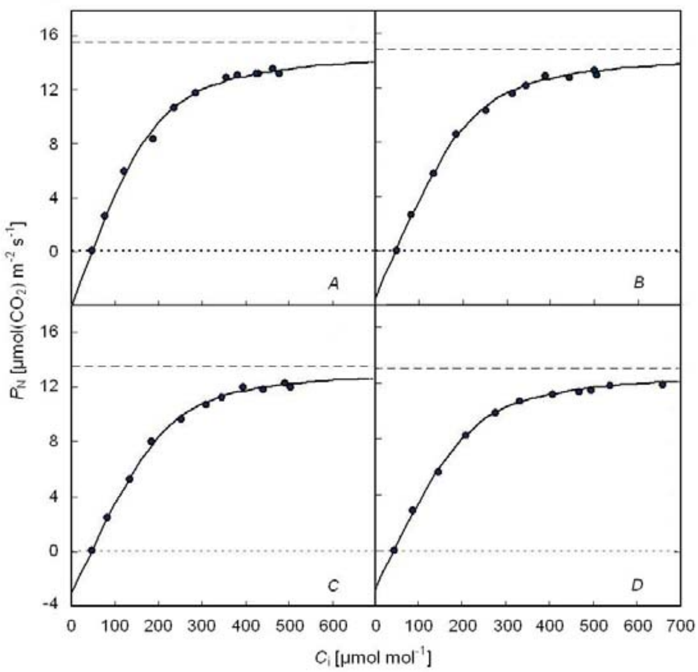

Fig. 2. Responses of leaf net photosynthetic rate (P_N) to intercellular CO_2 concentration (C_i) of four carrot cultivars: Cascade (*A*), Red Core Chantenay (*B*), Caro Choice (*C*), and Oranza (*D*) at 20 °C and 500 μmol m^{-2} s^{-1} irradiance. *The solid curves* were fitted using non-rectangular hyperbola model, and *the top broken lines* are the estimated maximum P_N.

among the cultivars ($p = 0.319$), although the increases in C_i for Oranza were relatively high at $C_a > 650$ µmol mol^{-1}, and this resulted in a significant cultivar×C_i interaction ($p = 0.016$).

The photosynthetic capacities of the cultivars were analyzed by fitting the P_N *vs.* C_i response curves to a non-rectangular hyperbola (Marshall and Biscoe 1980, Cannell and Thornley 1998). The P_N increased progressively with increase in C_i until CO_2 saturation at C_i approximately 350 µmol mol^{-1} (C_a 650 µmol mol^{-1}) for all cultivars except for Oranza where saturation occurred at C_i approximately 400 µmol mol^{-1} (C_a 650 µmol mol^{-1}) (Fig. 2). Above these C_i levels, P_N increased slightly with further increase in C_i. The photosynthetic parameters estimated from the model are similar for all four cultivars (Table 2). The curvatures of the curves ranged from 0.867 to 0.909. According to Cannell and Thornley (1998), the convexity factor varies from 0, describing a rectangular hyperbola, to 1, which describes a 'Blackman-type' response and can be assumed as an empirical factor determined by curve fitting. The initial slopes varied from 68 µmol m^{-2} s^{-1} for CC and Oranza to 91 µmol m^{-2} s^{-1} for Cascade but did not differ due possibly to the large variation in the data within cultivars.

Table 2. Estimated parameters for photosynthesis-intercellular CO_2 response curves for four carrot cultivars. The non-rectangular hyperbolic model parameters represent the convexity of the curves (θ), initial slope of the curves (α) [µmol m^{-2} s^{-1}], maximum net photosynthetic rate (P_{Nmax}) [µmol m^{-2} s^{-1}], and the dark respiration rate (R_D) [µmol m^{-2} s^{-1}]. CO_2 compensation concentration (Γ) [µmol mol^{-1}] was calculated from the fitted models. Parameter estimates within a column with the same letter are not significantly different at the 5 % level.

Cultivar	θ	α	P_{Nmax}	R_D	Γ
Cascade	0.867a	91a	15.50a	3.96a	45.0
Caro Choice	0.909a	68a	13.52a	2.93a	44.0
Oranza	0.898a	68a	13.31a	2.80a	42.1
Red Core Chantenay	0.897a	78a	14.96a	3.50a	46.0

According to Caemmerer and Farquhar (1981), the initial slope of the P_N *vs.* C_i curve at low C_i reflects the active sites of RuBPCO and is sometimes called the carboxylation efficiency. The values observed in our study compare well with those reported by Nederhoff and Vegter (1994) which ranged from 63.0 to 94.5 µmol m^{-2} s^{-1} for cucumber, sweet pepper, and tomato, and with other C_3 species including soybean, bean, and potato (Wullschleger 1993). However, lower values of 51 µmol m^{-2} s^{-1} were reported for cotton (Harley *et al.* 1992) and wheat (*Triticum aestivum* L.) (Harnos *et al.* 2002) leaves. The differences could be attributed, in part, to species differences, growth, and measurements conditions.

The CO_2-saturated P_N (P_{Nmax}) predicted by the nonlinear model for Cascade, CC, Oranza, and RCC were 15.50, 13.52, 13.31, and 14.96 µmol m^{-2} s^{-1}, respectively, and these values were not significantly different (Table 2). Typically, P_N is limited by one of these three process: (*1*) the capacity of RuBPCO to consume RUBP; (*2*) the capacity of the thylakoid reactions to provide ATP and NADPH to regenerate RUBP; and (*3*) the capacity of starch and sucrose synthesis to regenerate inorganic phosphates (P_i) from triose phosphates (Liu *et al.* 2002, Sage *et al.* 2002). RuBPCO capacity limits P_N at low C_i, limitation due to RuBP regeneration occuring at intermediate C_i, whereas P_i becomes a limiting factor at high C_i. In situations where P_N is limited by RuBP regeneration due to limitation imposed by electron transport, increasing C_i stimulates P_N (Sage *et al.* 1989). In contrast, when P_i regeneration becomes limiting, P_N is little or not affected, and may be inhibited by increasing CO_2 (Sharkey 1985). In the present study, limitations resulting from P_i regeneration were apparent at $C_i > 450$ µmol mol^{-1} for all cultivars suggesting that the rate of triose phosphate utilization for starch and sucrose synthesis, hence, P_i release was insufficient to allow further increases in P_N (Rajasekaran *et al.* 1997). We found no evidence of down-regulation of assimilation in response to increasing C_a as suggested in other studies (*e.g.*, Sharkey 1985, Sage *et al.* 1989).

The R_D for the cultivars correlated well with P_N indicating relatively low values for CC and Oranza, which had relatively low P_N, although the differences among cultivars were not significant. The Γ (C_i at which P_N is zero) was calculated from the model equation. The values ranged from 42 µmol mol^{-1} for Oranza to 46 µmol mol^{-1} for RCC and were consistent with the data for cucumber (Janoudi *et al.* 1993), wheat (Wheeler *et al.* 1993), sweet pepper (Nederhoff and Vegter 1994), and *Alstroemeria* (Leonardos *et al.* 1994) grown and measured under similar conditions.

Repeated measure analysis indicated no significant ($p = 0.573$) differences in g_s among cultivars and similarly the interaction between cultivar and C_a was not significant ($p = 0.638$). However, Oranza generally had relatively high g_s values among the four cultivars which presumably explains the corresponding high C_i relative to those for the other cultivars (Fig. 1*B*). Over all, increasing C_a from 50 to 350 µmol mol^{-1} increased g_s to a maximum (106 mmol m^{-2} s^{-1}) and thereafter g_s declined by 17 % when C_a was increased to 650 µmol mol^{-1} (Table 1). A three-fold increase in C_a from 350 to 1 050 µmol mol^{-1}

decreased g_s by 53 %. This is in agreement with several studies, which indicate that when stomata are exposed to increased CO_2 (above the present atmospheric) aperture or g_s generally declines (*e.g.*, Morison 1998), although the magnitude of the response in individual experiment may vary depending on the growth and measurement conditions (Field *et al.* 1995). The average decline in g_s for doubling CO_2 concentration for many C_3 species can be smaller or larger than 40 % (Morison 1998), thus, the values obtained in the present study are typical of C_3 plants. Mott (1988) demonstrated that stomata respond to C_i and Morison (1998) suggested that C_i could be the signal that links stomata aperture to mesophyll demand for CO_2. We observed maximum g_s at C_i 185–200 µmol mol^{-1} followed by a decline with further increase in C_i and is consistent with the results of Druță (2001).

The partial opening and closing of the stomata regulate water loss and in the process maintain leaf temperature within optimum range (Jones 1998) and also maintain the C_i:C_a ratio under elevated CO_2 concentration (Olivo *et al.* 2002). The response pattern for *E* with increasing C_a was similar to that for g_s (Table 1 and Fig. 1*C*) suggesting that changes in *E* were through the effect of stomatal size. The *E* reached maximum values (0.9–1.1 mmol m^{-2} s^{-1}) at 350 µmol mol^{-1} followed by a decline to 0.40–0.60 mmol m^{-2} s^{-1} when C_a was increased to 1 050 µmol mol^{-1} (Fig. 1*C*). Similarly, except for the 50 µmol mol^{-1} CO_2 treatment, the changes in g_s and also P_N maintained the C_i:C_a ratio for the individual cultivars (data not shown) supporting the suggestion that stomata operate in a manner that maintains the C_i:C_a ratio (Olivo *et al.* 2002). Thus, increasing C_a and hence C_i, generally had no significant influence on the C_i:C_a ratio.

The increase in P_N with C_a in addition to the decline in *E* at C_a > 350 µmol mol^{-1} increased the WUE for all the cultivars. The WUE increased linearly with increase in C_a (Fig. 1*D*) and repeated measure analysis detected no significant (p = 0.224) differences among cultivars. On average, increasing C_a from 50 to 350 µmol mol^{-1} improved WUE by 38 times and this increase could be attributed primarily to changes in P_N because g_s and hence *E* increased within this C_a range (Table 1). Increasing C_a from 350 to 650 µmol mol^{-1} increased WUE by 76 %, whereas a three-fold increase in C_a from 350 to 1 050 µmol mol^{-1} also resulted in a three-fold increase in WUE. Unlike the response at C_a < 350 µmol mol^{-1}, increase in WUE at C_a > 350 µmol mol^{-1} was associated with increase in P_N and a reduction in *E*, although the contribution due to the increase in P_N exceeded that of the decrease in *E*. Similar results was reported for bean (Radoglou *et al.* 1992) and sunflower (*Helianthus annuus L.*) (Tezara *et al.* 2002).

In summary, the four carrot cultivars responded similarly to CO_2 enrichment and did not differ in their photosynthetic capacities and other associated gas exchanges. Increasing C_a to about double the current atmosphere increased P_N by 43 % but P_N increased only slightly with further increases in C_a suggesting P_i regeneration capacity limited P_N. Carbon dioxide saturation occurred at C_a > 650 µmol mol^{-1} (C_i = 185–200 µmol mol^{-1}) with P_{Nmax} ranging from 13.31 to 15.50 µmol m^{-2} s^{-1}. The Γ values varied from 42 to 46 µmol mol^{-1} and are within normal range for C_3 plants. The g_s and *E* increased with C_a to a peak at 350 µmol mol^{-1} and thereafter declined by 53 and 47 %, respectively, at 1 050 µmol mol^{-1}. The C_i increased linearly with C_a and the C_i:C_a ratio remained fairly the same due presumably to the changes in P_N and g_s. The increase in P_N and also the decline in *E* at C_a > 350 µmol mol^{-1} increased WUE. For example, increasing C_a from 350 to 650 improved WUE by 76 %. These results suggest that future enrichment in the atmospheric CO_2 may lead to adjustments in P_N and g_s, which could improve carrot productivity and water utilization.

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