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BRIEF COMMUNICATION

Photosynthetic response of carrots to varying irradiances

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Abstract

Response to irradiance of leaf net photosynthetic rates (P_N) of four carrot cultivars: Cascade, Caro Choice (CC), Oranza, and Red Core Chantenay (RCC) were examined in a controlled environment. Gas exchange measurements were conducted at photosynthetic active radiation (PAR) from 100 to 1 000 μmol m^{-2} s^{-1} at 20 °C and 350 μmol(CO$_2$) mol^{-1}(air). The values of P_N were fitted to a rectangular hyperbolic nonlinear regression model. P_N for all cultivars increased similarly with increasing PAR but Cascade and Oranza generally had higher P_N than CC. None of the cultivars reached saturation at 1 000 μmol m^{-2} s^{-1}. The predicted P_N at saturation (P_{Nmax}) for Cascade, CC, Oranza, and RCC were 19.78, 16.40, 19.79, and 18.11 μmol(CO$_2$) m^{-2} s^{-1}, respectively. The compensation irradiance (I_c) occurred at 54 μmol m^{-2} s^{-1} for Cascade, 36 μmol m^{-2} s^{-1} for CC, 45 μmol m^{-2} s^{-1} for Oranza, and 25 μmol m^{-2} s^{-1} for RCC. The quantum yield among the cultivars ranged between 0.057–0.033 mol(CO$_2$) mol^{-1}(PAR) and did not differ. Dark respiration varied from 2.66 μmol m^{-2} s^{-1} for Cascade to 0.85 μmol m^{-2} s^{-1} for RCC. As P_N increased with PAR, intercellular CO$_2$ decreased in a non-linear manner. Increasing PAR increased stomatal conductance and transpiration rate to a peak between 600 and 800 μmol m^{-2} s^{-1} followed by a steep decline resulting in sharp increases in water use efficiency.

Additional key words: compensation irradiance; *Daucus carota*; net photosynthetic rate; nonlinear regression model; quantum yield; stomatal conductance; transpiration rate; water use efficiency.

The response of leaf or canopy photosynthesis to irradiance has been reported for many horticultural crops including cucumber (*Cucumis sativus* L.) (Warren Wilson *et al*. 1992, Janoudi *et al*. 1993, Nederhoff and Vegter 1994), aubergine (*Solanum melongena* L.) (Hand *et el*. 1993), sweet pepper (*Capsicum annuum* L.), and tomato (*Lycopersicn esculentum* Mill.) (Nederhoff and Vegter 1994). However, little is known about the effects of irradiance on photosynthetic capacity of carrot (*Daucus carota* var. *sativus*). Accurate assessment of these effects is essential to understand how to maximize carrot growth and yield through improved management practices and allow comparison with other crops that could be grown in similar environments. Generally, net photosynthetic rate (P_N) for single leaves or canopies of several horticultural crops increases with irradiance in a hyperbolic pattern typical of most plants possessing the C$_3$ photosynthetic pathway. These photon response curves have been extensively studied and described by exponential, asymptotic, or hyperbolic models (*e.g.*, Thornley 1998).

In the present study, we (*1*) evaluated the effects of increasing irradiance on leaf P_N of four carrot cultivars using repeated measures analysis, (*2*) modeled the relationship between irradiance and leaf P_N using the rectangular hyperbola model, and (*3*) compared the photosynthetic characteristics of the cultivars using nested rectangular hyperbola models.

Seeds of four carrot (*Daucus carota* L.) cultivars: Cascade, Caro Choice (CC), Oranza, and Red Core Chantenay (RCC) were sown in 15-cm diameter plastic pots containing *Pro-mix* (*Premier Horticulture*, Riviere-du-Loup, Quebec, Canada) in a controlled environment.

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Ten seeds of each cultivar were sown and seedlings were thinned to three at the first true leaf stage, *ca*. 7 d after emergence. Seedlings were watered daily to field capacity with tap water and each pot was fertilized weekly with 100 cm^3 solution containing 1.5 kg m^{-3} of NPK 15 : 15 : 30. Growth room conditions were maintained at a 16-h day length and mean day and night temperatures of 20 and 10 °C, respectively. Relative humidity was maintained at 70±2 %. The light source composed of a combination of high-pressure sodium lamps, cool white fluorescent lamps, and incandescent light bulbs provided a photosynthetic active radiation (PAR) of approximately 450±20 μmol m^{-2} s^{-1} at the top of the plant canopy. The CO_2 concentration in the growth room was 370±10 μmol(CO_2) mol^{-1}(air), which was monitored through a computerized infrared gas transmitter (*90DM3A*, *Vulcain*, New Stanton, PA, USA).

All measurements of P_N, stomatal conductance (g_s), intercellular CO_2 (C_i), and transpiration rate (E) were taken beginning 30 d after seedling emergence (approximately seven-leaf stage) on the youngest fully expanded intact leaves using a portable gas analyzer and associated leaf chamber (*LCA-4, Analytical Development Company*, Hoddesdon, UK) together with a portable Leaf Microclimate Control System (*Analytical Development Company*, Hoddesdon, UK). The Leaf Microclimate Control System provides a means of controlling and varying the microclimate of the leaf placed within the leaf chamber associated with the *LCA-4*. With this system the ambient air temperature in the chamber, the ambient irradiance on the leaf, and CO_2 concentration at the *LCA-4* air supply inlet can be varied. The gas analyzer is equipped with a gas-mixing subsystem, which provides an air supply within nearly constant CO_2 and water vapor concentrations within the leaf chamber. The analyzer was operated at an airflow rate of 400 μmol s^{-1}. Leaf temperature was measured using a leaf temperature sensor attached to the leaf chamber.

Leaf gas exchange was determined at 10 levels of PAR (100, 200, 300, 400, 500, 600, 700, 800, 900, and 1 000 μmol m^{-2} s^{-1}) at 350±10 μmol mol^{-1}(CO_2), leaf temperature of 20 °C, and relative humidity of 65 %. Initially, the light canopy in the growth room was raised to provide PAR of 100 μmol m^{-2} s^{-1} at the surface of the leaflets placed in the leaf chamber. Irradiance was increased in steps by lowering the light canopy to increase the incident PAR to 1 000 μmol m^{-2} s^{-1}. Five min was allowed for a steady-state condition at each PAR prior to measurement. Five measurements were recorded automatically at 60 s intervals for each PAR 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* is 16 s. The leaf areas for the individual leaves used for measurements were determined using leaf area meter (*Li-3000, Licor*, Lincoln, NE, USA). Gas exchange measurements were calculated on leaf area basis.

The values were analyzed using repeated measures analysis (RMA). The design for the RMA was a two factor (cultivar with 4 levels, and PAR with 10 levels) factorial in four time blocks, and the response variables were P_N, C_i, g_s, and E. For each cultivar, the five response measurements taken on each plant at each PAR were averaged prior to analysis. Instantaneous water use efficiency (WUE) was also computed as P_N/E. Since the response measurements for the 10 PAR levels were measured repeatedly on the same leaflet, the independence assumption on the error terms for the ANOVA was likely to be violated (Potvin *et al.* 1990, Littell *et al.* 1998). Consequently, the error term was assumed to be 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 values were back transformed. The appropriate covariance structure was determined to be autogressive [AR(1)] using the Akaike information criterion (AIC) and Schwarz Bayesian criterion (SBC) (Littell *et al.* 1998). The analysis was completed using the Mixed Procedure of *SAS* (SAS Institute 1999).

For each cultivar, plot of P_N against PAR suggested an asymptotic regression model, which is similar to the rectangular hyperbola model proposed by Thornley (1998) for modeling leaf photosynthesis as a function of PAR. Therefore, for each cultivar, P_N (Y) as a function of PAR (X) was modeled using the rectangular hyperbola. Following this, a nested nonlinear regression with incremental parameters model was used for comparing pairs of cultivars in terms of the model parameters. The analysis was completed using the *NLIN* procedure of *SAS* (SAS Institute 1999). The general form of the rectangular hyperbola model is:

$$Y = \frac{\alpha X \; P_{Nmax}}{\alpha X + P_{Nmax}} - R_D + \varepsilon \tag{1}$$

where Y is P_N, α is the initial slope of PAR response curve at low PAR, often called photosynthetic efficiency or quantum yield, X is PAR incident on leaf surface, P_{Nmax} is asymptote of photosynthesis at high PAR, R_D is dark respiration rate, and ε is the error term assumed to be normally distributed with zero mean, constant variance and independent of one another. The compensation irradiance at PAR level where Y is zero was calculated from the fitted model.

Repeated measure analysis of variance showed that irradiance significantly affected all the parameters (response variables) measured. No significant interaction occurred between cultivar and irradiance for all measured responses indicating that the cultivars responded similarly to increasing irradiance. Hence, the values at various

PAR were averaged over cultivars and also for the four cultivars over irradiance (data not shown). Significant increases in P_N for every 100 µmol m^{-2} s^{-1} increase in irradiance were observed until PAR reached 700 µmol m^{-2} s^{-1}. At this PAR (700 µmol m^{-2} s^{-1}), P_N increased 5-fold compared with that for the 100 µmol m^{-2} s^{-1}. Increases in P_N at irradiance >700 µmol m^{-2} s^{-1} PAR were relatively small. The differences in P_N among the cultivars were significant ($p = 0.032$) and could be attributed to the higher assimilation rates of Cascade and Oranza compared with CC at PAR >400 µmol m^{-2} s^{-1}. For example, the P_N for Cascade and Oranza at 600 µmol m^{-2} s^{-1} were 29 and 19 %, respectively, higher than that for CC.

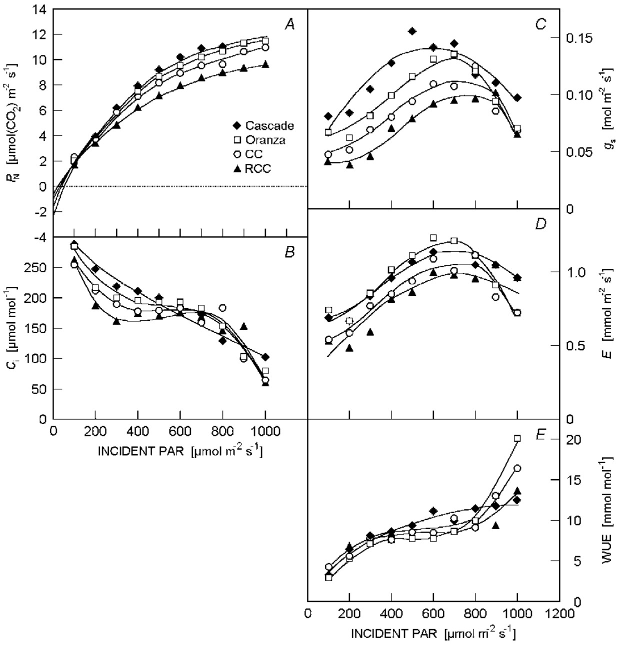

Fig. 1. Responses of leaf net photosynthetic rate, P_N (*A*), intercellular CO$_2$ concentration, C_i (*B*), stomatal conductance, g_s (*C*), transpiration rate, E (*D*), and instantaneous water use efficiency, WUE (*E*) in four carrot cultivars to changing irradiance at 20 °C and 350 µmol mol^{-1} CO$_2$ concentration. The regression lines in *A* were fitted using the rectangular hyperbola model. Means of four blocks, each block is the average of five measurements.

P_N for all cultivars increased hyperbolically in response to increased irradiance (Fig. 1*A*). The photosynthetic-irradiance response curves observed in this study are typical of many C$_3$ plants and consistent with the results of previous reports (Hand *et al.* 1993, Leonardos *et al.* 1994, Miller *et al.* 2001, Jiang *et al.* 2003). The values were fitted to rectangular hyperbola, Eq. (1), to facilitate the analysis of the responses in terms of model parameters and to test for differences in parameter estimates. None of the cultivars reached photon saturation at the highest PAR that could be reached in the growth room (1 000 µmol m^{-2} s^{-1}), although the magnitude of increase in P_N decreased at irradiance >700 µmol m^{-2} s^{-1}.

Several studies on vegetables including those of Hand *et al.* (1993) for aubergine and Warren Wilson *et al.* (1992) for tomato and cucumber did not reach photon saturation below 900 µmol m^{-2} s^{-1}. Under high CO$_2$ concentration, Warren Wilson *et al.* (1992) observed photon saturation only at 2 500 µmol m^{-2} s^{-1}. Similarly, potato (*Solanum tuberosum*) cultivar DTO-33 did not reach photon saturation at 1 300 µmol m^{-2} s^{-1} PAR (Midmore and Prange 1992).

The estimated maximum P_N under ambient CO$_2$ concentration (350 µmol mol^{-1}) (P_{Nmax}) for the cultivars varied from 16.40 to 19.79 µmol m^{-2} s^{-1}, with Cascade and Oranza having significantly higher P_{Nmax} than CC (Table 1). Quantum yield ranged from 0.033 mol(CO$_2$) mol^{-1}(PAR) for CC to 0.057 mol mol^{-1} for Cascade and these values did not differ significantly. The values obtained in the present study compare well with reported values, which range between 0.026–0.075 mol mol^{-1} for many C$_3$ plants (Acock *et al.* 1978, Leonardos *et al.* 1994, Miller *et al.* 2001).

Table 1. Estimated values with the standard errors in parenthesis of quantum yield (α), photon saturated net photosynthetic rate (P_{Nmax}), and dark respiration rate (R_D) for irradiance response curves of four carrot cultivars fitted to rectangular hyperbola. The compensation irradiances (I_c) were calculated from the models. Parameter estimates within a column with the same letter are not significantly different at the 5 % level.

Cultivar	α	P_{Nmax} [µmol m^{-2} s^{-1}]	R_D [µmol m^{-2} s^{-1}]	I_c [µmol m^{-2} s^{-1}]
Cascade	0.057 (0.015)a	19.78 (0.80)a	-2.66 (1.24)a	54
Caro Choice	0.033 (0.003)a	16.40 (0.41)b	-1.11 (0.35)a	36
Oranza	0.043 (0.006)a	19.79 (0.62)a	-1.76 (0.62)a	45
Red Core Chantenay	0.035 (0.006)a	18.11 (0.77)ab	-0.85 (0.60)a	25

R_D (P_N at PAR of 0 µmol m^{-2} s^{-1}) did not differ among the cultivars due primarily to the large standard errors, especially for Cascade (Table 1). The calculated I_c from the model equation varied among cultivars. Cascade had the highest value (54 µmol m^{-2} s^{-1}), which was more than twice that for RCC (25 µmol m^{-2} s^{-1}). Differences in I_c among the cultivars were primarily caused by the different R_D. Thus, RCC with low R_D (in absolute magnitude) requires less photons to photosynthesize rapidly enough to balance the CO_2 being lost compared with Cascade with relatively high R_D. The observed I_c values are within the normal range of C_3 plants including tomato, sweet pepper, and cucumber (Acock *et al.* 1978, Warren Wilson *et al.* 1992, Nederhoff and Vegter 1994, Peek *et al.* 2002).

Measured C_i for all cultivars decreased as irradiance increased to 400 μmol m^{-2} s^{-1} but except for Cascade, C_i stabilized between 400 and 800 μmol m^{-2} s^{-1} followed by a steep decline to 58, 62, and 77 μmol mol^{-1} for CC, RCC, and Oranza, respectively, at 1 000 μmol m^{-2} s^{-1} (Fig. 1*B*). Unlike the other cultivars, the C_i for Cascade declined linearly with increasing irradiance reaching 101 μmol mol^{-1} at 1 000 μmol m^{-2} s^{-1}. The sharp decline in C_i suggests rapid decrease in stomatal aperture in response to high irradiance, which presumably limited CO_2 diffusion as indicated in the relatively low C_i for CC, RCC, and Oranza compared with Cascade. The C_i for CC was generally low and may have contributed to the low P_N observed in this cultivar. A strong cubic relationship was observed between C_i and P_N indicating that large increases in P_N occurred at $C_i > 200$ μmol mol^{-1}, moderate increases between 200 and 120 μmol mol^{-1}, and slight increases at C_i below 120 μmol mol^{-1} (values not shown). Thus, the slight increases in P_N at higher PAR > 600 μmol m^{-2} s^{-1} could partly be due to the low C_i, which possibly limited ribulose-1,5-bisphosphate carboxylase activity (Walcroft *et al.* 1997).

Low C_i could be due to limitation in CO_2 diffusion as a result of decreased g_s. Stomata regulate C_i and control water loss, which in turn maintain leaf temperature within optimal range (Jarvis and Davies 1998, Jones 1998, Morison 1998). In the present study, g_s and consequently E for all cultivars increased with increasing irradiance reaching a maximum between 600 and 800 μmol m^{-2} s^{-1} (Fig. 1*C,D*). At irradiance > 800 μmol m^{-2} s^{-1}, g_s declined presumably due to stomata sensitivity to higher irradiance or as a means to control water loss. Repeated measure analysis of variance indicated that the g_s for Cascade was significantly higher than that for CC and RCC, whereas Oranza had similar g_s to the other cultivars (values not shown).

Jarvis and Davies (1998) indicated that the relationship between increases in P_N and g_s at fixed ambient CO_2 concentration is linear because stomata maintain C_i, hence CO_2 concentration gradient across the leaf epidermis. Our data supported this observation at low PAR (< 600 μmol m^{-2} s^{-1}) (not shown), but g_s declined at PAR > 700 μmol m^{-2} s^{-1} as P_N continued to increase with increasing irradiance, suggesting that the decrease in g_s did not limit P_N substantially.

In a study on the dynamics of changes in P_N and g_s in response to changes in irradiance in *Phaseolus* leaves, large changes in g_s had no effect on P_N (Jones 1998) but this could happen provided C_i is not limiting. In our study, the decline in g_s primarily reduced E as a means of controlling water loss. Prior to the decline in E, WUE for CC, Oranza, and RCC increased with irradiance up to 400 μmol m^{-2} s^{-1} and remained stable between 400 and 800 μmol m^{-2} s^{-1} (Fig. 1*E*). However, the WUE for Cascade increased with irradiance following a quadratic relationship. No significant differences in WUE were observed among cultivars. The steep decline in E in turn led to a sharp increase in WUE for CC, Oranza, and RCC. Thus, the rapid responses in g_s to higher PAR (>800 μmol m^{-2} s^{-1}) observed in these three cultivars may represent an adaptation to minimize water loss resulting in high WUE. In contrast, the WUE pattern for Cascade appeared relatively less efficient at higher PAR, but it may reflect an adaptation to maximize carbon gain at low WUE.

In conclusion, the data indicate that P_N for the four carrot cultivars increased with increasing irradiance in a similar manner and none of the cultivars reached saturation at 1 000 μmol m^{-2} s^{-1}. This implies that perhaps carrots grown under Canadian Maritimes field conditions do not reach their P_{Nmax} during most part of the growing season days probably as a result of the frequent cloud cover. The increases in P_N with increasing irradiance decreased in magnitude at PAR > 800 μmol m^{-2} s^{-1} which could be related to the increasing importance of the low C_i. However, the decline in g_s was not the primary factor limiting P_N at higher irradiance but rather controlled water loss leading to a sharp increase in WUE. Cascade and Oranza had the highest P_{Nmax}, possibly due to the relatively high quantum yields for these cultivars compared with those for RCC and CC. I_c for the cultivars varied; the value for Cascade was more than two times that for RCC and correlated with the R_D values.

References

Acock, B., Charles-Edwards, D.A., Fitter, D.J., Hand, D.W., Ludwig, L.J., Warren Wilson, J., Withers, A.C.: The contribution of leaves from different levels within a tomato crop to canopy net photosynthesis: An experimental examination of two canopy models. – J. exp. Bot. **29**: 815-827, 1978.

Hand, D.W., Warren Wilson, J.W., Acock, B.: Effects of light and CO_2 on net photosynthetic rates of stands of aubergine and *Amaranthus*. – Ann. Bot. **71**: 209-216, 1993.

Janoudi, A.K., Widders, I.E., Flore, J.A.: Water deficits and environmental factors affect photosynthesis in leaves of cucumber (*Cucumis sativus*). – J. amer. Soc. hort. Sci. **118**: 366-370, 1993.

Jarvis, A.J., Davies, W.J.: The couple response of stomatal conductance to photosynthesis and transpiration. – J. exp. Bot. **49**: 399-406, 1998.

Jiang, H., Wang, X.-H., Deng, Q.-Y., Yuan, L.-P., Xu, D.-Q.: Comparison of some photosynthetic characters between two hybrid rice combinations differing in yield potential. – Photosynthetica **40**: 133-137, 2002.

Jones, H.G.: Stomatal control of photosynthesis and transpiration. – J. exp. Bot. **49**: 387-398, 1998.

Leonardos, E.D., Tsujita, M.J., Grodzinski, B.: Net carbon dioxide exchange rates in *Alstroemeria* 'Jacqueline' at varying irradiances, carbon dioxide concentrations, and air temperatures. – J. amer. Soc. hort. Sci. **119**: 1265-1275, 1994.

Littell, R.C., Henry, P.R., Ammerman, C.B.: Statistical analysis of repeated measures data using SAS procedures. – J. anim. Sci. **76**: 1216-1231, 1998.

Midmore, D.J., Prange, R.K.: Growth responses of two *Solanum* species to contrasting temperatures and irradiance levels: relations to photosynthesis, dark respiration and chlorophyll fluorescence. – Ann. Bot. **69**: 13-20, 1992.

Miller, A.M., van Iersel, M.W., Armitage, A.M.: Whole-plant carbon exchange responses of *Angelonia angustifolia* to temperature and irradiance. – J. amer. Soc. hort. Sci. **125**: 606-610, 2001.

Morison, J.I.L.: Stomatal response to increased CO_2 concentration. – J. exp. Bot. **49**: 443-452, 1998.

Nederhoff, E.M., Vegter, J.G.: Photosynthesis of stands of tomato, cucumber and sweet pepper measured in greenhouse under various CO_2 concentrations. – Ann. Bot. **73**: 353-361, 1994.

Peek, M.S., Russek-Cohen, E., Wait, D.A., Forseth, I.N.: Physiological response curve analysis using nonlinear mixed models. – Oecologia **132**: 175-180, 2002.

Potvin, C., Lechowicz, M.J., Tardif, S.: The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. – Ecology **71**: 1389-1400, 1990.

SAS Institute: SAS OnlineDoc®, Version 8. – SAS Institute, Cary 1999.

Thornley, J.H.M.: Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. – Ann. Bot. **81**: 421-430, 1998.

Walcroft, A.S., Whitehead, D., Silvester, W.B., Kelliher, F.M.: The response of photosynthetic model parameters to temperature and nitrogen concentration in *Pinus radiata* D. Don. – Plant Cell Environ. **20**: 1338-1348, 1997.

Warren Wilson, J., Hand, D.W., Hannah, M.A.: Light interception and photosynthetic efficiency in some glasshouse crops. – J. exp. Bot. **43**: 363-373, 1992.