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Whole-plant Net CO_2 Exchange of Raspberry as Influenced by Air and Root-zone Temperature, CO_2 Concentration, Irradiation, and Humidity

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Abstract. **The influence of irradiance, CO_2, and temperature on whole-plant net CO_2 exchange rate (NCER) of *Rubus idaeus* L. 'Heritage' micropropagated raspberries was examined. Within the set of environmental conditions examined, irradiation was the most important factor, accounting for 58% of the whole-plant irradiance/CO_2 concentration/temperature NCER model variation, followed by CO_2 concentration (28%) and temperature (2.5%). Net photosynthesis (Pn) required irradiance levels >600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPF* for saturation, greatly increased under CO_2 enrichment (up to 1500 $\mu L \cdot L^{-1}$), and was optimum at a whole-plant temperature of 20 °C. Temperature effects were partitioned in an experiment using varying air and root-zone temperatures (15, 20, 25, 30, and 35 °C) under saturated light and ambient CO_2 levels (350 $\mu L \cdot L^{-1}$). Air and root-zone temperature influenced Pn, with maximum rates occurring at an air × root-zone temperature of 17/25 °C. The contribution of air and root-zone temperature to the NCER model varied, with air and root-zone temperature contributing 75% and 24%, respectively, to the total model variation (R^2 = 0.96). Shoot dark respiration increased with air and root-zone temperature, and root respiration rates depended on air and root-zone temperature and shoot assimilation rate. Humidity also influenced Pn with a saturated vapor pressure deficit threshold >0.25 kPa resulting in a Pn decrease. Quantifying the physiological response of raspberries to these environmental parameters provides further support to recent findings that cool shoot/warm root conditions are optimum for raspberry plant growth.**

Plant growth depends on the balance between C gain during photosynthesis and C loss through respiratory processes (Dutton et al., 1988; McCree, 1986). Crop productivity, however, is often restricted as a consequence of unfavorable physical environment conditions. Quantifying the response of net C assimilation to various physical environmental factors (e.g., radiation, temperature, CO_2 concentration, and humidity) contributes to an understanding of how to maximize plant growth and yield potential and results in the development of management strategies to attain optimum physical environment conditions.

Insufficient information is available regarding the whole-plant physiological response of raspberries (*Rubus idaeus*) to temperature, radiation, CO_2 concentration, and humidity. Past studies have focused primarily on floricane and primocane competition and the effect on light interception (Braun et al., 1989; Palmer et al., 1987) and dry-matter partitioning (Waister and Wright, 1989). Although recent studies have examined the effects of CO_2 concentration, temperature, and radiation in seasonal photosynthesis patterns and stomatal versus nonstomatal limitations studies, these experiments were limited to leaf studies (Fernandez, 1994), which may not represent the behavior of the entire plant or canopy (Dutton et al., 1988).

Although the optimum whole-plant air temperature for net photosynthesis (Pn) and net growth in raspberries is 15 to 20 °C (Fernandez and Pritts, 1994; Privé, 1991), the optimum root-zone temperature remains unresolved. Cool root-zone temperatures have been thought optimum for raspberry growth (Clark, 1940). Studies by Privé (1991) and Trinka (1991), however, indicated that these results may have been due to groundcover moisture conservation properties, and that warm root-zone temperatures may be optimum for raspberry growth. This unclear quantification of optimum root-zone temperature and results from an elevated daily root-zone temperature study with apples imply that net CO_2 exchange rate (NCER) may also be influenced by root-zone temperature (Behboudian et al., 1994). Hence, the objectives of this project were to 1) determine how whole-plant NCER is influenced by CO_2 concentration, whole-plant temperature, irradiation, and humidity and 2) quantify and differentiate the influence of air and root-zone temperature on NCER in raspberries.

Materials and Methods

Plant material. Dormant *Rubus idaeus* 'Heritage' tissue culture plantlets (Nourse Nurseries, South Deerfield, Mass.) were planted to minimize variability in growth patterns. The plug plantlets were potted at weekly intervals in 15-cm-diameter (1.74-L) pots containing Promix-BX (Les Tourbières Premier LTÉE, Rivière du Loup, Que.) starting in December 1993 for the whole-plant root-zone/air temperature study and in December 1994 for the whole-plant CO_2 concentration/irradiation/temperature study. Plants were placed on benches in a greenhouse with 22 ± 3 °C day and 17 ± 1 °C night temperatures and maintained as one unbranched primocane per pot. Plants were exposed to an 18-h photoperiod with sufficient supplemental irradiance (photosynthetic photon flux of about 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$) provided by overhead 1000-W, high-pressure sodium (HPS) lamps (Lumalux LU1000; GTE Sylvania Canada Ltd, Drummondville, Que.) to maintain whole-plant NCER above the compensation point. Plant material was watered and fertilized as required (20N–8.7P–16.6K at 200 mL/plant), grown for a period of <120 days to a cane height of 112 ± 3 cm (about 30 nodes), and was in a vegetative state before being placed in the chambers.

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Whole-plant photosynthesis. Whole-plant net CO_2 exchange was monitored in a controlled environment using a computer-controlled whole-plant gas analysis system originally designed by Dutton et al. (1988) and recently modified by Leonardos et al. (1994). The system consisted of plexiglass chambers operating in a semi-closed mode. Individual environmental variables within each chamber (irradiation, whole-plant temperature, saturated vapor pressure deficit, and CO_2 concentration) were independently controlled (Dutton et al., 1988, Leonardos et al., 1994). Light was supplied by HPS sodium lights (Lumalux LU1000; GTE Sylvania Canada Ltd), which provided a maximum photosynthetic (400 to 700 nm) photon flux density (PPF) of 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as measured by quantum sensors (LI-Q3991-4; LI-COR, Lincoln, Neb.) located at the top of the plant canopy.

Several modifications were made to the original system used by Leonardos et al. (1994) to allow for cane height and isolation and temperature control of the root zone (Fig. 1). Two air-tight plexiglass plant holding chambers measuring $155 \times 72 \times 60$ cm (height $\times$ width $\times$ depth) were built to accommodate cane height. Three root compartments were placed in each chamber and sealed to the bottom of the chamber and the upper diffuser panel (Fig. 1). The root compartments consisted of an outer 30-cm ABS plastic casing, 0.94-cm-diameter heating/cooling coil and 4- to 1.9-cm-wide ventilation tubes with urethane foam insulation between the outer casing/ventilation tubes and the coil. Coolant fluid and air lines were connected parallel with the supply going into the bottom and the return feed coming from the top of each root compartment (Fig. 1). Root-zone temperature and coolant fluid temperatures were also computer controlled and were monitored with linear thermistors (YSI 44018; Yellow Springs Industrial Co., Yellow Springs, Ohio). Changes in root-zone temperature were regulated by a relay attached to an in-line heater (model 220100; Temro Division, Bull Canada, Winnipeg, Man.) and a transducer (model T6000; Fairchild, Winston-Salem, N.C.), which was attached to a coolant supply mixing valve (Fig. 1).

Carbon dioxide concentration was monitored using an infrared gas analyzer (IRGA) (model 200; Analytical Development Co., Hoddesdon, England) while the chamber was in open mode. Carbon dioxide concentration inside the chambers could be maintained at a preset concentration by adding pure CO_2 with a mass flow controller (MKS Instruments, Nepean, Ont.) or being lowered to beneath ambient levels with a soda scrubber (Fisher Scientific, 6- to 12-mesh soda lime, Toronto, Ont.).

The chamber was kept in a semi-closed mode while estimating NCER, and CO_2 concentration was monitored with a IRGA (LI-6262; LI-COR). Pure CO_2 was injected into the chambers to compensate for depletion due to plant metabolic activity via a second mass flow controller (30 standard $cm^3 \cdot min^{-1}$, MKS Instruments), and NCER was calculated as previously described by Dutton et al. (1988).

Influence of CO_2 concentration, irradiation, and whole-plant temperature on whole-plant NCER. The influence of irradiance, CO_2 concentration, and whole-plant temperature on whole-plant NCER was studied by varying one environmental factor at a time while the other factors were set at predetermined levels. A split-split-plot experimental design comprised of four replications was used with the whole-plot factor consisting of CO_2 concentration (100, 300, 600, 1000, and 1500 $\mu L \cdot L^{-1}$), the split-plot factor being irradiance (0, 100, 200, 600, 1000, and 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ measured from the top of the canopy) and the split-split-plot factor consisting of whole-plant temperature (12, 17, 22, 27, 32 °C). Net CO_2 readings were calculated every 5 min, humidity levels were maintained at a saturated vapor-pressure deficit (SVPD) of 1.0 kPa, and the leaves were harvested and the leaf area determined using a leaf area meter (LI-3100; LI-COR.) to determine NCER on a leaf area basis.

Influence of root-zone and air temperature on whole-plant NCER. The influence of root-zone and air temperature on whole-plant NCER was studied by varying air temperature at a specified root-zone temperature while irradiance was maintained at either 0 or 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, humidity levels were maintained at a SVPD of 1.0 kPa, and CO_2 levels were maintained at 350 $\mu L \cdot L^{-1}$. A split-split-plot experimental design comprised of four replications was used with the whole-plot factor consisting of root-zone temperature (15, 20, 25, 30, 35 °C) and the split-plot factor consisting of air temperature (15, 17, 20, 25, 30, 35 °C).

Shoot NCER measurements were obtained by first isolating the root systems in a ventilated, self-contained subchamber with two plexiglass yokes and sealing the plexiglass yoke, diffuser panel, and stem with lanolin paste (Fisher Scientific, Toronto, Ont.) (Fig. 1). Each run lasted over a period of 2 d, with the plant being allowed to acclimatize at a specified root-zone temperature for at least 6 h before recording data to avoid potential alteration in photosynthesis and C export associated with mechanical stress (Pappas and Mitchell, 1985; Pickard and Minchin, 1990).

After obtaining shoot NCER measurements, the whole plant was then exposed to the same environmental variables, and root respiration

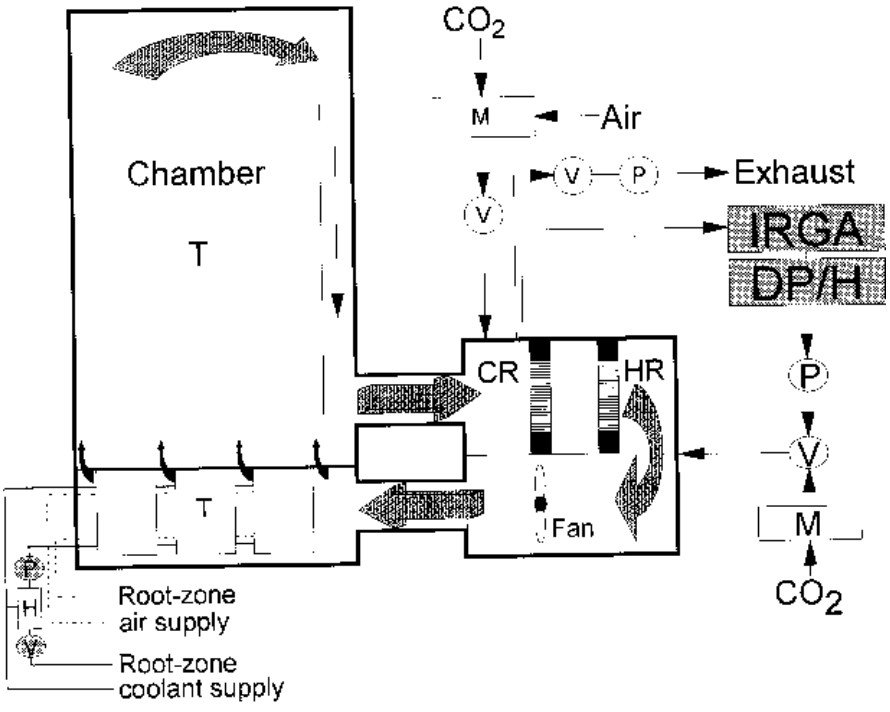

Fig. 1. Whole-plant, computer-controlled growth chamber for measuring shoot, root and whole-plant net C exchange rate (NCER). CR = coolant radiator, DP/H = digital dewpoint/humidity analyzer, H = heater, HR = heating radiator, IRGA = infra red gas analyzer, M = mixing valve, P = pump, T = thermistor, V = valve.

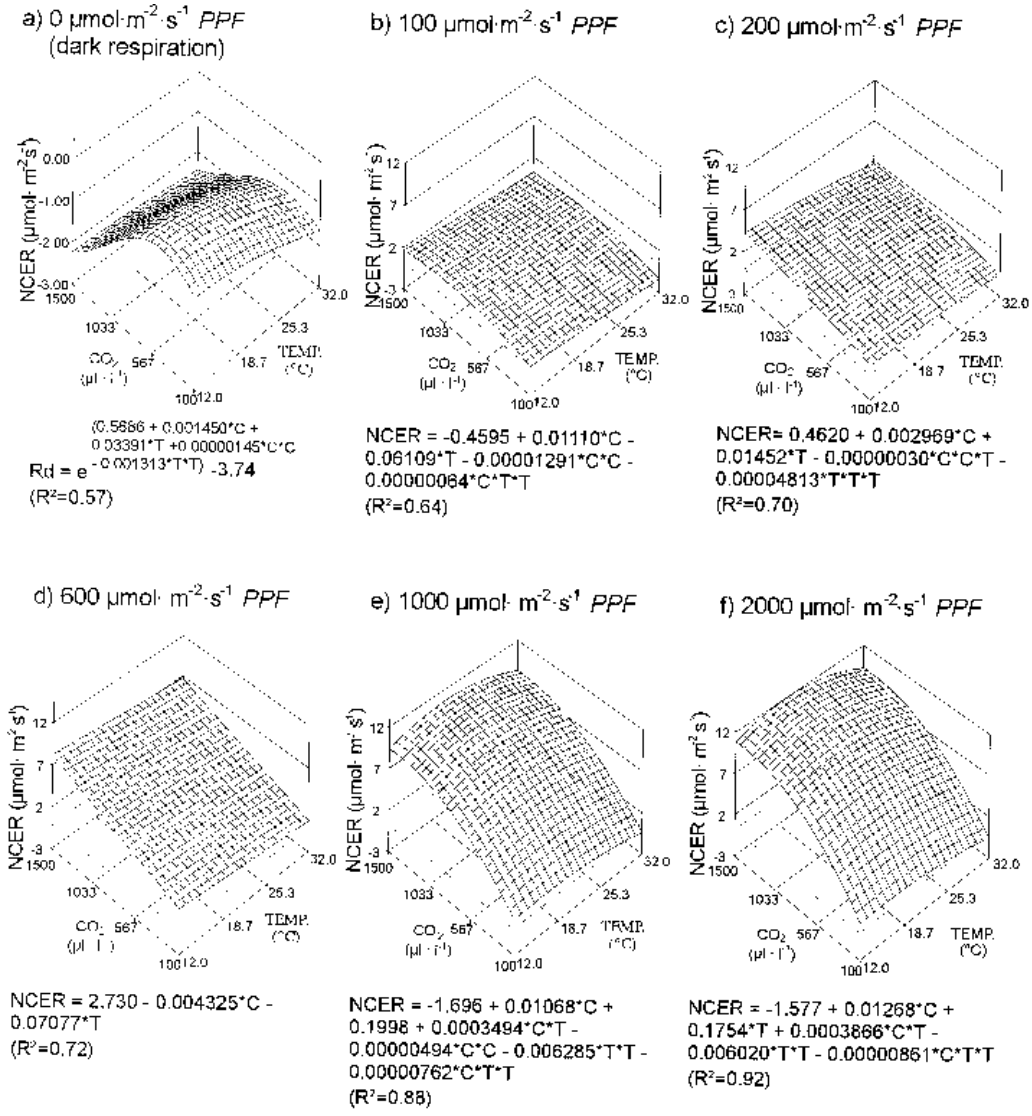

Fig. 2. Response surfaces of whole-plant net CO_2 exchange rate (NCER) (µmol CO_2/m² per s) versus CO_2 concentration (C) (µL CO_2/L) and whole-plant temperatures (T) at various photosynthetic photon flux (µmol·m^{-2}·s^{-1}). Response surfaces were generated using polynomial equations for each irradiance level.

was estimated by calculating the difference between the two measurements. NCER adjustments for media microbial activity and oxidation were estimated by exposing pots containing only media to the root-zone temperatures used in this study. Pots containing only media were set aside at the initiation of the experiment and watered as required.

Influence of whole-plant temperature and SVPD on whole-plant NCER. The influence of air temperature and SVPD on whole-plant NCER was studied while maintaining light intensity at 2000 µmol·m^{-2}·s^{-1} and CO_2 levels of 350 µL·L^{-1}. A split-plot experimental design was used with the whole-plot factor consisting of air temperature (12, 20, 28 °C) and the split-plot factor consisting of SVPD (0.25, 0.50, 0.75, 1.0, and, if possible, 1.5, 2.0, 2.5, and 3.0 kPa). Prior results indicated that there was no confounding influence of SVPD on C assimilation by gradually reducing SVPD from saturated to nonsaturated conditions (data not reported). Plants were placed into the whole-plant chambers and allowed to equilibrate at a randomly assigned air temperature and near saturated vapor pressure conditions. SVPD in the chambers was monitored and gradually reduced by condensing and removing water from the condensation radiator.

Data analysis. Analysis of variance was completed using SAS's general linear models (GLM) procedure (SAS Institute, Cary, N.C.). Models were initially fitted to a polynomial function with variables omitted if nonsignificant (i.e., $P > |T| > 0.10$). The normality of a model was than tested with SAS's univariate procedure. Regression coefficients were also obtained using SAS's GLM procedure and response surfaces generated using SAS graphics.

Results

Carbon dioxide, irradiation, and temperature NCER model. The analysis of variance of the whole-plant NCER model indicated that 87.0% ($R^2 = 0.87$) of the total experimental variation was explained by a second-order polynomial function (Table 1). Irradiance was the most important factor accounting for 57.7% of the variation in the NCER model (Table 1). Carbon dioxide concentration was the next most important factor accounting for 27.7% of the NCER model variation (Table 1). Although significant, whole-plant temperature accounted for only 2.46% of the model variation (Table 1). A CO_2 × irradiation interaction accounted for the remaining 12.1% of the model variation (Table 1).

Carbon dioxide, irradiation, and whole-plant temperature NCER response surfaces. Six response surfaces were generated to illustrate the influence of whole-plant temperature and CO_2 concentration on whole-plant NCER at varying irradiances (Fig. 2). Dark respiration increased exponentially with elevated whole-plant temperatures but always had a change in respiration rate over a 10 °C interval (Q_{10}) of <2 (Fig. 2a). A significant effect of CO_2 concentration was also observed on dark respiration with minimum rates occurring at a CO_2 concentration of 570 µL·L^{-1} and maximum rates at a CO_2 concentration of 1500 µL·L^{-1} (Fig. 2a).

The light compensation point and light saturation point were also influenced by CO_2 concentration and whole-plant temperature. Reduced irradiation levels were required to reach the light compensation point with low whole-plant temperatures and elevated CO_2 concentrations (Fig. 2 b and c). The light saturation point was also influenced by elevated CO_2 concentration and whole-plant temperature. Irradiance levels >600 µmol·m^{-2}·s^{-1} were required for light saturation (Fig. 2f), and maximum NCER values were observed at a CO_2 concentration of 1500 µL·L^{-1} and a whole-plant temperature of about 20 °C (Fig. 2g).

Root-zone and air temperature effects on net photosynthesis (shoot). Air and root-zone temperature were important factors

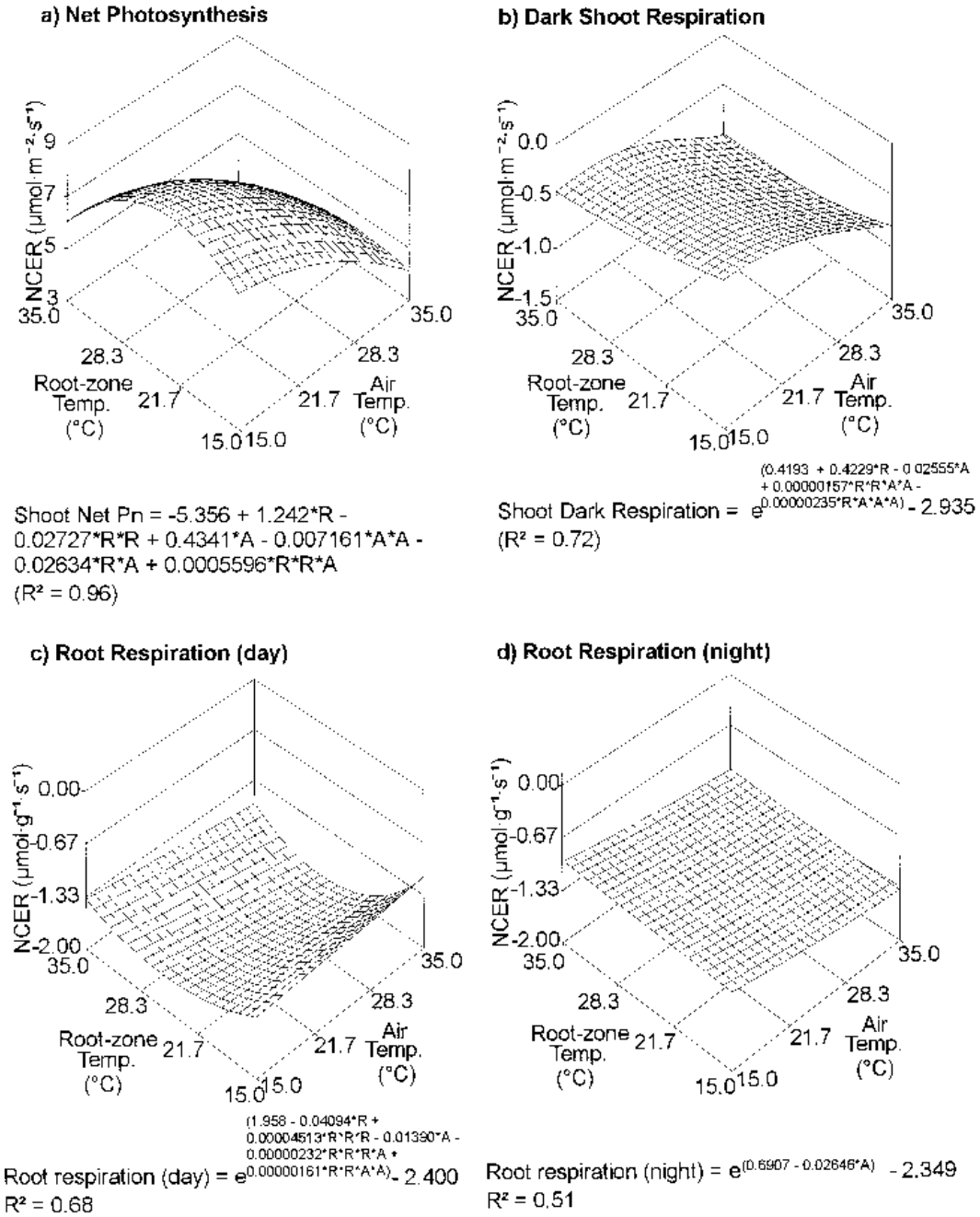

Fig. 3. Response surfaces of whole-plant net carbon exchange rate (NCER) versus root-zone temperature (R) and air temperature (A) at a photosynthetic photon flux (*PPF*) of 0 or 2000 µmol·m^{-2}·s^{-1}.

governing Pn, accounting for 74.7% and 24.1%, respectively, of the variation in the NCER model (data not shown) as illustrated in Fig. 3a. The air/root-zone Pn response surface differed significantly from the whole-plant study (Fig. 2), with maximum Pn rates occurring at a whole-plant temperature of 20 °C for the CO_2/irradiance/temperature model (Fig. 2f) and at an air/root-zone temperature of 17/25 °C for the air/root-zone model (Fig. 3a).

Root-zone and air temperature effects on shoot dark respiration. Air and root-zone temperature influenced shoot dark respiration. Root-zone temperature had a smaller effect on shoot dark respiration with a Q_{10} of <1.1 from 15 to 25 °C and also <1.1 from 25 to 35 °C (Fig. 3b). Air temperature had a greater effect on shoot dark respiration with a Q_{10} of <1.1 from 15 to 25 °C and a Q_{10} of 1.1 to 1.5 from 25 to 35 °C (Fig. 3b).

Root-zone and air temperature effects on root respiration (light and dark). Root respiration significantly differed between conditions of saturated irradiance (i.e., day) (Fig. 3c) and darkness (i.e., night) (Fig. 3d). Day root respiration rates were significantly greater than night rates with maximum rates occurring at a 25 °C root-zone temperature (Fig. 3 c and d). Day root respiration also had greater Q_{10} rates over the temperature ranges examined than night root respiration.

Influence of whole-plant temperature and SVPD (kPa) on net photosynthesis (Pn). Whole-plant temperature and SVPD influenced NCER under saturated irradiance with maximum Pn values being attained under cool temperatures (12 and 20 °C) and low saturated vapor pressure deficits (i.e., 0.25 kPa) (Fig. 4). A significant temperature × SVPD interaction occurred, with the greatest effects of a high SVPD on whole-plant Pn being observed at a low whole-plant temperature (Fig. 4).

Discussion

Whole-plant NCER model. The whole-plant NCER model provides valuable insight into physical environment effects on C assimilation. Irradiance was the most important factor in the irradiance/CO_2 concentration/whole-plant temperature NCER model, accounting for 58% of the variation in the NCER model followed by CO_2 concentration (28%) and whole-plant temperature (2.5%) (Table 1). In other reports examining the influence of irradiance, CO_2 concentration and temperature under similar physical environment conditions, irradiance, CO_2 concentration, and whole-plant temperature accounted for 58%, 23%, and 14%, respectively, of the total NCER model variation in *Alstromeria* (Leonardos et al., 1994); 82%, 10%, and 1%, respectively, in carnation (Enoch and Sacks, 1978); and 70%, 20%, and 5%, respectively, in roses (Jiao et al., 1991b). Therefore, the whole-plant temperature response of 'Heritage' raspberries was similar to that of roses (Jiao et al., 1991b) and carnation (Enoch and Sacks, 1978) but less sensitive to temperature than *Alstromeria* (Leonardos et al., 1994). However, the raspberry NCER model differed from others by being more sensitive to CO_2 concentration, especially in the presence of light with a CO_2 × irradiation interaction comprising over 12% of the total model variation (Table 1).

Temperature and CO_2 temperature effects on whole-plant dark

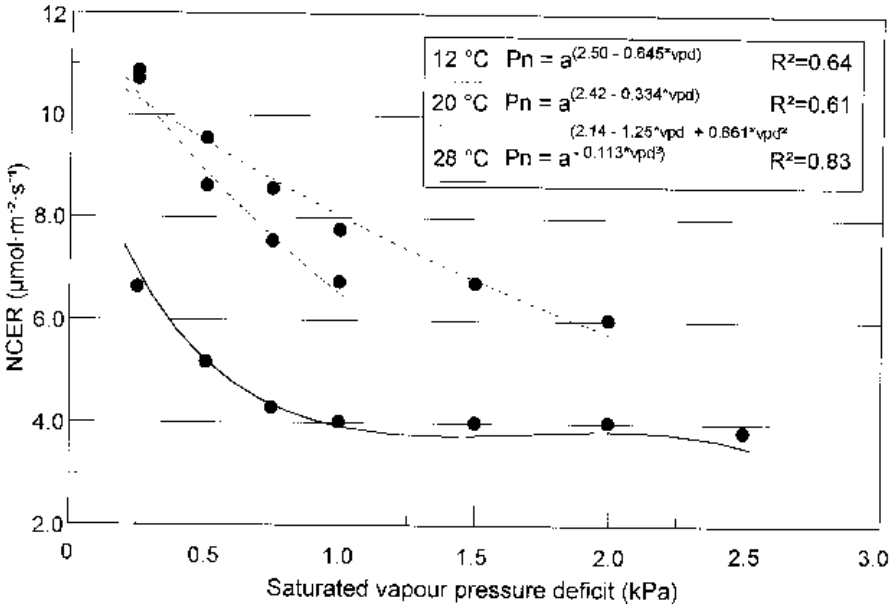

Fig. 4. Influence of whole-plant temperature and saturated vapor pressure deficit on net photosynthesis (Pn) at photosynthetic photon flux (PPF) of 2000 µmol·m^{-2}·s^{-1}.

respiration. Whole-plant dark respiration increased exponentially with temperature, but, regardless of CO_2 concentration, always had a Q_{10} of <1.5 (Fig. 2a). Although other examples of plants with low Q_{10} values exist (e.g., subterranean clover) (Fukai and Salisbury, 1977), the results obtained in this study are below the normal Q_{10} range found in most plant species of 2.0 and 2.5 (Amthor, 1989).

Whole-plant dark respiration was also affected by CO_2 concentration. Results similar to Amthor et al., (1992) were observed with minimal respiration rates occurring at a CO_2 concentration of about 600 µL·L^{-1} (Fig. 2a). This may have been due to short-term, direct, inhibitory effects on enzyme activities and possibly CO_2 diffusion rates (Amthor, 1991; Wullschleger et al., 1994). However, the reduction in whole-plant dark respiration rate did not persist with increased CO_2 concentration. Maximum whole-plant respiration rates were observed at a CO_2 concentration of 1500 µL·L^{-1} CO_2 and may have been an indirect result of increased substrate supply accumulation while the plant was rapidly assimilating C under an elevated CO_2 concentration (Fig. 2a) (Thomas and Griffen, 1994).

Carbon dioxide and temperature effects on whole-plant net photosynthesis. Whole-plant temperature results similar to those of Privé (1991) and Fernandez and Pritts (1994) were found with Pn increasing until an optimum temperature of about 20 °C (Fig. 2f). Temperatures >20 °C resulted in a decrease in Pn. This was less likely to be a result of altered CO_2 diffusion into the leaf (data not reported) or the light-driven split of H_2O (photophosphorylation) (Foyer, 1984) than to alteration of the CO_2 fixation and reduction reactions (Hall and Keys, 1983). The decrease in Pn was largely due to respiratory losses in the form of increased dark respiration (Fig. 2a) and probably also to higher photorespiration rates (Edwards et al., 1983; Gardner et al., 1985). Increased photorespiration rates occur with a lower dissolved CO_2:O_2 ratio reacting with ribulose bis-phosphate carboxylase (i.e., RuBISCO) (Edwards et al., 1983; Hall and Keys, 1983). Therefore, the flat and convex whole-plant NCER response to temperature was, in part, due to the promoting effect of temperature and the offsetting effect of total respiration over much of the temperature range (i.e., 15 to 30 °C) in which C_3 plants grow.

The photosynthetic rates were also influenced by CO_2 concentration. Results similar to those of Fernandez (1994) were found with maximum Pn rates at 1500 µL·L^{-1} (Fig. 2f). The increase in net photosynthesis with elevated CO_2 concentration was likely caused by a rapid diffusion of CO_2 molecules resulting in an accelerated rate of carboxylation by RuBISCO and also a reduction in photorespiration (Hall and Keys, 1983). Increased C assimilation under elevated CO_2 concentrations also resulted in an increase in quantum efficiency (moles of CO_2 reduced per mole of photons absorbed) with lower irradiance levels being required to reach the light compensation point (Fig. 2 b and c) and higher irradiance levels being needed to saturate photosynthesis (Fig. 2 d–f).

Root-zone and air temperature effects on net photosynthesis. Photosynthesis is one of the most temperature-sensitive factors controlling plant growth (Jones, 1992). The air and root-zone temperature study illustrated how the whole-plant CO_2/irradiance/temperature model underestimated and oversimplified the importance of whole-plant temperature. Under ambient conditions, the influence of temperature on Pn was greatly improved by separating and isolating the response of the shoot and root-zone regions (Fig. 3a). Air and root-zone temperature were important factors influencing Pn, with maximum rates occurring at an air/root-zone temperature of 17/25 °C (Fig. 3a). The results support the findings of Privé (1991) and Trinka (1991) that raspberries are sensitive to root-zone temperatures and that cool shoot (17 °C) and warm root-zone (25 °C) conditions may be optimum for growth and development.

Possible explanations of how root-zone temperature influenced C assimilation include an alteration in water uptake, modification of the endogenous plant growth regulator balance, or absorption of nutrients (Behboudian et al., 1994). Water uptake was altered in the present study with transpiration rates decreasing with supraoptimum (i.e., >25 °C) root-zone temperatures (data not shown). This may have been a result of decreased levels of cytokinin-like substances in the roots and leaves (Gur et al., 1972) and also a possible increase in the synthesis of ABA resulting in stomatal closure (Behboudian et al., 1994). Other possible reasons for the root-zone temperature influence on net Pn include the mechanistic aspects of ion absorption and translocation (Natr, 1992).

The effect of root-zone temperature on Pn also presents additional potential factors influencing the midday decline associated with the diurnal photosynthetic response curves of many woody plants (Fernandez and Pritts, 1994; Hodges, 1967; Kozlowski et al., 1991; Lakso, 1986). This midday decline has been attributed to an accumulation of sucrose in the leaves of red clover (Grub and Mächler, 1990), starch and sucrose in *Amaranthus* (Blechschmidt-schneider et al., 1989), and starch in red raspberry (J.S. Cameron, personal communication). This carbohydrate accumulation can result in a feedback inhibition in the photosynthetic cycle, possibly due to increased CO_2 diffusion resistance towards the carboxylation enzymes (Grub and Mächler, 1990; Ho, 1992), a light transmission interference within the chloroplast (Ho, 1992), or biochemical effects of sugar or starch accumulation (Blechschmidt-schneider et al., 1989; Grub and Mächler, 1990). This decline in assimilation could also occur if either air or root-zone temperatures became supraoptimum (i.e., greater then air/root-zone tempera-

Table 1. Mathematical model used to represent whole-plant CO_2 exchange rate (NCER) response of 'Heritage' raspberries. The second-order polynomial function was obtained by fitting the NCER data obtained at various CO_2 concentrations (C) (100 to 1500 $\mu L \cdot L^{-1}$), whole-plant temperatures (T) (12 to 32 °C) and irradiances (I) (0 to 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Analysis of variance indicated that the NCER model and all regression coefficients were significant at $P \leq 0.001$.

Source	df	SS	%	Coefficient
Model	7	15145.93	100	
Error	1153	2527.82		
Corrected total	1159	17163.29		R^2=0.87
Intercept	1			–3.81426032
C	1	3565.43	23.5	0.00672849
C × C	1	632.86	4.18	–0.00000345
T	1	295.55	1.95	0.19249193
T × T	1	76.74	0.507	–0.006028601
I	1	6926.48	45.7	0.007310289
I × I	1	1823.57	12.0	–0.000003166
C × I	1	1825.29	12.1	0.000003567

tures of 17/25 °C) resulting in a feed forward decline in assimilation due to mechanisms such as a low nutrient supply or an alteration in ionic and plant growth regulator relations (Schulze, 1990). More research however, is required to determine the mechanisms involved with root-zone temperature effects on Pn.

Root-zone and air temperature effects on shoot dark and root respiration. Air temperature and root-zone temperature influenced shoot dark respiration. Although significant, the influence of root temperature on shoot dark respiration was minimal with a Q_{10} of <1.2 (Fig. 3b). As with Pn, the influence of root-zone temperature on shoot dark respiration may have been a result of increased ion uptake and subsequent nutrient supply at elevated temperatures (Amthor, 1989).

Despite having shoot dark respiration rates comparable to other plant species at cool temperatures, the plant material used in this experiment differed notably from other plant species with Q_{10} values <1.1 from 15 to 25 °C and <1.5 from 25 to 35 °C (Fig. 3b). These Q_{10} values were unusually low, with most plant species having Q_{10} values of about 2 (Johnson and Thornley, 1985). The low Q_{10} values obtained in this study may have been due to the developmental stage of the plant material used. The greatest sink demand for raspberries occurs when primocane growth is rapid, root growth is increasing, and fruiting begins (Fernandez and Pritts, 1994). All plant material used was in a vegetative state and, hence, did not have any reproductive sinks present. In roses, the reproductive sink (i.e., developing bud) can account for 45% of shoot C loss (Jiao et al., 1991a), and, when physiologically mature, the raspberry aggregate fruit has the highest respiratory rates of all small fruit (Lutz and Hardenburg, 1968).

Root respiration rates differed significantly between illuminated (i.e., day) and nonilluminated (night) conditions (Fig. 3 c and d). Maximum root respiration rates were observed during the illuminated conditions and were influenced by root-zone and air temperature (Fig. 3c). Minimum root respiration rates were observed during nonilluminated conditions and were influenced only by air temperature (Fig. 3d). This diurnal root respiration rate difference illustrates the dependence of root respiration rate on recent CO_2 assimilation by the shoot and translocation to the root (Amthor, 1989; Plaut and Reinhold, 1969). The influence of shoot irradiation on root respiration, however, could also be partially mediated by plant growth regulators (Huck et al., 1962) or some other light factor (Lambers and Posthumus, 1980). One possible light factor may be reduced N, which is available to the root system during the illuminated periods when nitrate is transported to the leaves in the transpiration stream, reduced by photoprocesses, and translocated through the phloem back to the root in a reduced form (Amthor, 1989).

Whole-plant temperature and SVPD effects on net photosynthesis. Optimum conditions for photosynthesis occur when the stomata are open, a condition favored by humid air and low CO_2 partial pressures inside the leaf (Grodzinski, 1992). There was a whole-plant temperature and SVPD influence on NCER, with maximum Pn values being attained under cool temperatures (12 to 20 °C) and low SVPD (i.e., 0.25 kPa) (Fig. 4). A SVPD >0.25 kPa resulted in a decline in Pn at all temperature regimes with the greatest decline occurring at 28 °C (Fig. 4). The reduction in Pn was probably a result of nonstomatal and stomatal factors, with Pn rates decreasing at a SVPD of <0.25 kPa (Fig. 4). A decrease in transpiration rates and subsequent stomatal closure occurred only after a SVPD of about 0.5 kPa had been attained (data not shown).

The SVPD threshold of only 0.25 kPa is far below the 1.0 kPa threshold, which has been determined for greenhouse tomatoes (Romero-Aranda and Longuenesse, 1995). This very low threshold illustrates that SVPD is a very important factor regulating NCER in raspberries, especially in temperate areas such as northeastern North America, which experiences hot, summer days with high midday SVPDs. Therefore, unlike most greenhouse commodities (Romero-Aranda and Longuenesse, 1995; Grodzinski, 1992), SVPD appears to be an important factor regulating NCER in raspberries and must be further examined in future whole-plant NCER models.

Insights and Implications. Raspberries have presented persistent problems by not attaining their full yield potential, with actual harvest indexes being <5% of preharvest yield components (Braun et al., 1989; Dale, 1989; Fernandez and Pritts, 1994). This may have been partially due to a simultaneous convergence of a large sink demand in the middle of the growing season consisting of growth and development of the root, apical meristem, and reproductive structures (Fernandez and Pritts, 1994). This midseason sink demand often coincides with a reduction in net CO_2 assimilation rate and source available for export as a result of supraoptimal (i.e., >20 °C) temperatures and other possible limiting physical environment conditions (e.g., a large SVPD) (Fernandez and Pritts, 1994). Therefore, even with a large leaf : fruit ratio, raspberries exhibit characteristics of a source-limited plant with strong yield component compensation.

An improved understanding of the combined effects of irradiance, CO_2 concentration, temperature, and, to a lesser extent, SVPD on raspberry NCER was obtained in this study. Although only one developmental stage was examined in this study and the

source–sink dynamics of the primocane fruiting 'Heritage' raspberry will differ from those of summer fruiting raspberries (Fernandez and Pritts, 1994), the physical environment effects on source availability will still apply. However, the magnitude of this response may differ among cultivars with a tremendous amount of genetically based physiological variation in the subgenus *Idaeobatus*, which contains 195 species (Ourecky, 1975).

This study provides valuable insight into cultural methods to optimize yield. The whole-plant CO_2 concentration/temperature/irradiance model verified results of Privé (1991) and quantitatively illustrated the importance of optimizing light interception and distribution within the canopy. The proportion of shaded leaves must be kept to a minimum by possibly horizontally training the canopy (Palmer et al., 1987) or optimizing cane density and maintaining narrow hedgerow widths. Results from the air/root-zone study illustrated the importance of isolating and determining the optimum conditions in the shoot and root-zone with maximum assimilation rates occurring at a air/root-zone temperature of 17/25 °C. Several management options exist to moderate air temperature and include the use of floating rowcovers early in the growing season (Trinka and Pritts, 1992) and the use of micromist overhead irrigation systems. In conjunction with lowering air and foliage temperatures via latent energy, a micromist system could also maintain a high humidity level and reduce saturated vapor pressure gradients, which are both important factors influencing assimilation. Root-zone temperature could be elevated through the use of plastic films and reduced through the use of straw mulch to attain near optimum root-zone temperatures (Percival et al., 1995). These options need to be examined further to develop management strategies that are practical, effective, and cater to the optimum physical environmental thresholds for raspberry assimilation, growth and development.

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