

# Effect of Radiation and Temperature on Cranberry Photosynthesis and Characterization of Diurnal Change in Photosynthesis

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**ABSTRACT.** Cranberry [*Vaccinium macrocarpon* (Ait.)] yield has been associated with photosynthate supply. However, the impact of temperature and radiation on photosynthesis of the cranberry plant is not well understood. The objective of this experiment was to characterize the photosynthetic response to radiation and temperature in order to develop a model for estimation of cranberry photosynthetic rates. Two cranberry cultivars, 'Stevens' and 'Ben Lear', were tested for photosynthetic response at air temperatures ranging from 15 to 35 °C and radiation intensities from 200 to 1200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Depending on temperature, maximum photosynthesis ( $P_{\text{max}}$ ) was  $\approx 10$  or  $12 \mu\text{mol CO}_2/\text{m}^2/\text{s}$  (net photosynthesis) and the saturating radiation level was estimated to be 600 to 800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Cranberry quantum yield was estimated as 0.03 mol  $\text{CO}_2/\text{mol photon}$ . Both models; Blackman and the nonrectangular hyperbola with a  $\Theta$  (angle of curvature) of 0.99 were a good fit for measured photosynthetic rates under controlled environment conditions. The disparity between modeled predicted values, and observed values in the field around midday, indicates a reduction in potential photosynthetic rates in a diurnal cycle that is consistent with the phenomenon of midday depression.

Cranberry is an important economic fruit crop in the north coastal regions of the United States as well as in Wisconsin and parts of Canada. The commercial cranberry [*Vaccinium macrocarpon* (Ait.)] is indigenous to acidic soils and is found naturally in marshes and river banks of coastal regions. It grows as a slow growing, creeping vine and is along with the other important native North American fruit crop, blueberry [*Vaccinium corymbosum* (L.)], a member of the Ericaceae family.

Despite its economic importance, studies on cranberry yield prediction models have shown little success. Early yield studies (Eaton and Kyte, 1978; Eaton and MacPherson, 1978; Shawa et al., 1981) have concentrated on the relationships between yield components (e.g., flower number, fruit set, fruit weight) and yield rather than on the relationship between assimilate supply and yield. Studies with flower and fruit removal have indicated that assimilate limitation may play a role in the low fruit set (Birrenkott and Stang, 1990; Patten and Wang, 1994; Roper and Kleuh, 1994; Roper et al., 1992). In a study in which photosynthesis was manipulated through changes in  $\text{CO}_2$  concentrations, greater photosynthesis during flowering and fruit set was found to have a significant and positive impact on fruit yield (Kumudini, 2001).

Although photosynthetic supply is important to yield, very little is known about cranberry photosynthesis. The optimal abiotic environment for plant photosynthesis has been shown to be species specific (Salisbury and Ross, 1992). However, there is a paucity of current information on the effect of either temperature or radiation intensity on cranberry carbon assimilation.

Forsyth and Hall (1967) reported changes in dissolved oxygen

concentration associated with photosynthesis and respiration of submerged cranberry leaves at different temperatures. They observed that increasing temperature, increased both photosynthesis and respiration. However, the use of submerged leaves in their study limits the extrapolation of these finding for aerial leaves or the estimation of photosynthetic productivity on a leaf area basis. Bonn et al. (1969) used a custom designed system to calculate photosynthetic rates of cranberry leaves under different radiation levels. The radiation levels used were too low for extrapolation to field conditions.

The objective of this experiment was to develop a model which characterizes the photosynthetic response of the American cranberry to changes in radiation and temperature in order to calculate cranberry leaf photosynthetic response under field conditions.

## Materials and Methods

### Plant material

**CONTROLLED ENVIRONMENT EXPERIMENT.** Cuttings of the two commercial cultivars; 'Stevens' and 'Ben Lear' were grown in 5-cm containers in an outdoor, irrigated section of the Philip Marucci research facility (Chatsworth, N.J.) in 2001 and 2002. After cuttings were 2 to 3 months old, selected plants were moved to one of two controlled environment chambers (EGC model GC15, equipped with two lamp banks for high radiation capabilities, Environmental Growth Chamber, Chagrin Falls, Ohio) at the beginning of the day of the experiment. The temperature in the Growth Chambers were preset to 15, 20, 25, 30, or 35 °C at the beginning of each day and maintained at that temperature for the duration of the test. Two temperatures were tested each day of the experiment; therefore, it took 3 d to complete one replication. The temperature at the canopy level was verified using a psychrometer (Psychro-Dyne, model 595, Belfort Instruments Co., Baltimore, Md.) each time the radiation level was changed within the growth chamber. The plants were first placed in the dark at the preset temperature and maintained for at least 1 h to

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allow for acclimation. The radiation levels tested in the growth chamber were 0, 200, 400, 600, 800, and 1200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in random order within the chamber. Plants were allowed to acclimate at each radiation intensity for at least 30 min before measurement. Gas exchange measurements were made only after the plants were acclimated for at least 1 h at a specific temperature and after 30 min at a specific radiation level.

**DIURNAL GAS-EXCHANGE EXPERIMENT.** Plants were selected from 2 to 3 month old cuttings grown in pots under irrigation in a section of the Philip Marucci research facility (Chatsworth, N.J.) in 2001 and 2002 (as in plant material for the controlled environment experiment). These plants were left under ambient (field) conditions to measure diurnal changes in gas exchange. Gas exchange measurements were taken on these plants at one hour intervals beginning at 0900 HR EST and ending at 1600 HR EST on 2 Aug. 2001, 5 Aug. 2001, 1 July 2002, and 2 July 2002. Bright, sunny days with clear sky conditions were selected. While diurnal gas exchange measurements were made, the plants were irrigated every 1 to 2 h.

### Gas-exchange measurements

**CONTROLLED ENVIRONMENT EXPERIMENT.** Only fully expanded leaves borne on nonherbaceous stem (runner) from the current year were selected. Each plant was acclimated for 1 h in the dark before the first measurement and kept well watered. Gas exchange measurements were made with an external quantum sensor (LI-6400; LI-COR Inc., Lincoln, Nebr.) with fluorometer chamber (LI-6400-40). A thin wire grid, which minimized shading was custom made to maintain cranberry leaves stable within the chamber. The chamber was sufficient to fit two leaves ( $\approx 0.5 \text{ cm}^2$  leaf area) at each reading. The flow rate was set at 150  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and the chamber temperature was set at the temperature setting of the growth chamber (i.e., either 15, 20, 25, 30 or 35 °C). The  $\text{CO}_2$  concentration was set at 400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  on the reference side. The fluorometer light source was used to simulate the radiation level within the growth chamber (i.e., either 0, 200, 400, 600, 800, and 1200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). After completion of gas exchange measurements, the leaf area was measured by scanning the leaves alongside a coin of known area and then using Optimas 6.0 (MediaCybernetics Co. Carlsbad, Calif.) image analysis software to quantify leaf area. Quantum yield ( $\phi$ ) was calculated from the linear portion of the light response curve (0 to 200  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ).

**DIURNAL GAS-EXCHANGE EXPERIMENT.** The leaf material was selected on the same basis as for the controlled environment experiment. A maximum of two leaves fit in the fluorometer chamber at each measurement. Three plants of each cultivar were selected in each of the four replications. Gas-exchange measurements were made with the external quantum sensor every hour beginning at 0900 HR and ending at 1600 HR EST. The flow rate was set at 150  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and the  $\text{CO}_2$  concentration was set at 400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  set at the reference side. A thermometer guarded from direct solar radiation was used to monitor ambient temperature and the external quantum sensor was used to measure ambient radiation levels. At the beginning of each hourly measurement, the chamber temperature was set to simulate ambient air temperature within the chamber and the fluorometer light source was used to simulate ambient solar radiation intensity within the chamber.

### Light-response model

A number of models have been proposed to fit the photosynthetic light response of various plant species. In the current experi-

ment four models were tested for fit to cranberry photosynthetic light response: Negative exponential which has no biological significance Eq. [1], the rectangular hyperbola (Maskell, 1928) Eq. [2], Blackman response curve (Blackman, 1905) Eq. [3], and the nonrectangular hyperbola (Rabinowitch, 1951) Eq. [4] where  $x = (I_A \times \phi) / P_{\text{max}}$ . The symbol  $I_A$  represents absorbed radiation (assumed to be 85% of incident photosynthetically active radiation ( $PAR$ )). The symbol  $\phi$  represents quantum yield. The symbol  $P_{\text{max}}$  represents the maximum photosynthetic rate achieved at a particular temperature. In Eq. [4], the symbol  $\Theta$  represents the curvature of the line and the closer it is to 1 the more it approximates Eq. [3].

$$\text{Photosynthesis} = P_{\text{max}} \cdot (1 - \exp(-x)) \quad [1]$$

$$\text{Photosynthesis} = P_{\text{max}} \cdot x / (1 + x) \quad [2]$$

$$\text{Photosynthesis} = P_{\text{max}} \cdot x \text{ when } x \leq 1, \text{ else } P_n = P_{\text{max}} \quad [3]$$

$$\text{Photosynthesis} = P_{\text{max}} \cdot (1 + x - (1 + x^2) - 4.x..)/2\Theta \quad [4]$$

### Statistical analysis

**CONTROLLED ENVIRONMENT EXPERIMENT.** The experimental design was a randomized complete block design. There were two sub sample plants for each cultivar, two cultivars and two replications in time for a total of four plants at each of the radiation and temperature levels. The data were analyzed using the SAS GLM procedure (ver. 8.0, SAS Institute Inc., Cary, N.C.).

**DIURNAL GAS EXCHANGE EXPERIMENT.** The experimental design was a randomized complete block design with replication in time. There were three plants per cultivar, two cultivars in each of four replications. The data was analyzed using the SAS GLM procedure. The regression relationship also used the SAS GLM procedure using photosynthetic rates as the dependent variable and days as a class variable. Sequentially greater polynomials of stomatal conductance ( $g_s$ ), were tested until the highest significant polynomial was determined.

## Results and Discussion

**CONTROLLED ENVIRONMENT EXPERIMENT.** The three way interaction of  $C \times T \times PAR$  was not significant (Table 1). There was a significant temperature and  $PAR$  interaction effect for all variables measured. Leaf photosynthetic rates increased with temperature and radiation intensity under controlled environment conditions. The maximum photosynthetic rate ( $P_{\text{max}}$ ) at the lower temperatures (15 to 25 °C), was  $\approx 12 \mu\text{mol CO}_2/\text{m}^2/\text{s}$  and was reached at a saturating photosynthetic photon flux density ( $PPFD$ ) level of 800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , while at high temperatures ( $\geq 30$  °C),  $P_{\text{max}}$  was around 14  $\mu\text{mol CO}_2/\text{m}^2/\text{s}$  and was reached at the saturating  $PPFD$  level of 600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Fig. 1). Similar saturating  $PPFD$  values

Table 1. Analysis of variance for controlled environment experiment, statistical significance of sources of variation for photosynthesis and stomatal conductance.

Source	Photosynthesis	Stomatal conductance	Leaf internal $\text{CO}_2$
Cultivar (C)	NS	NS	NS
Temperature (T)	NS	*	*
$C \times T$	NS	NS	NS
Radiation ( $PAR$ )	***	***	***
$T \times PAR$	*	**	**
$C \times PAR$	*	NS	*
$C \times T \times PAR$	NS	NS	NS

NS,\*,\*\*,\*\*\*Nonsignificant or significant at  $P \leq 0.05, 0.01$  or  $0.001$ , respectively.

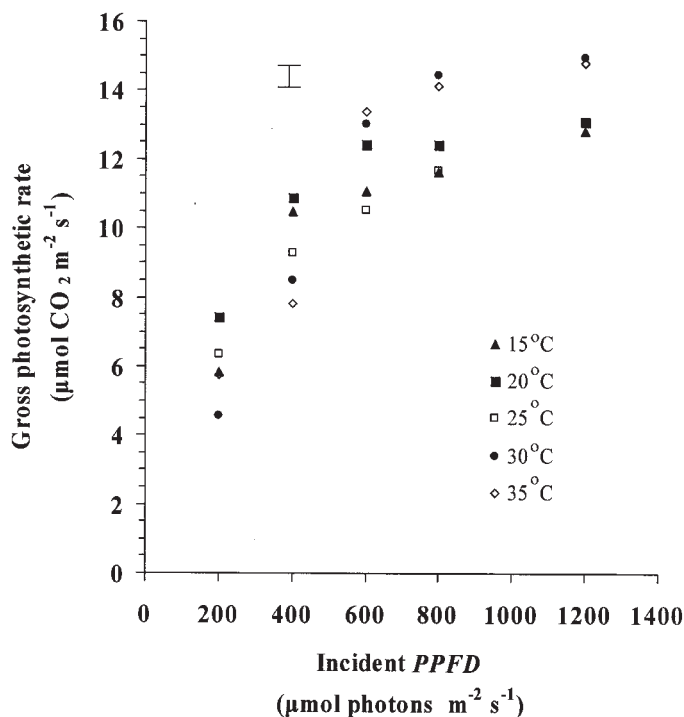


Fig. 1. Gross photosynthetic rates of American cranberry, 'Stevens' and 'Ben Lear' at each of the light levels, and temperature settings tested. The bar represents standard error of the means;  $n = 4$ .

were reported in related species as well as in a previous report on the cranberry cultivar Searles. The saturating PPF level of rabbiteye blueberry (*Vaccinium Ashei* Reade) was reported as  $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , the highbush blueberry was reported to be between  $600$  to  $800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and that of the cultivar Searles was  $700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Davies and Flore, 1986; Moon, et al., 1987; Stang and Struckmeyer, 1985).

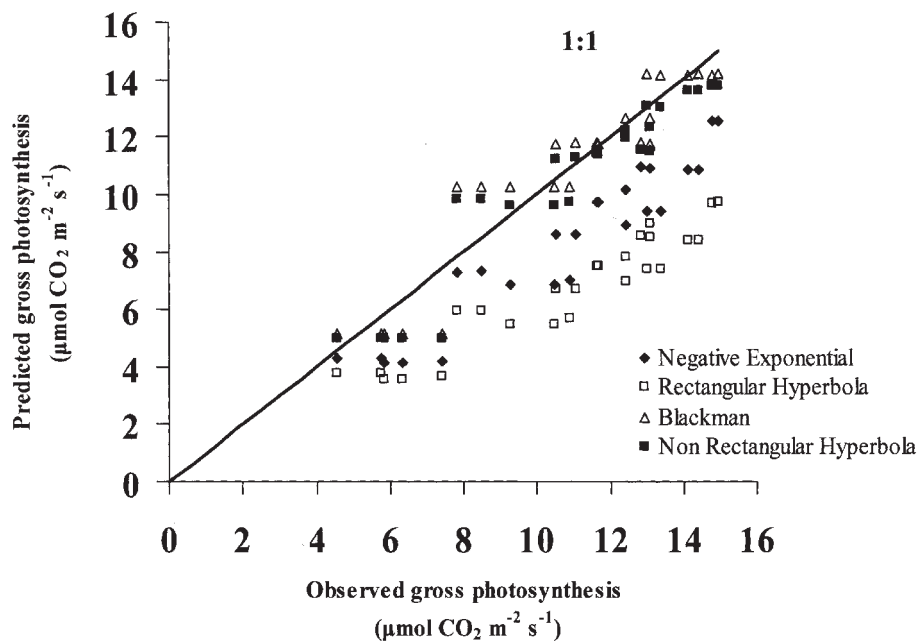
The calculated quantum yield was not significantly different for the temperatures tested and did not vary with cultivar (data not shown). Therefore, the model mean for quantum yield was used ( $0.03 \text{ mol CO}_2/\text{mol photon}$ ) for the calculations of the photosynthetic response models. The low photosynthetic rates under low radiation and the small differences due to temperature may have resulted in a lack of a discernible temperature effect on quantum yield. The  $\phi$  value obtained was lower than that estimated from the data in the study by Bonn et al. (1969). The current estimate corroborates well with the report of  $0.03 \text{ mol CO}_2/\text{mol photon}$  by Davies and Flore (1986) for the related rabbiteye blueberry. Singaas et al. (2001) suggested that  $\phi$  values should be consistent and high across all plant species, and questioned low  $\phi$  values (as in Davies and Flore, 1986) as possibly due to errors in estimation of the linear portion of the light response curve and/or insufficient time for intercellular  $\text{CO}_2$  levels to stabilize. Both in the current study and that conducted by Davies and Flore (1986), the plants were acclimated for at least 30 min. Further, in the current study the linear portion of the light response curve was measured at each temperature. The value from a closely related

species (Davies and Flore, 1986) and our measurement of quantum yield to reduce measurement errors would suggest that the value of  $0.03 \text{ mol CO}_2/\text{mol photon}$  for the  $\phi$  of cranberry is reliable.

The estimated  $\phi$ , and the  $P_{\text{max}}$  values were utilized in deriving the various mathematical models for predicting photosynthetic rates. The nonrectangular hyperbola model had the highest  $R^2$  value and the Blackman response was closest to a 1:1 relationship, although both models were close to a 1:1 relationship between predicted and observed photosynthetic rates. A nonrectangular hyperbola is the same as a Blackman response curve when  $\Theta = 1$ . Both the Blackman response equation and the nonrectangular hyperbola (with  $\Theta = 0.99$ ) fit the observed data well (Fig. 2).

**DIURNAL GAS-EXCHANGE EXPERIMENT.** Field net photosynthetic rates reported for midday are close to values reported by Hagi-dimitriou and Roper (1995) and modeled by Bland et al. (1996). However, early morning measurements are higher than previously reported (Fig. 3a and b). A distinct diurnal trend in leaf photosynthetic rates was observed. Photosynthetic rates tend to be higher in the early morning followed by a decline in photosynthetic rates around midday (without a decline in ambient temperature or radiation) and then a recovery stage. The predicted (based on the nonrectangular hyperbola model using ambient radiation and temperature data) versus observed data for field photosynthetic measurements were consistent at the start of the day, but then diverged at midday, yet appeared to come closer to predicted values later in the day (Fig. 3a and b). Predicted values indicate the potential for photosynthesis, therefore the decline in observed values around midday suggests that factors distinct to midday reduced potential photosynthetic rates. The observed values form a diurnal pattern of photosynthetic rates which is consistent with a phenomenon known as midday depression. Midday depression has been reported to occur in a number of horticultural crops (Correia et al., 1990; Demming-Adams et al., 1989; Küppers

Fig. 2. Four models: Negative exponential  $Y = 0.83x + 0.50$   $R^2 = 0.89$ , rectangular hyperbola  $Y = 0.59 + 0.26$   $R^2 = 0.88$ , nonrectangular hyperbola  $Y = 0.94 + 0.24$   $R^2 = 0.91$ , Blackman (1905) response  $Y = 0.98x + 0.222$   $R^2 = 0.89$  of predicted gross photosynthetic rates versus observed photosynthetic rates (data from controlled environment experiment) of american cranberry 'Stevens' and 'Ben Lear'. The solid line represents the ideal 1:1 relationship between modeled and observed values.



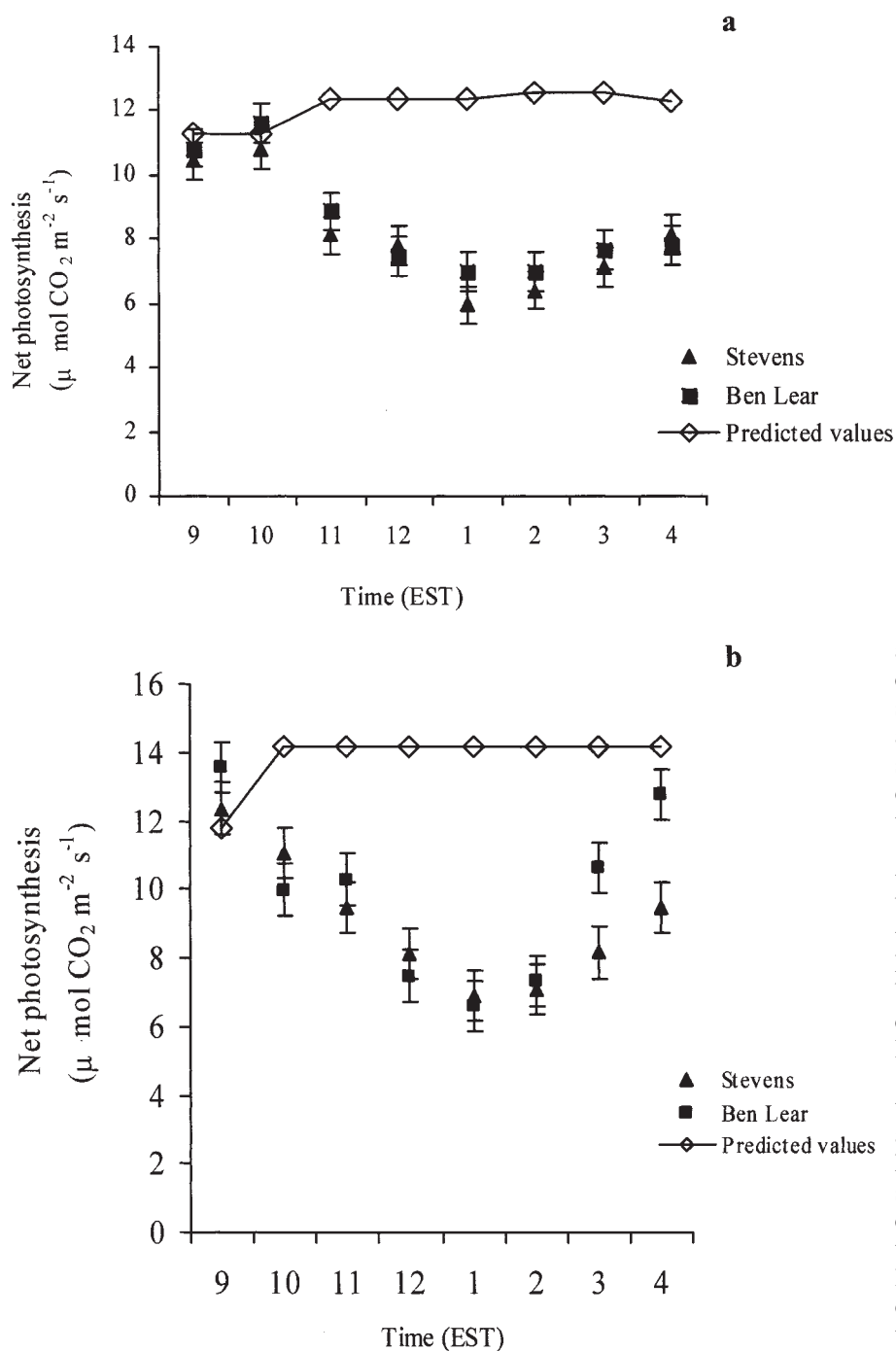


Fig. 3. Diurnal change in predicted values (from a nonrectangular hyperbola model with  $\phi = 0.99$ ) based on ambient air temperature and radiation and observed net photosynthetic rates for cultivars Stevens and Ben Lear on two representative days from each year (a) 2 Aug. 2001 and (b) 1 July 2002. Bars represent standard errors of the mean;  $n = 3$ .

et al., 1986; Tenhunen et al., 1984) but has not been previously reported in cranberry. Midday depression is observed in field grown plants and is characterized by a decline in photosynthetic rates around solar noon. Studies on midday depression have suggested that the decline in photosynthetic rates and its recovery depends on the environmental conditions and can therefore vary daily (Küppers et al., 1986; Tenhunen et al., 1984). Consistent with this suggestion, the data from the current study also indicated a significant day effect (Table 2). Extrapolation of the current

study to a cranberry canopy must take into account the microclimatic conditions within a cranberry canopy. Consequently, relevance to a cranberry canopy is predicated on further studies at the canopy level. In a study on photosynthetic rates of individual cranberry uprights, a vertical stem with several leaves arranged in a whorl, Hagedimitriou and Roper (1995) noted that photosynthetic rates peaked 2 to 3 h following sunrise. These observations lend support for the idea that midday depression may also be apparent at the upright, and possibly, canopy level.

Midday depression has been thought to be the consequence of either stomatal limitation, biochemical limitations from photo-inhibition, or enzymes involved in the dark reactions of photosynthesis. Correia et al. (1990) and Demming-Adams et al. (1989) have suggested that increasing water stress and vapor pressure deficit in mid afternoon, feed-back inhibition from carbohydrate accumulation, or decreased carboxylation efficiency may contribute to midday depression. These factors can directly or indirectly affect  $g_s$ . Further research is required to clearly state a cause and effect relationship between cranberry stomatal conductance and photosynthetic decline during midday depression.

A second-order polynomial best described the relationship (model  $R^2 = 0.64$ ,  $P \leq 0.0001$ ) between stomatal conductance and photosynthetic rate (Fig. 4a and b). Earlier research has reported that  $g_s$  of the American cranberry is either limited or responds slowly to environmental conditions (Croft et al., 1993; Hattendorf and Davenport, 1996; Sawyer, 1932). Sawyer (1932) noted that stomates of the cultivated cranberry do not open fully but are more slit-like and although they occur in high density, they only occur on the abaxial surface of the leaves. Faraq and Palta (1989) examined cranberry stomates and determined that they are sunken and covered with a thick layer of epicuticular wax. These and other characteristics led researchers to consider that this species' stomatal conductance resembles that of xeromorphic plants (Croft et al., 1993; Faraq and Palta, 1989; Hattendorf and Davenport, 1996). Consequently, cranberry stomatal limitations may likely be associated with the observed midday depression.

Consistent with the report by Hattendorf and Davenport (1996) and Bland et al. (1996), the  $g_s$  reported here were not as low as that cited by Croft et al. (1993). The current data reported midday  $g_s$  values of between 0.06 and 0.30  $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  depending on the day and the cultivar. Hattendorf and Davenport (1996) did not routinely irrigate their experimental material but also reported similar values with a mean  $g_s$  value of  $\approx 0.04 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (converted value using a temperature of 25 °C) for their stand of a mixture of 'Stevens' and 'Crowley'. In the current study, the plants were well irrigated during the course of the experiment, possibly explaining the higher values. Davies and Flore (1986)

Table 2. Analysis of variance for field experiment, statistical significance of sources of variation for photosynthesis and stomatal conductance.

Source	Photosynthesis	Stomatal conductance
Day (D)	***	***
Cultivar	NS	NS
C × D	NS	NS
Hour (H)	**	NS
C × H	NS	NS
D × H	NS	NS
D × C × H	*	***

ns,\*,\*\*,\*\*\*Nonsignificant or significant at  $P \leq 0.05$ , 0.01 or 0.001, respectively.

reported midday  $g_s$  values of between 0.08 and 0.20  $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the related rabbiteye blueberry. The current data on  $g_s$  appears to be comparable to other reports. There was a positive linear relationship between  $g_s$  and photosynthetic rate when  $g_s$  was below  $\approx 0.15 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . The optimal  $g_s$  for photosynthesis was  $\approx 0.2 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Fig. 4a and b).

DeMoranville et al. (1996) found that although solar radiation accounted for some of the variability in cranberry fruit mass accumulation, most of the variability (>80%) was due to moderate temperatures between 16 and 30 °C. Their results have an interest-

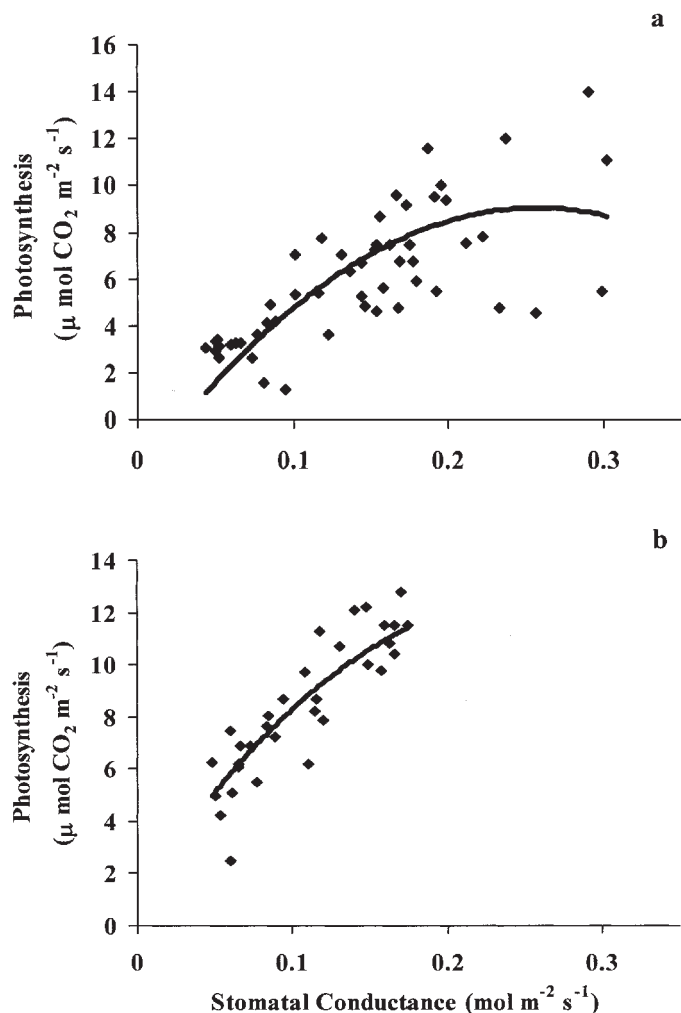


Fig. 4 Relationship between stomatal conductance and photosynthetic rate of American cranberry 'Stevens' and 'Ben Lear' measured under field conditions on two representative days: a) 2 Aug. 2001,  $Y = 89.6x + (-174.3x^2) - 2.45$ , and b) 2 July 2002  $Y = 89.6x + (-174.3x^2) + 1.08$ ;  $n = 3$ .

ing perspective if the impact of solar radiation and temperature on cranberry fruit mass accumulation as acting through its impact on photosynthesis is considered. Low saturating light levels for cranberry photosynthesis (600 to 800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) means that even under partially cloudy conditions, saturating light levels may be obtained. Furthermore, if midday depression is due to duration of high light intensity, the relationship between light intensity and assimilation would be complex resulting in it accounting for little of the variability in fruit mass accumulation while temperature played a more important role. High temperature and radiation stress may also impact plant water status which again would likely result in stomatal closure and thereby reduce photosynthesis. If the impact of temperature and radiation conditions on cranberry fruit mass accumulation, as reported by DeMoranville et al. (1996), was the result of its affect on photosynthesis, then understanding the impact of environmental factors on photosynthesis, especially those factors controlling midday depression will be important in increasing cranberry yield.

## Conclusion

Saturating light level for both cranberry cultivars tested were in the region of 600 to 800  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , depending on temperature. The  $\phi$  of cranberry was estimated to be 0.03  $\text{mol CO}_2/\text{mol photon}$ , close to values reported for related species. Both the nonrectangular hyperbola and the Blackman response models fit the observed controlled environment data. In the field, the predicted values from the nonrectangular hyperbola model, based on ambient radiation and temperature, fit only the early morning data. By midday, the observed data were consistently lower than the predicted values, but rose again by late afternoon to levels closer to the predicted. Based on this response, it is concluded that cranberry leaves experience midday depression. Values for well watered cranberry leaf stomatal conductance were found to range from 0.06 and 0.30  $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , which are close to some previously reported values.

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