Leaf Gas Exchange Characteristics of Red Raspberry Germplasm in a Hot Environment

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Abstract. Net CO_2 assimilation (A), evapotranspiration (ET), and stomatal conductance (g_s) were determined in two experiments for 14 and 18 raspberry (*Rubus* sp.) genotypes, respectively, grown in 4-L containers and exposed to 35 °C daytime temperatures 2 weeks and 4 weeks after placement in growth chambers. Measurements were taken on two successive leaves on the same primocane between the third and seventh node (≈75% to 85% of full leaf expansion). In Expt. 1, selections from Louisiana exhibited higher A (3.10–5.73 μmol·m^{-2}·s^{-1}) than those from Oregon (0.50–2.65 μmol·m^{-2}·s^{-1}). In Expt. 2, the genotype × time interactions were nonsignificant, and time of measurement did not affect A or ET ($P \leq 0.05$). Assimilation ranged from 2.08 to 6.84 μmol·m^{-2}·s^{-1} and varied greatly among genotypes, indicating that diverse A levels exist at high temperatures in raspberry germplasm. NC 296, a selection of *R. coreanus* Miq. from China, and 'Dormanred', a southern-adapted raspberry cultivar with *R. parvifolius* Hemsl. as a parent, had the highest A rates. Evapotranspiration and g_s did not differ among genotypes. Average g_s for all genotypes declined from 234 mmol·m^{-2}·s^{-1} in week 2 to 157 mmol·m^{-2}·s^{-1} in week 4. Our findings, coupled with plant performance under hot conditions, can be used to identify potential parental raspberry germplasm for breeding southern-adapted cultivars.

Interest in red raspberry (*Rubus idaeus* L.) in the southern states has increased recently (Clark and Rom, 1997), but the region suffers from a lack of southern-adapted cultivars with commercial quality (Moore, 1997). Currently available cultivars developed outside of the South are not well-adapted for several reasons, including high light intensities and hot summer temperatures (Moore, 1997). Southern Asiatic countries traditionally have been the source of *Rubus* plant material with tolerance to heat and drought. North American researchers have been the leaders in introducing wild species to the commercial genetic base for incorporation of heat tolerance (Jennings et al., 1991). Unfortunately, commitment to the development of heat-tolerant, commercial-quality cultivars has not been sustained. Considerable efforts (Hull, 1969; Overcash, 1972; Williams, 1950) have proved only mildly successful, but these researchers have generated many selections from their breeding programs. Yet, no efficient procedure exists to identify those selections that have inherited heat tolerance or to determine which species have the most to offer a breeding program. Gas exchange characteristics of *Rubus* germplasm may indicate adaptation to hot conditions.

Donnelly and Vidaver (1984) reported results on a raspberry selection (BC 72-1-7, a cross of 'Haida' x 'Canby', later released as 'Algonquin') with the maximum rate of A between 6.3 and 9.5 μmol·m^{-2}·s^{-1}. No studies have evaluated genotype response at high temperatures in the South. A few studies have focused on established cultivars in general, such as 'Amity', 'Autumn Bliss', 'Heritage', 'Meeker', and 'Titan' (Cameron and Hartley, 1989; Fernandez and Pritts, 1994; Goulart, 1989; Hunt et al., 1991; Klauer et al., 1992; Percival et al., 1996; Privé et al., 1997). Cameron and Hartley (1989) examined gas exchange characteristics of 'Amity' leaves after partial defoliation and discovered that A, g_s, and transpiration increased after one-third or two-thirds of the total leaf area on one leaf were removed. Gas exchange rates reported for whole leaves in this study were 8.9 μmol·m^{-2}·s^{-1} (A), 99.3 mmol·m^{-2}·s^{-1} (g_s), and 2.6 mmol·m^{-2}·s^{-1} (transpiration). In 'Titan' and 'Heritage', Goulart (1989) found that A and g_s increased as soil water content increased from deficit to high levels. Hunt et al. (1991) determined that maximum assimilation levels were achieved at 1000 to 1200 μmol·m^{-2}·s^{-1} photosynthetically active radiation (*PAR*) when 'Titan' leaflets reached 75% to 85% of full expansion. The highest levels of CO_2 assimilation were reached from 0700 to 1000 HR in a study conducted by Klauer et al. (1992) on 'Meeker'.

Fernandez and Pritts (1994), Percival et al. (1996), and Privé et al. (1997) examined gas exchange response to temperature, but response to high temperature was not the major focus of these studies. Fernandez and Pritts (1994) found that gas exchange of primocane leaves on 'Titan' declined as temperature increased from 15 to 40 °C. Assimilation rate at 20 °C was ≈8 μmol·m^{-2}·s^{-1}, whereas at 35 °C it declined to ≈4 μmol·m^{-2}·s^{-1}. Similar results were reported by Percival et al. (1996) for whole-plant A of 'Heritage'. However, Privé et al. (1997) stated that high A and g_s rates were obtained at both warm (≈30 °C) and cool (≈15 °C) temperatures. They also reported a wide range in g_s throughout the season; the mean for leaves in the absence of a subtending fruiting or flowering lateral was 159 ± 110 mmol·m^{-2}·s^{-1}.

The objectives of this study were to examine gas exchange characteristics among a broad range of genotypes that had not been studied previously and to determine if any expressed qualities contributed to heat tolerance.

Materials and Methods

Fourteen diverse genotypes from varying origins were used in Expt. 1 (Table 1), and 18 genotypes were used in Expt. 2 (Table 2). Many of these genotypes are native to regions where summer conditions are hot and humid, as in the upper South. These were obtained from the U.S. Dept. of Agriculture, Agricultural Research Service (USDA, ARS) National Clonal Germplasm Repository and the USDA, ARS, Northwest Center for Small Fruit Research, both at Corvallis, Ore., from North Carolina State Univ., and from Glen Melcher, a private *Rubus* breeder in Louisiana. Plants were potted in 4-L pots in a Universal Mix media (Strong-Lite Hort. Prod., Pine Bluff, Ark.) containing a controlled-release fertilizer (Osmocote 18N–2.6P–9.9K, 14 g/pot) and grown in the greenhouse for several months until the experiment was initiated. Plants were placed in three 2.13-m^2 Conviron 3244 growth chambers (Winnipeg, Man., Canada) on 3 July 1998 for Expt. 1 and 22 May 1998 for Expt. 2. Growth chamber temperatures were 35 °C day (16-h photoperiod) and 25 °C night to approximate conditions for the southern United States.

Measurements were taken 2 and 4 weeks after placement in the growth chamber with a CIRAS-1 (PP-Systems, Hitchens, Herts, U.K.) portable infrared gas analyzer (IRGA) and Parkinson leaf cuvette (2.5 cm^2) on two leaves per primocane. Leaves were at 75% to 85% of full expansion at the time of measurement. The air flow rate within the cuvette was set at 200 mL·min^{-1} with 350 mL·L^{-1} CO_2 and 50% of ambient water vapor. Leaf and chamber temperature were maintained by a thermoconductive peltier plate, set at 35 °C, and measured using an infrared temperature sensor. *PAR* was maintained between 1000–1500 μmol·m^{-2}·s^{-1} during measurements, the reported light saturation level for *Rubus* (Hunt et al., 1991; Rom and Clark, 1991). Stability in measurement was reached between 1 and 2 min. Plants were watered as needed, and no water stress was experienced prior to or during

enclosure in the growth chamber. Measurements were taken on the same day of the week between 0800 and 1200 HR.

Expt. 1 consisted of one growth chamber containing 14 entries with one plant only of each entry. On each date data from two separate leaf measurements were averaged for both experiments. Analysis of variance was performed using the LSMEANS statement in the MIXED procedure of SAS (Cary, N.C.) for Expt. 2. Proc CORR was used to determine correlations. The experimental design was a randomized incomplete block, with two or three replications (plants) of each of 18 entries. Each growth chamber was considered a block.

Results and Discussion

For Expt. 1, means from one plant averaged over two times of measurement were generated for A, ET, and g_s. This provided insight as to the photosynthetic capabilities of previously untested selections and species that could not be included in Expt. 2 because of a shortage of plant material. ORUS selections generally placed low, whereas Louisiana genotypes were among the highest performers, for all dependent variables (Table 1). *Rubus innominatus* Moore exhibited surprisingly high ET and g_s rates (data not shown) in relation to its low rate of A. 'Dormanred' had a lower A rate than in Expt. 2, perhaps because of later

measurement dates or variation among plants used. Melcher 92-3-34 and 96-2-41 are offspring from crosses that include at least one red raspberry parent with heat tolerance. Gas exchange measurements for these genotypes may reflect heat tolerance inherited from the parental material (Hancock et al., 1992). Melcher 93-5-41 is a cross between OR 1030, an Oregon-developed red raspberry selection of uncertain origin (F.J. Lawrence, personal comm.), and *R. occidentalis* L., the North American black raspberry. It displayed lower rates for all variables than did the other Melcher genotypes. This result is consistent with the data for the ORUS selections in both studies.

Interactions between genotype and time of measurement were nonsignificant in Expt. 2. Evapotranspiration and g_s did not differ among genotypes (data not shown). Average stomatal conductance declined from 234 to 157 mmol·m^{-2}·s^{-1} from the second to the fourth week. Assimilation varied from a high of 6.84 for NC 296 to a low of 2.08 μmol·m^{-2}·s^{-1} for ORUS 1728-1 (Table 2). NC 296, 'Dormanred', 'Mandarin', and 'Jingu Jeugal' (S. Korean breeding program) displayed the highest A rates. The ORUS series, all siblings, differed both within and among selections, with A varying from 2.08 (ORUS 1728-1) to 4.59 μmol·m^{-2}·s^{-1} (ORUS 1728-5). Even though all of the ORUS series were selected in Oregon and subjected to identical experimental conditions in this study, the variation expressed was significant.

Fernandez and Pritts (1994) found that primocanes of 3-year-old potted 'Titan' red raspberry plants had A rates of ≈4 μmol·m^{-2}·s^{-1} at 35 °C. Percival et al. (1996) found similar results with whole-plant net CO_2 exchange of 'Heritage' red raspberry. The results of our study are similar, as 4 μmol·m^{-2}·s^{-1} was near the median A rate for the 18 genotypes. However, the wide variation among the genotypes is noteworthy. Keep (1972) noted that wild raspberry populations vary widely in several physiological and morphological traits, such as leafing and flowering times, leaf shape, and spine density. Our findings indicate that variation within *Rubus* species in gas exchange characteristics is also significant.

Several genotypes in the replicated study were hybrids of *R. parvifolius*, but not the same clones. *Rubus parvifolius* is reported to be adaptable to high temperature (Moore, 1997). 'Dormanred', a *R. parvifolius* derivative, is adapted to the southern United States, and in this study exhibited a high A rate, especially in comparison with ORUS 1728-1. This high A rate may contribute to the adaptation of 'Dormanred' to high temperature. The wide range in A among the 10 *R. parvifolius*-derived genotypes in our study may reflect variation in adaptation of *R. parvifolius* genotypes to high temperature or in their specific combining abilities in hybridizations with other genotypes. It could also reflect the fact that the parents of the ORUS series were selected

Table 1. Genotype, parentage, location where genotype was selected, and assimilation rates (A) of raspberry germplasm at 35 °C in Expt. 1.

Parentage	Location	Genotype	A
Bababerry x Dormanred	Louisiana	Melcher 92-3-34	5.73
Mandarin x Melcher 94-3-206	Louisiana	Melcher 96-2-41	4.60
Dorsett x *R. parvifolius*	Mississippi	Dormanred	3.64
OR 1030 x *R. occidentalis*	Louisiana	Melcher 93-5-41	3.10
R. parvifolius 1658-2236 x Tulameen	Oregon	ORUS 1730-4	2.65
(*R. innominatus* O.P.) x O.P.	N. Carolina	NC 405	2.25
	Jiangxi, Japan	*R. innominatus* (NC 1768)	1.83
R. parvifolius 1658-2236 x Tulameen	Oregon	ORUS 1730-6	1.73
[NC 86-14-1(*R. trivialis* Michx.) x Glen Prosen]	N. Carolina	NC 354	1.58
	Japan	*R. phoenicolasius* Maxim.	1.58
R. parvifolius 1659-2239 x Tulameen	Oregon	ORUS 1728-2	1.45
R. parvifolius 1659-2239 x Tulameen	Oregon	ORUS 1728-3	1.30
R. coreanus 1634-1923 x Meeker	Oregon	ORUS 1725-3	0.55
R. coreanus 1634-1923 x Meeker	Oregon	ORUS 1725-6	0.50

Table 2. Genotype, parentage, location where genotype was selected, and assimilation rates (A) of raspberry germplasm at 35 °C in Expt. 2.

Parentage	Location	Genotype	A
R. coreanus (RUB 1635 O.P.)	SW China	NC 296	6.84 a[z]
Dorsett x *R. parvifolius*	Mississippi	Dormanred	6.42 ab
(*R. parvifolius* x Taylor) x Newburgh	N. Carolina	Mandarin	5.69 a–c
R. crataegifolius Bge.	S. Korea	Jingu Jeugal	5.04 b–d
NC 177 (*R. innominatus* O.P.) x Comox	N. Carolina	NC 365	4.68 c–e
R. parvifolius 1659-2239 x Tulameen	Oregon	ORUS 1728-5	4.59 c–e
	Jiangxi, China	*R. innominatus*	4.47 c–f
R. parvifolius 1658-2236 x Tulameen	Oregon	ORUS 1730-5	3.98 c–g
	Honshu, Japan	*R. parvifolius*	3.73 d–g
R. parvifolius 1659-2239 x Tulameen	Oregon	ORUS 1728-4	3.39 d–g
R. parvifolius 1658-2236 x Tulameen	Oregon	ORUS 1730-2	3.35 d–g
R. parvifolius 1658-2236 x Tulameen	Oregon	ORUS 1730-3	3.32 e–g
	Honshu, Japan	*R. illecebrosus* Focke	3.28 e–g
R. coreanus 1634-1923 x Meeker	Oregon	ORUS 1725-1	3.15 e–g
R. parvifolius 1658-2236 x Tulameen	Oregon	ORUS 1730-1	2.71 fg
Sunrise x Taylor	Maryland	Sentry	2.60 fg
R. coreanus 1634-1923 x Meeker	Oregon	ORUS 1725-2	2.58 fg
R. parvifolius 1659-2239 x Tulameen	Oregon	ORUS 1728-1	2.08 g

[z]Mean separation by *t* test, $P \leq 0.05$. n = two to three replicate plants/genotype; two sample leaves/replication.

under Pacific Northwest rather than Southern conditions. Variation in A among offspring from the cross *R. parvifolius* x 'Tulameen' (ORUS 1728-1, 1728-4, and 1728-5) is noteworthy. Also, NC 296, ORUS 1725-1, and ORUS 1725-2, all of which had *R. coreanus* collected from the same Chinese location as a parent, differed considerably. NC 296 was selected in North Carolina, whereas ORUS 1725-1 and 1725-2 were selected in Oregon. This difference in environment could have contributed to the difference in A.

Assimilation had a significant relationship, but was not strongly correlated with either ET ($R = 0.52$, $P \leq 0.0001$) or g_s ($R = 0.46$, $P \leq 0.0001$). This suggests that at high temperature nonstomatal inhibition of A occurs, as reported previously (Fernandez and Pritts, 1994; Privé et al., 1997). Evapotranspiration was strongly correlated with g_s, as was expected ($R = 0.95$, $P \leq 0.0001$).

Although measurement of a larger range of genotypes would be needed to more precisely quantify the variation in A in red raspberry germplasm, our data indicate that variability in A exists among the genotypes tested. Also, A is inhibited by nonstomatal factors at high temperatures, as evidenced by the correlation data, implying that photosynthetic activity is being controlled by physiological processes unrelated to stomatal function. Photosynthetic mechanisms of woody species can show a high degree of plasticity to temperature variation even within a single population (Tranquillini, 1979). Therefore, net photosynthesis may not be a good indicator of yield or other traits (Elmore, 1980; Zelitch, 1982). The next logical step would be to test the responses of the genotypes at high field temperatures to determine how they compare with those in a controlled environment.

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