

Leaf Gas Exchange Response of ‘Arapaho’ Blackberry and Six Red Raspberry Cultivars to Moderate and High Temperatures

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Abstract. Leaf gas exchange of six red raspberry (*Rubus idaeus* L.) and one blackberry (*Rubus* L. subgenus *Rubus* Watson) genotypes growing in 12-L containers was measured at four temperatures (20, 25, 30, and 35 °C) once a month for 3 months in growth chambers by infrared gas analysis. Measurements were taken on three successive leaves on the same primocane between the third and seventh nodes (≈75% to 85% of full leaf expansion). The plants were grown in ambient (field) conditions except when measurements were taken. Maximum daily ambient temperatures rose as high as ≈37 °C during this period. Net CO₂ assimilation (A), evapotranspiration (ET), and stomatal conductance (g_s) were measured during June, July, and August. Significant differences ($P \leq 0.01$) in A were found among the seven genotypes. ‘Arapaho’ blackberry displayed the highest mean A rate at all temperatures. Only in the raspberry cultivars Nova and Reveille did the rate of A drop significantly when temperature increased from 20 to 30 °C. ‘Reveille’ was also the only cultivar in which A significantly declined between 30 and 35 °C. The ET increased significantly over the four temperatures in four cultivars (‘Arapaho’, ‘Heritage’, ‘Nova’, and ‘Southland’). The ET rate at 35 °C was higher for ‘Arapaho’ than for all other cultivars. ‘Autumn Bliss’, ‘Dormanred’, and ‘Reveille’ did not change significantly as the temperature rose from 20 to 35 °C. Stomatal conductance of ‘Heritage’ and ‘Arapaho’ did not change significantly between 20 and 35 °C, whereas that of ‘Autumn Bliss’ and ‘Reveille’ declined almost 50% when temperature increased to 30 or 35 °C.

Interest in red raspberry production has grown in the southern states in recent years (Clark and Rom, 1997). However, there are no commercially viable, southern-adapted cultivars available to satisfy the increasing demand (Moore, 1997). Most cultivars have been bred in cooler, more northerly areas and have limited adaptation in the South, where high temperatures pose serious problems. Additional obstacles are loss of hardiness due to fluctuating winter temperatures, disease, and high light intensities (Hull, 1961; Lawrence, 1980; Moore, 1997).

Few studies on red raspberry have focused on the leaf gas exchange capabilities at high temperatures. Fernandez and Pritts (1994) observed that CO₂ assimilation (A) declined in both floricanes and primocane leaves of potted ‘Titan’ red raspberry as temperature increased,

with primocane leaves exhibiting higher A rates at all temperature levels. At 30 °C, A in primocane leaves was nearly 6 μmol·m⁻²·s⁻¹. As temperature increased to 35 °C, A declined to ≈4 μmol·m⁻²·s⁻¹ and at 40 °C it dropped to around 2 μmol·m⁻²·s⁻¹. Percival et al. (1996) found that an air temperature of 35 °C yielded a whole-plant A rate of ≈4 μmol·m⁻²·s⁻¹ in ‘Heritage’. They concluded that maximum A was reached between 17 and 20 °C, while temperatures above 20 °C reduced it. Privé et al. (1997) reported that high net carbon exchange rates could be attained at warm temperatures (25 to 30 °C) in potted ‘Autumn Bliss’. The objective of our study was to assess the gas exchange capabilities of a broader range of *Rubus* germplasm over moderate to high temperatures.

Dormant plants from virus-tested stock of red raspberry cultivars were obtained from two local nurseries: Pense Nurseries and Simmons Berry Farm, both in Mountainburg, Ark. The blackberry plants were obtained from the University of Arkansas Agricultural Research and Extension Center, Fayetteville (Table 1). The first ‘Arapaho’ plants did not produce any growth, and were replaced with 1-month-old plants 1 month later.

Thirty-five total plants were potted in 12-L pots with a Universal Mix media (Strong-Lite Hort. Prod., Pine Bluff, Ark.) and a controlled-release fertilizer (Osmocote 18N–2.6P–9.9K, 51 g/pot) on 17 Apr. 1998 and placed in ambient field conditions on the same day at Fayetteville, Ark. There were five replications per cultivar, with a block consisting of a single plant of each cultivar. They were drip irrigated at the rate of 4-L per hour for 1 h per day from 0800 to 0900 HR. Plants were also watered to saturation the night before measurements were taken. Beginning in June, leaf gas exchange measurements were undertaken. These consisted of CO₂ assimilation (A), evapotranspiration (ET), and stomatal conductance (g_s). On the morning of the day measurements were to be taken, one block of pots was transported to the Rosen Alternative Pest Control Center (APC) building and placed in a 70 × 105 × 70-cm (height × width × depth) growth chamber (Conviron 3244, Winnipeg, Manitoba, Canada) at a randomly selected temperature of 20, 25, 30, or 35 °C. The plants were allowed to acclimate to the temperature for 1 h before any measurements were taken (Fernandez and Pritts, 1994; Moon et al., 1987). Lighting was provided inside the growth chamber, but humidity could not be controlled. A CIRAS-1 portable infrared gas analyzer (PP-Systems; Hitchens, Herts, U.K.) with a Parkinson leaf cuvette (2.5 cm²) was used to take gas exchange measurements. The cuvette temperature was set at the same temperature as that of the growth chamber. Leaf and cuvette temperatures were maintained by a thermoelectric peltier plate and measured using an infrared temperature sensor. Photosynthetically active radiation (PAR) was set at 1500 μmol·m⁻²·s⁻¹, considered a saturating light level for raspberries (Fernandez and Pritts, 1994; Hunt et al., 1991; Rom and Clark, 1991). The air flow rate inside the cuvette was set at 200 mL·min⁻¹ with 350 mL·L⁻¹ CO₂ and 50% of ambient water vapor.

Table 1. Origin and parentage of cultivars used in this study.

Cultivar	Origin	Parentage
Arapaho	Clarksville, Ark.	Ark. 631 x Ark. 883 (Moore and Clark, 1993)
Autumn Bliss	East Malling, England	Complex involving <i>R. strigosus</i> Michx., <i>R. arcticus</i> L., <i>R. occidentalis</i> L. and several red raspberry cultivars (Keep et al., 1984)
Dormanred	State College, Miss.	<i>R. parvifolius</i> x Dorsett (Overcash, 1972)
Heritage	Geneva, N.Y.	(Milton x Cuthbert) x Durham (Ourecky, 1969)
Nova	Kentville, Nova Scotia	Southland x Boyne (Brooks and Olmo, 1983)
Reveille	College Park, Md.	[VPI 1 (Indian Summer x Sunrise)] x September (Brooks and Olmo, 1968)
Southland	Raleigh, N.C.	N.C. 237 x Md. S420-5 (Hull, 1969)

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Measurements were taken on five consecutive days during a 1-week period, with one block measured per day, during 23–27 June, 20–24 July, and 17–21 Aug. For each plant, data for three individual leaves on one primocane were averaged for each temperature. Leaves were ≈75% to 85% of full expansion, from the third to the seventh node. Measurements were taken between 0800 and 1230 HR to avoid any diurnal response, which has been reported in raspberry (Fernandez and Pritts, 1994; Hunt et al., 1991; Klauer et al., 1992).

A total of three growth chambers were used: the first to allow the plants to acclimate to the desired temperature (1 h), the second to measure the gas exchange (one pot at a time), and the third to allow the plants to acclimate to the next randomly selected temperature to be measured. Once a plant was measured, it was immediately placed into the next growth chamber for acclimation. Plants were rotated until gas exchange had been measured at all temperatures for each cultivar, then the block of plants was taken back to the field.

The design of the study was a randomized complete block with five replications per cultivar. The data were analyzed as a split-plot in time for A, ET, and g_s . Fixed effects were cultivar, temperature, month, and all interactions involving these effects. Random effects were block, interactions involving block, and residual error. The data analysis was performed with the Statistical Analysis Systems Program (SAS Institute, 1989). Analysis of variance was calculated by the MIXED procedure and mean separation was by *t* test at $P \leq 0.01$. Trend analysis was done using the contrast statement in the MIXED procedure.

Results

Previous reports for both primocane-fruiting (Privé et al., 1997) and floricane-fruiting (Fernandez and Pritts, 1994) potted field-grown raspberries indicated that leaf gas exchange was constant throughout the growing season on primocane leaves. Privé et al (1997) also found that fruiting did not affect leaf gas

exchange in ‘Autumn Bliss’ primocanes. In the current study, leaf gas exchange measurements were taken only on primocane leaves, thus avoiding seasonal fluctuations reported on floricane leaves (Fernandez and Pritts, 1994).

For all three dependent variables (A, ET, and g_s), the cultivar \times temperature interaction was significant ($P \leq 0.01$). There was also a significant interaction of month \times temperature for ET. No other interactions were significant for any of the dependent variables.

Assimilation rates at temperatures of 20 to 25 °C (Table 2) for all cultivars except ‘Dormanred’ were within rates (6 to 12 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) reported by other researchers (Donnelly and Vidaver, 1984; Fernandez and Pritts, 1994; Klauer et al., 1992). ‘Arapaho’ displayed higher A rates than the raspberry cultivars in accordance with previous findings (Andersen, 1989; Rom and Clark, 1991).

Similar declines in A were observed for all cultivars as temperature increased above 25 °C (Table 2), even though A rates were not identical for all cultivars. The A rates of all genotypes was highest at 20 or 25 °C. The average decline among raspberries was 40% between 20 and 35 °C, with the rate in ‘Reveille’ declining nearly 50%. No other raspberry cultivar had as significant a decline. In contrast, the blackberry ‘Arapaho’ exhibited only a 22% decline in A rate as temperature rose 25 °C to 35 °C.

Significant variation in A occurred among the cultivars at a given temperature (Table 2). At 20 °C, ‘Arapaho’ and ‘Reveille’ had the highest A rates, while ‘Dormanred’, ‘Heritage’, and ‘Autumn Bliss’ had the lowest rates.

Trend analysis across all cultivars showed a negative linear relationship between A and temperature ($P \leq 0.0001$). This was expected as similar results were reported by other researchers (Fernandez and Pritts, 1994). Individual cultivar trend analysis showed a negative linear relationship for all raspberries reflecting lower A rate with increased temperature (Table 3). Contrast trend analysis comparisons among cultivars revealed that the slopes were not significantly different except

for those involving ‘Reveille’, which had a slope similar only to ‘Southland (data not shown). Response in ‘Arapaho’ was quadratic probably because of the increase between 20 and 25 °C prior to a decline between 25 and 35 °C (Table 2).

The ET rates observed in this study across all temperatures were within the range (2 to 6 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) reported by other researchers for red raspberry (Cameron and Hartley, 1989) and blackberry cultivars (Andersen, 1989). Similar increases in ET were observed with increasing temperature for the blackberry cultivar Arapaho, and the red raspberry cultivars Heritage, Nova, and Southland (Table 2). Although small increases in ET were observed in ‘Autumn Bliss’, ‘Dormanred’, and ‘Reveille’, they were not significant. The increase in ‘Arapaho’ (52%) was especially dramatic over the temperature range used in this study. In comparison, ‘Southland’ was the red raspberry cultivar with the greatest increase in ET (38%).

Cultivar by temperature analysis indicated that all cultivars were similar in ET at 20 and 25 °C, except ‘Dormanred’ in which ET remained constant (Table 2). At 30 °C, the ET rate of ‘Arapaho’ was greater than those of all raspberry cultivars except ‘Heritage’, ‘Nova’, and ‘Southland’; at 35 °C it was significantly higher than those of all raspberry cultivars.

Trend analysis revealed positive linear relationships between temperature and mean ET for all cultivars ($P \leq 0.0001$). Individual cultivar trend analysis determined that ‘Arapaho’, ‘Heritage’, ‘Nova’, and ‘Southland’ had positive linear relationships with temperature. The other individual cultivars displayed no significant trend for ET (Table 3).

Differences in ET among temperatures in June were significant (Table 4); however, in July, 20 °C differed only from 30 and 35 °C. There were no significant differences among temperatures in August.

No differences in ET were observed at 20 °C among months (Table 4), but at 25 °C, values for June were significantly higher than those for July or August. The ET rates at 30 °C differed among all months, with higher values in June and lowest values in August. At 35 °C,

Table 2. Effects of temperature and *Rubus* genotype on mean CO₂ assimilation (A), evapotranspiration (ET), and stomatal conductance (g_s) over 3 months.

Temp (°C)	Cultivar						
	Arapaho	Autumn Bliss	Dormanred	Heritage	Nova	Reveille	Southland
	<i>Assimilation ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)</i>						
20	9.83 ab A ^z	6.14 a C	4.65 a C	6.13 a C	6.60 ab BC	8.77 a A	8.31 a AB
25	11.40 a A	6.77 a BC	4.04 ab D	6.09 a CD	7.15 a BC	8.37 a BC	8.55 a B
30	10.24 ab A	5.05 ab BC	3.81 ab C	4.81 ab BC	5.32 bc BC	6.42 b B	7.03 ab B
35	8.86 b A	3.74 b BC	2.81 b C	3.79 b BC	4.15 c BC	4.60 c B	5.46 b B
	<i>Evapotranspiration ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)</i>						
20	2.90 c AB	3.03 a A	2.14 a B	2.85 b AB	2.70 b AB	3.23 a A	2.84 c AB
25	3.54 c A	3.46 a A	2.13 a B	3.19 ab AB	3.23 b AB	3.59 a A	3.53 bc A
30	4.74 b A	3.55 a BC	2.52 a C	3.71 ab AB	3.66 ab A–C	3.61 a BC	3.83 b AB
35	6.06 a A	3.81 a BC	2.82 a C	4.29 a B	4.25 a B	3.75 a BC	4.61 a B
	<i>Stomatal conductance ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)</i>						
20	211 a AB	232 a AB	161 a B	214 a AB	210 a AB	260 a A	234 a A
25	213 a A	237 a A	113 ab B	203 a A	197 ab A	246 a A	220 ab A
30	201 a A	146 bc AB	84 b B	150 a AB	150 ab AB	150 b A	165 bc A
35	202 a A	121 c BC	79 b C	137 a A–C	131 b BC	114 b BC	152 c AB

^zSignificant differences among temperatures within cultivars are indicated by lower case letters. Significant differences among cultivars within temperatures are indicated by uppercase letters. Means with the same letter are not significantly different as determined by *t* test, $P \leq 0.01$.

Table 3. Significance of F in cultivar trend analysis across month and temperature for CO₂ assimilation (A), evapotranspiration (ET), and stomatal conductance (g_s).

Cultivar	Trend	A	ET	g _s
Arapaho	Linear	NS ^z	0.0001	NS
	Quadratic	0.0010	NS	NS
Autumn Bliss	Linear	0.0001	NS	0.0001
	Quadratic	NS	NS	NS
Dormanred	Linear	0.0036	NS	0.0001
	Quadratic	NS	NS	NS
Heritage	Linear	0.0010	0.0009	0.0051
	Quadratic	NS	NS	NS
Nova	Linear	0.0001	0.0001	0.0012
	Quadratic	NS	NS	NS
Reveille	Linear	0.0001	NS	0.0001
	Quadratic	NS	NS	NS
Southland	Linear	0.0001	0.0001	0.0001
	Quadratic	NS	NS	NS

^zNS nonsignificant ($P \leq 0.01$).

ET values in June were significantly different from those in July and August, but the differences between July and August values were not significant.

Stomatal conductance rates measured in our study were similar to those reported in other studies of red raspberry (Cameron and Hartley, 1989; Privé et al., 1997) and blackberry cultivars (Andersen, 1989). All raspberries except 'Heritage' showed significant declines in g_s as temperatures increased (Table 2), with 'Dormanred', 'Autumn Bliss', and 'Reveille' showing the sharpest declines (51%, 49%, and 46%, respectively). 'Arapaho' showed no significant differences in g_s over the temperature range 20 to 35 °C.

At each temperature, g_s varied significantly among cultivars (Table 2). 'Dormanred' had the lowest g_s at all temperatures. At 20 °C, only 'Reveille' and 'Southland' had values significantly higher than that of 'Dormanred', but at 25 °C, values for all cultivars were significantly higher than that of 'Dormanred'. 'Arapaho' had the highest g_s at 30 °C, though it was not significantly different from any of the raspberries except 'Dormanred'. 'Arapaho', 'Southland', and 'Heritage' had the highest g_s at 35 °C.

Trend analysis indicated a negative linear relationship between g_s and temperature ($P \leq 0.0001$) for each raspberry cultivar and for the mean of all cultivars, whereas (Table 3), the blackberry 'Arapaho' showed no significant regression response for g_s.

Assimilation trends and rates at high temperatures observed in our study were consistent with the results of other researchers (Fernandez and Pritts, 1994; Percival et al., 1996). All cultivars experienced declines in A as temperature increased from 25 to 35 °C and the decreases were nearly parallel for all cultivars of both red raspberry and blackberry. These findings support the data presented elsewhere in the literature for heat tolerance of temperate fruit crops (Hancock et al., 1992; Sams and Flore, 1982).

Differences in A were observed between the red raspberries and the blackberry. 'Arapaho' showed a dramatic increase in A from 20 to 25 °C, suggesting a potentially higher temperature optimum for A than in red raspberries (Cameron et al., 1993; Percival et al., 1996). However, g_s remained stable from

20 to 35 °C for this blackberry, suggesting that g_s is not acting as a limiting factor to A at temperatures up to 35 °C. Similar results have been observed in heat-adapted *Ilex* sp. (Ranney and Ruter, 1997). The extreme increase in ET as temperature increased is probably due to the large vapor pressure deficit (VPD) that was created as temperature rose, but the relative humidity remained constant.

The red raspberry 'Reveille', which has been recommended for southern conditions (Swartz et al., 1992) though not bred in the deep South, showed a precipitous decline in both A and g_s, but no significant difference in ET at higher temperatures. This lack of an increase in ET would result in insufficient evaporative cooling, creating a higher leaf temperature, which in turn could have led to the strong declines in A and g_s. The same trends were seen in 'Autumn Bliss', where A and g_s decreased, but ET was not significantly affected by temperature. This may reflect the fact that 'Autumn Bliss' originated in the United Kingdom which has a cool climate without extreme temperatures.

'Dormanred', a southern-adapted red raspberry, displayed the lowest A rates. Stomatal conductance for 'Dormanred' decreased as A decreased; however, the decline was greater for g_s. Evapotranspiration was not affected significantly by temperature. If reasoning is consistent with the conclusions made for 'Reveille' and 'Autumn Bliss', then a higher leaf temperature could result and similar declines in A and g_s would be observed. However, the decline of A in 'Dormanred' was small in comparison with the decline in 'Reveille'. This may reflect a different adaptation mechanism of 'Dormanred' to high temperatures than in other red raspberry cultivars.

'Heritage' is a widely adapted, primocane-fruited red raspberry that has been grown in the upper South. It displayed moderate A rates in comparison with the other raspberry cultivars in this study. Stomatal conductance did not differ with temperature, suggesting that it sustains relatively constant stomatal function in various temperature regimes, which could explain its wide area of adaptation. 'Nova', along with its parent 'Southland', performed in a very similar manner to 'Heritage'. This is mildly surprising since 'Southland' is a southern-adapted cultivar (Moore, 1997), but 'Nova'

Table 4. Evapotranspiration (ET) (mmol·m⁻²·s⁻¹) for 3 months and four temperatures averaged over seven *Rubus* genotypes.

Temp (°C)	Month		
	June	July	August
20	3.38 d A ^z	2.49 b A	2.57 a A
25	4.28 c A	2.97 abB	2.47 a B
30	5.26 b A	3.43 a B	2.31 a C
35	6.50 a A	3.53 a B	2.64 a B

^zSignificant differences among temperatures within months are indicated by lowercase letters. Significant differences among months within temperatures are indicated by uppercase letters. Means with the same letter are not significantly different as determined by *t* test, $P \geq 0.01$.

has 'Boyne' in its ancestry, a northern-adapted cultivar from Canada.

Distinct groupings of genotypes and their responses to elevated temperatures were detected in this study. However, all cultivars had similar A, ET and g_s responses to high temperatures. No cultivars were found to adapt to heat simply through the measurements reported, although acclimation may be seen in the ET rates as months progressed. Adaptation to heat is probably related to gas exchange processes, but our study suggests that other factors play a more important role.

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