Calorespirometric Evidence for Adaptation of Blackbrush and Shadscale to Growth Season Temperatures in Cold Deserts

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CALORESPIROMETRIC EVIDENCE FOR ADAPTATION

OF BLACKBRUSH AND SHADSCALE TO GROWTH

SEASON TEMPERATURES IN COLD DESERTS

By

Heidi Ann Summers

A thesis submitted to the faculty of

Brigham Young University

in partial fulfillment of the requirements for the degree of

Master of Science

Department of Plant and Animal Sciences

Brigham Young University

April 2005

BRIGHAM YOUNG UNIVERSITY

GRADUATE COMMITTEE APPROVAL

Of a thesis submitted by

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This thesis has been read by each member of the following graduate committee and by majority vote has been found to be satisfactory.

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BRIGHAM YOUNG UNIVERSITY

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2000 m elevation. Tissue and seeds from the two species were collected from several
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ACKNOWLEDGMENTS

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Coleogyne ramosissima Torr. (blackbrush) and *Atriplex confertifolia* [Torr. & Frem.] Wats. (shadscale) are cold desert shrubs from different families that often grow together in the Great Basin and the Colorado Plateau in the life zone between 800 and 2000 m elevation. Tissue and seeds from the two species were collected from several localities. Metabolic heat and carbon dioxide production rates were measured with calorespirometry on tissue from field-grown plants and on seedlings at temperatures from 5 to 35°C at 5°C intervals. Blackbrush adapts to higher temperatures earlier than does shadscale, and once it has adjusted to higher temperatures, anabolic rates keep rising with increasing temperature while for shadscale rates flatten out or drop off between 25 and 35°C. Both species are metabolically adapted to temperatures during the growth season determined by the historical rainfall pattern.

Keywords: calorespirometry, *Coleogyne ramosissima* (blackbrush), *Atriplex confertifolia* (shadscale), temperature

ACKNOWLEDGMENTS

INTRODUCTION

This study is a further test of the hypothesis that plant respiration is closely adapted to the environmental temperatures of the plant's growth season in the native location. Optimal respiratory adaptation maximizes fitness by producing maximum growth rate at the most frequently encountered temperature during the growth season. In previous studies this hypothesis has been tested by comparing temperature responses of respiration and growth to growth-season environmental temperature distributions for crop plants grown in different seasons and locations—cabbage and tomato, lettuce, soybean (Criddle and Hansen 1999); maize (Taylor et al. 1998); oats (Ellingson et al. 2003)—and for wild plants adapted to different locations—redwoods, bitterbrush, sagebrush, rabbitbrush (Criddle et al. 1994); eucalyptus (Criddle and Hansen 1999); cheatgrass (Hemming et al. 1999). This study tests another prediction of the hypothesis, namely that unrelated species, coexisting in the same locations, with the same growth season imposed by water availability, will have the same respiration and growth responses to temperature.

Blackbrush (*Coleogyne ramosissima* Torr.) is a shrub in the Rosaceae family with many woody branches (hence the name ramosissima) that turn black when wet or with age. The leaves are small, only 3–12 mm long and less than 2 mm wide (Welsh et al. 1987). This desert shrub grows in the transitional zone between warm and cold deserts in the southwestern United States at elevations between 760 and 1,980 m (Ackerman et al. 1980; Ackerman and Bamberg 1974; Bradley 1964). Blackbrush is foraged by desert bighorn sheep year-around and by mule deer during winter. Goats and sheep may graze on blackbrush during spring, but it is not eaten much by cattle (Bradley 1964; Callison et al. 1985). Blackbrush seeds provide food for both rodents and birds (Pendleton et al.

1995; Lei and Walker 1997), and the plant provides important ground cover and habitat for small mammals (Ackerman et al. 1980). Blackbrush is very slow-growing and very long-lived, some shrubs having been recorded as old 400 years (Callison and Brotherson 1985). It flowers from late March to early May for two to three weeks but only in good years when fall and winter precipitation (snow) is sufficient. The resource reserves of the plant determine the size of the mast seed crop, and periods between mast crops often exceed five years (Ackerman et al. 1980). *Coleogyne* is a monotypic genus that grows over a wide geographic and elevational range. *C. ramosissima* exists only as a diploid with a chromosome count of 2n=16 (McArthur and Sanderson 1985). Stebbins and Major (1965) described it as a paleoendemic species with little variation, perhaps on its way to extinction. However, paleoecological evidence indicates that blackbrush has a sufficient gene pool to have evolved different ranges of tolerance (Wells 1983) and to have successfully migrated along environmental gradients in response to climatic changes (Phillips and Van Devender 1974; Spaulding 1990). Populations of blackbrush also show differences in plant size and germination characteristics (Pendleton et al. 1995). Such evidence argues against classifying the species as paleoendemic and on the way to extinction. Blackbrush is still an ecotonal species and can be upset by frequent large fires, road building and mining, and invasion by exotic species (Pendleton et al. 1995).

Shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.) is a shrub in the Chenopodiaceae family that does well in alkaline and saline soils (often at lower elevations than blackbrush) and is found from Canada to Mexico (Ackerman et al. 1980; Ackerman and Bamberg 1974). Shadscale has small rigid branches that bear grayish leaves covered with water-holding bladder hairs and then taper to become woody and

spiny. The ovate leaves are up to 2 cm long and deciduous. Male and female flowers appear in the spring on separate plants (Welsh et al. 1987). Shadscale is also an important forage plant (Sanderson et al. 1990) and provides important ground cover and habitat for small mammals (Ackerman et al. 1980). The species consists of five ploidy races from diploid to decaploid. Similarity between shadscale plants of different chromosome numbers and a lack of close relatives indicate that the ploidy races of *A. confertifolia* are autoploid (Stutz and Sanderson 1983), but ecological differences appear among some ploidy races (Stutz and Sanderson 1983; Sanderson et al. 1989), indicating rapid adaptation to new, or changed, environments (Sanderson et al. 1990).

While blackbrush and shadscale often occur together, there are important differences between the species. Shadscale is a faster growing shrub than blackbrush, and while blackbrush is monotypic, shadscale has ploidy races from diploid to decaploid and therefore appears to adapt more rapidly to change than blackbrush. These differences can be explored by looking at the plants' metabolism.

Respiration consists of catabolism, which liberates the energy for life from photosynthate, and anabolism, which uses the gradients thus produced to drive the reactions of growth, reproduction, defense, etc. By means of calorespirometric measurements, catabolism and anabolism can be separately characterized (Hansen et al. 2002). Metabolic and growth responses to environmental temperatures can thus be determined. These responses are hypothesized to match diurnal and seasonal temperatures and temperature variability of the environment to which the plant is adapted (Smith et al. 1999). The rate of respiration multiplied by the efficiency controls growth

rate; therefore determination of these properties as a function of temperature can be used to demonstrate adaptation to a particular locale (Hansen et al. 2002).

The hypothesis to be tested is that respiratory metabolism is closely adapted to the environment, and thus two different plants from disparate families that grow together and have the same growth season will have similar respiratory responses to temperature. The objective of this research is to measure the respiration rate and respiration efficiency as functions of temperature for both blackbrush and shadscale and relate those measurements to their environment.

MATERIALS AND METHODS

Meristematic tissue and young leaves (ca. 100 mg fresh weight) were placed in an ampule of an isothermal calorimeter (Hart Scientific Model 7707 or Calorimetry Sciences Corporation Model 4100). After thermal equilibration of 15 minutes at a given temperature, the heat rate (R_q) was measured for an additional 15 minutes to verify a steady state. A small vial with 50 μL of 0.4 M NaOH was then placed in the ampule with the tissue, followed by another 15-minute equilibration and a 15-minute measurement period. The vial of NaOH was removed and R_q measured again. The measurement with the NaOH gives the sum of the heat rate from metabolism (R_q) plus the heat rate from carbonate formation. This measurement minus the average R_q from the first and third measurements yields the rate of CO_2 production (R_{CO_2}) (Criddle and Hansen 1999). These measurements were repeated on a given sample at temperatures ranging either downward from 20 to 10°C or upward from 20 to 35°C in five-degree increments. Figure 1A is representative of R_q and R_{CO_2} data.

Predicted growth rate is

$$R_{SG}\Delta H_B = -(1-\gamma_s/4)\Delta H_{O_2}R_{CO_2} - R_q \qquad (1)$$

where R_{SG} is the specific anabolic (or growth) rate, and ΔH_B is the enthalpy change for

the reaction

$$C_{sub} + (N, P, K, etc.) \rightarrow C_{bio} + xO_2 \qquad (2),$$
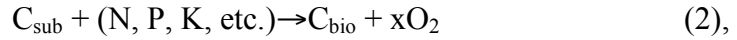
i.e. the difference in the heats of combustion per C-mole of biomass (C_{bio}) and

photosynthate (C_{sub}) (Hansen et al. 2002). γ_s is the oxidation number of carbon in the

respiratory substrate, and ΔH_{O_2} is in general Thornton's constant (Thornton 1917), -

455 ± 15 kJ mol^{-1} O_2, or specifically the heat of combustion of the substrate per mole of

O_2. Equation 1 shows that growth can occur only at those temperatures where $-(1-$

$\gamma_s/4)\Delta H_{O_2}R_{CO_2}$ exceeds R_q (Criddle et al. 1997). $(1-\gamma_s/4)$ is a conversion factor that

depends on substrate carbon oxidation state. We assume the substrate is carbohydrate,

with $\gamma_s = 0$ and $\Delta H_{O_2} = -470$ kJ mol^{-1} O_2, yielding $-470R_{CO_2}$ in µW mg^{-1} dw. An example

of $R_{SG}\Delta H_B$ data is shown in Fig 1B.

The calorespirometric ratio R_q/R_{CO_2} is a measure of efficiency for growth driven

by aerobic respiration (Figure 1C). Equation 3

$$R_q/R_{CO_2} = -(1-\gamma_s/4)\Delta H_{O_2} - \Delta H_B[\varepsilon/(1-\varepsilon)] \qquad (3)$$

shows how the calorespirometric ratio is related to ε, the substrate carbon conversion

efficiency (Hansen et al. 2002). In aerobic systems with carbohydrate substrate, decreases

in R_q/R_{CO_2} indicate a decrease in the catabolic/anabolic ratio, and hence an increasing

efficiency for producing anabolic products.

Metabolic data were obtained for various populations. Seeds were gathered from

different populations of blackbrush, germinated at 15°C after a pre-chill treatment

(Pendleton and Meyer 2004), and grown in a growth chamber at 25°C. Leaf tissue was also collected from established populations in the wild. Although seeds were also gathered from different populations of shadscale, germinated, and planted in the greenhouse, the seedlings died due to fungal infection. Thus, shadscale data are for leaf tissue collected from established populations in the wild only. Where possible, shadscale accessions of different ploidy levels were compared. Replicates were run as often as possible and range from two to six.

RESULTS

Figure 2 shows R_{CO_2} plotted against R_q for unaveraged data of *Atriplex confertifolia*; Figure 3 does the same for *Coleogyne ramosissima*. The scatter around the least squares line is largely due to differences in measurement temperature. The average efficiency without regard to temperature (represented by slope) for blackbrush does not differ significantly from that of shadscale. However, the maximum rates (R_{CO_2} and R_q) for blackbrush are less than half those of shadscale (note the difference in scale in Figures 2 and 3), showing that blackbrush grows more slowly than shadscale primarily because of a lower respiration rate. For shadscale, the CO_2 and heat rates are related to ploidy, but ploidy appears to have little or no effect on the metabolic efficiency.

Anabolic rates ($R_{SG}\Delta H_B$) differ systematically within *Atriplex confertifolia* populations according to ploidy (Table 1). Within each shadscale population, predicted growth rates, whatever the optimum temperature happens to be, decrease with increasing ploidy. Shadscale races with higher ploidy grow more slowly than those with lower

ploidy. Because tissue samples were collected from the different populations at different times and were therefore at different physiologic stages, rates cannot be compared between populations since rates change with the changing season (see Figure 4).

For shadscale tissue collected in Moab from late April through early June, the highest anabolic rate ($R_{SG}\Delta H_B$) occurs in May and the lowest in June (Figure 4). The difference in rates between May and June is quite marked, with rates in June about half as high as those in May. $R_{SG}\Delta H_B$ suddenly drops off at 35°C for tissue collected in April, indicating increased tolerance for higher temperatures as the season progresses, although the optimum changes little through the season.

Blackbrush leaf tissue collected from Moab showed a shift in temperature for optimum metabolism and growth ($R_{SG}\Delta H_B$) over the three-month period. In March, optimum growth occurred between 25 and 30°C and by May shifted to 35°C, apparently in response to rising average temperatures. In blackbrush, the highest rates were also seen in tissue collected in May, while leaf tissue collected in April showed rates almost as low as leaf tissue collected in June (Figure 5). The anomalously high rates measured in March compared with April may relate to flowering, which occurred from mid-April to mid-May when the plants' resources were diverted from leaf growth to reproduction. Floral tissue (buds and young flowers) collected in April had a much higher $R_{SG}\Delta H_B$ than did leaf tissue collected at the same time (Figure 6).

There was a difference in the response to temperature between blackbrush populations taken from higher and lower elevations. Figure 7 shows the averaged calorespirometric ratio (R_q/R_{CO_2}) for blackbrush tissue grown from seed from populations at higher elevations (Island in the Sky, 1866 m; Little Rockies, 1646 m; and Beaver Dam

summit, 1450 m) and at lower elevations (Kyle Canyon, 1280 m; Winchester Hills, 1189 m). Blackbrush seedlings grown from seed from higher elevations had the lower R_q/R_{CO_2}, and therefore greater efficiency for producing anabolic products, at 20°C while blackbrush from lower elevations had peak efficiency at 25°C.

DISCUSSION

C. Hart Merriam observed in 1894 that different "life zones" could be characterized with increases in altitude from desert to mountaintop on the San Francisco peaks in northern Arizona. Thus different species characterize the life zone at a particular altitude. Sonoran desert plants such as creosote bush, Joshua tree, and catclaw acacia are found at elevations below 800 m, and the next zone in elevation is characterized by blackbrush, ephedra, and shadscale. Sagebrush and cohorts are found above 1500 m, juniper and pinyon pine at about 2000 m, and oak and maple at higher elevations (2500 m). Douglas fir and aspen are at 3000 m, and close to timberline is found Englemann spruce. The lines are not sharp between life zones, but the species are known to ecologists to be generally characteristic for a given zone (Whittaker 1970). The dominant environmental variable that changes with altitude is temperature, and temperature is one of the most significant determinants of plant growth rate, though other factors such as toxins, water, and mineral availability may interact with it. In desert climates, for instance, it is temperature and water availability that generally dictate which plants grow in a particular habitat as well as growth season.

Diploid *Atriplex confertifolia* are found above the level of the Pleistocene lakes, while polyploids grow in the valley bottoms and sides. These polyploids probably formed as the lakes disappeared and new habitats opened up (Stutz and Sanderson 1983). In general, polyploid tissues of shadscale have a lower rate of cell division and growth, which may be advantageous where moisture supplies are too low to support taller plants (Sanderson, McArthur, and Stutz 1989), and indeed, *Atriplex confertifolia* plants with higher ploidy numbers are generally smaller, particularly than diploid plants (Stutz and Sanderson 1983). Increased ploidy is also correlated with increased osmotic capability (Sanderson, McArthur, and Stutz 1989). The data in Table 1, showing decreasing $R_{SG}\Delta H_B$ with increasing ploidy, fit well with these observations.

Blackbrush seeds have shown variation, according to habitat, in germination response. Populations from lower (warmer) elevations have lower primary seed dormancy and shorter chilling requirements than populations from higher elevations (Pendleton and Meyer 2004; Lei 1997). Elevation also has a clear role in metabolic response to temperature ($p \leq 0.01$) for blackbrush populations (Figure 7), and so while *Coleogyne ramosissima* has commonly been assumed to be a paleoendemic species lacking in genetic variation following the original postulation by Stebbins and Major (1965), there is clearly genetic variation among blackbrush populations.

Both the shadscale and blackbrush tissue collected in Moab showed the highest specific anabolic rates in May (Figures 4 & 5), indicating that they have both adapted to their environment so they grow most when average temperatures are warmer, but when water is still available. However, they do show differences in their adaptation. Blackbrush adapts to higher temperatures earlier in the season than does shadscale, and

once it has adjusted to higher temperatures, anabolic rates keep rising with increasing temperatures, even in June (Figure 6), while for shadscale, anabolic rates flatten out or even drop off slightly between 25 and 30°C (Figure 4). Blackbrush should therefore be able to carry out anabolic activity in Moab even in the heat of summer as long it has sufficient water. In agreement with this, blackbrush, unlike many other desert shrubs, has been shown to be able to utilize rare summer rainfall events efficiently (Lin et al. 1996; Gebauer and Ehleringer 2000).

SUMMARY

For *Atriplex confertifolia*, an increase in ploidy (2x to 10x) predicts a decrease in specific growth rate, which may be part of the physiological adaptation of shadscale polyploids to new habitats. In Moab, tetraploid shadscale becomes tolerant to higher temperatures more slowly than blackbrush and continues to show optimum specific growth rates at 25°C while the temperature for optimum specific growth rate increased for blackbrush throughout the season. So, while both shrubs in the Moab environment have adapted to maximize specific growth rate in May, they still show some differences. One notable difference between metabolic responses of the two species is that, in general, specific anabolic rates of shadscale are double those of blackbrush.

While blackbrush shrubs in Moab were in flower from mid-April to mid-May, floral tissue had much higher metabolic rates and predicted anabolic rates than did vegetative tissue, and specific growth rates of vegetative tissue in April decreased relative to March and May.

Coleogyne ramosissima germinated from seeds collected at higher elevations (1866 - 1450 m) had optimum metabolic growth at 20°C, while plants from lower elevations (1280 - 1189 m) had optimal predicted metabolic growth at 25 to 30°C, indicating genetic adaptation to growth season temperature for the environment in which the population grows.

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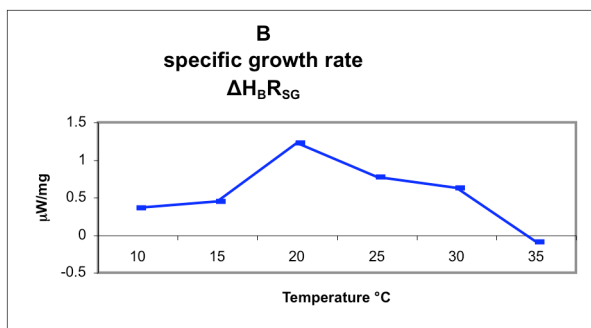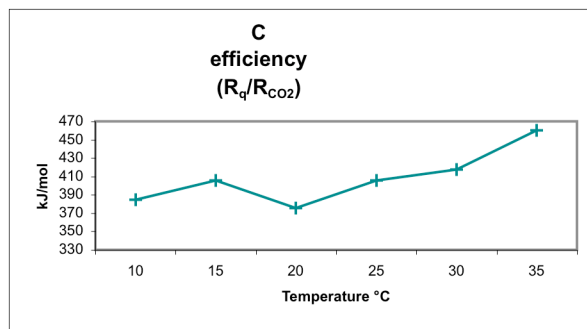Thornton, W.M. 1917. The relation of oxygen to the heat of combustion of organic compounds. Philos. Mag. 33: 196–203.
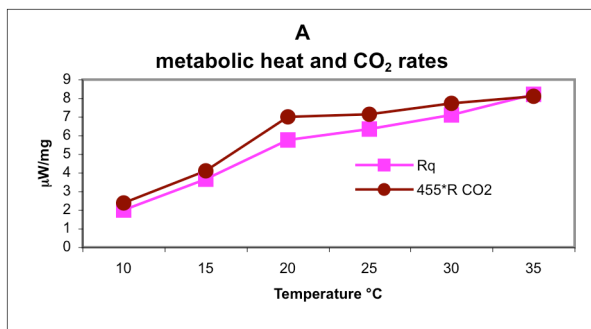
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Table 1. Predicted growth rates ($R_{SG}\Delta H_B$) for ploidy races of shadscale populations. Bolded numbers indicate optimum growth rate.

Location	ploidy	Temp (°C) $R_{SG}\Delta H_B(\mu W)$					
		10°	15°	20°	25°	30°	35°
Lake Mead	2x	0.63	1.13	1.63	**4.45**	2.67	2.08
	4x	0.71	1.06	1.94	**3.13**	2.70	1.65
	8x	0.27	0.55	0.87	**1.98**	1.25	1.21
Four Corners	2x	0.09	0.14	0.65	**0.71**	0.51	0.62
	4x	0.09	0.14	0.30	**0.43**	0.39	0.16
	6x	0.15	0.29	**0.39**	0.27	0.33	0.36
Bigwater	2x	—	—	3.24	**3.56**	2.32	2.24
	4x	0.29	0.72	**1.27**	0.96	0.74	0.62
Cliff Dwellers	4x	0.26	0.63	**1.89**	0.92	0.74	0.16
	6x	—	—	1.28	**1.40**	0.99	0.27
Millard Co.	2x	0.15	0.36	**0.86**	**0.82**	0.45	0.16
	4x	0.18	0.30	0.74	**0.87**	**0.84**	0.68
	8x	0.05	0.22	**0.76**	**0.76**	0.53	0.54
	10x	0.11	0.28	**0.75**	**0.71**	0.33	0.45

A
metabolic heat and CO_2 rates

μW/mg — Temperature °C

Rq
455*R CO2

C
efficiency
(R_q/R_{CO2})

kJ/mol — Temperature °C

B
specific growth rate
$\Delta H_B R_{SG}$

μW/mg — Temperature °C

Figure 1. Blackbrush tissue grown from seed collected at Beaver Dam Summit: [A] metabolic heat rate (R_q) and rate of CO_2 (R_{CO_2}); [B] ratio of R_q/R_{CO_2} or efficiency for metabolically-driven growth; [C] specific growth rate ($R_{SG}\Delta H_B$) calculated from R_{CO_2} and R_q ($R_{SG}\Delta H_B =455\ R_{CO_2}- R_q$). Data has been averaged.

Figure 2. Rate of CO$_2$ evolution (R$_{CO_2}$) plotted against metabolic heat rate (R$_q$) for leaf tissue from the different ploidy races of *Atriplex confertifolia*. The gray line represents the heat of combustion of carbohydrate, y=(1/470)x.
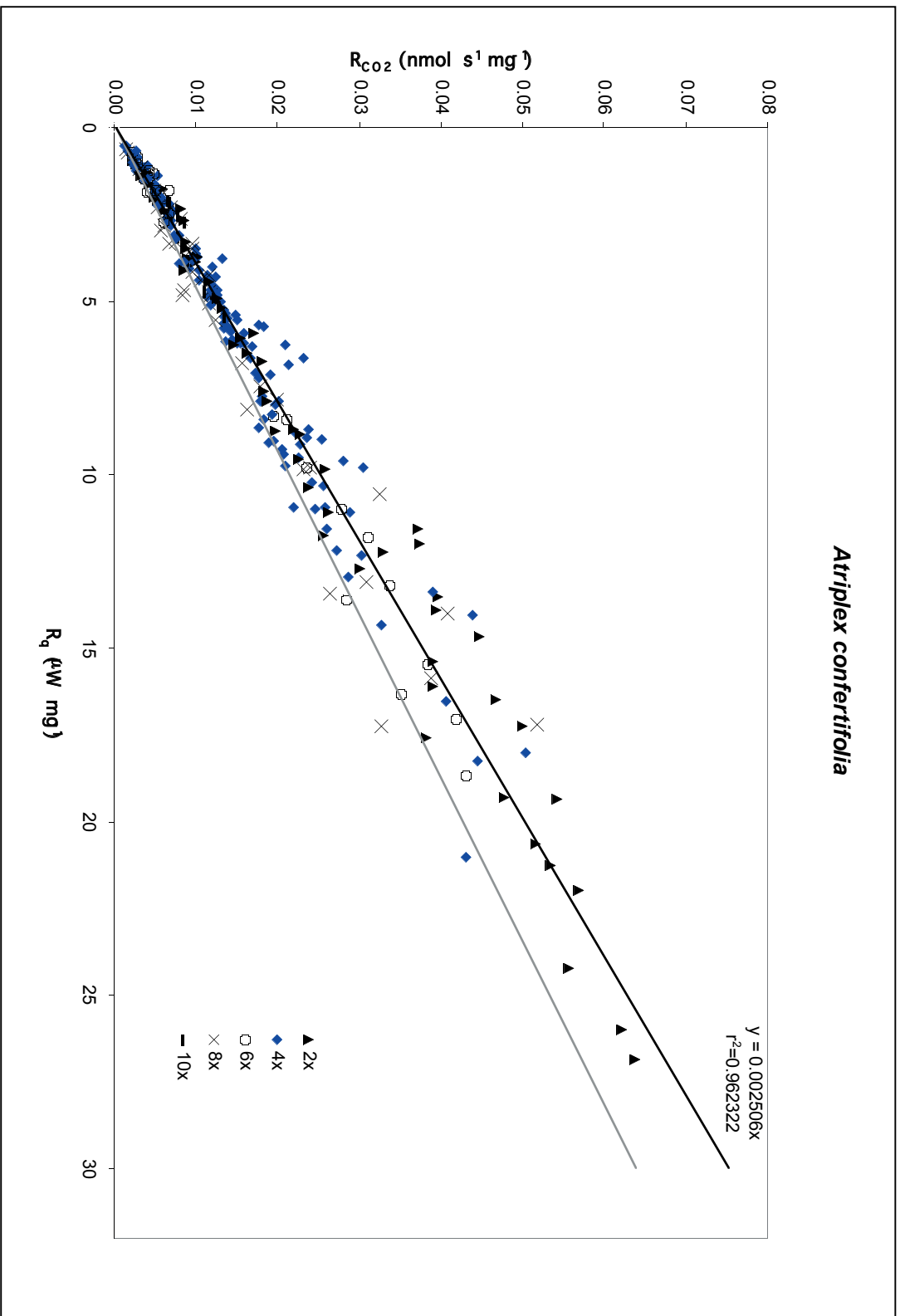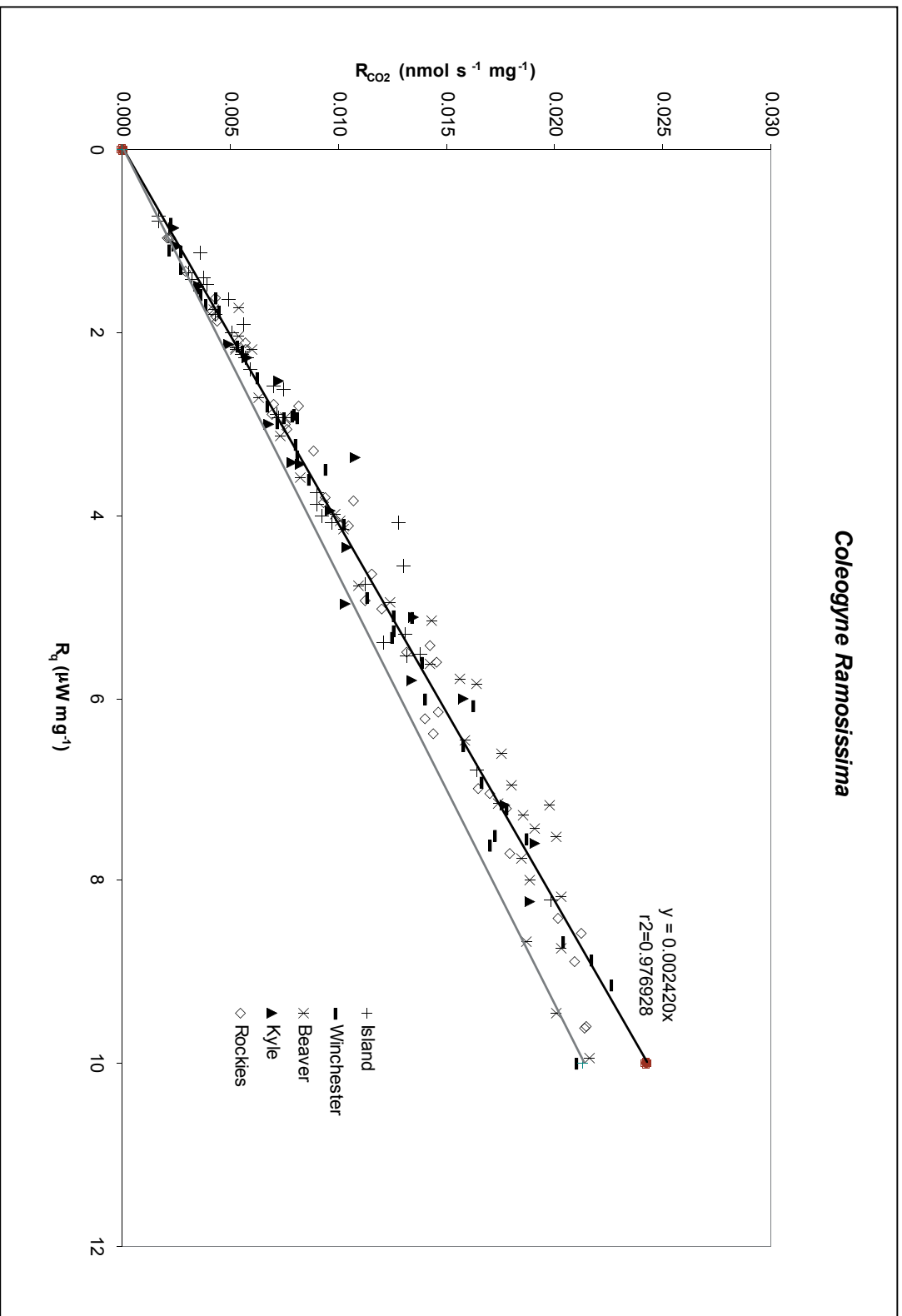
Figure 3. Rate of CO$_2$ evolution (R$_{CO_2}$) against metabolic heat rate (R$_q$) for leaf tissue from the different populations of *Coleogyne ramosissima*. The gray line represents the heat of combustion of carbohydrate, y=(1/470)x.

Coleogyne Ramosissima

y = 0.002420x
r2=0.976928

+ Island
— Winchester
✳ Beaver
▲ Kyle
◇ Rockies

R$_{CO_2}$ (nmol s^{-1} mg^{-1})

R$_q$ (μW mg^{-1})

Figure 4. Specific growth rate ($R_{SG}\Delta H_B$), calculated from metabolic heat and CO_2 rates, in microwatts (µW) per mg dry weight for shadscale collected from Moab, late April to early June. The bars indicate the standard error [SE=$\sqrt{(MSE*2/r)}$] that applies to data points at each temperature.
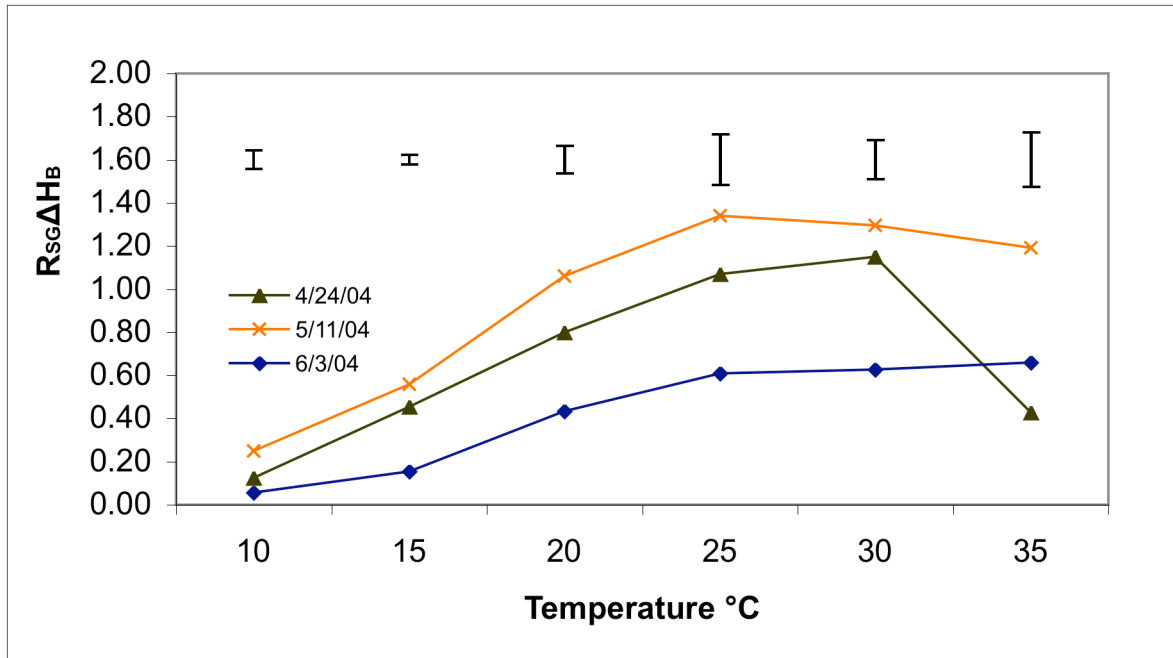
Figure 5. Specific growth rates ($R_{SG}\Delta H_B$) as a function of temperature for blackbrush tissue collected from Moab 3/9/2004 (not in flower), 4/24/2004 (flowering), 5/11/2004 (flowering), and 6/3/2004 (past flowering—in fruit). The bars indicate the standard error [SE=$\sqrt{(MSE*2/r)}$] that applies to data points at each temperature.
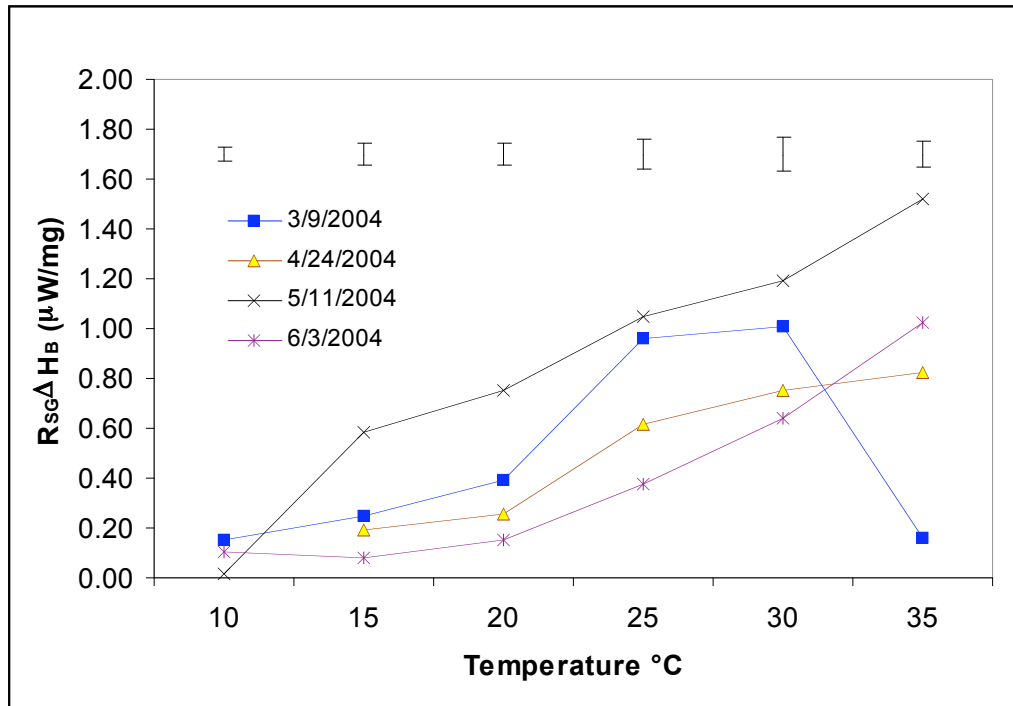
Figure 6. $R_{SG}\Delta H_B$ as a function of temperature for blackbrush floral and leaf tissue, respectively, collected 4/24/2004 from Moab. The bars indicate the standard error [SE=√ (MSE*2/r)] that applies to data points at each temperature.
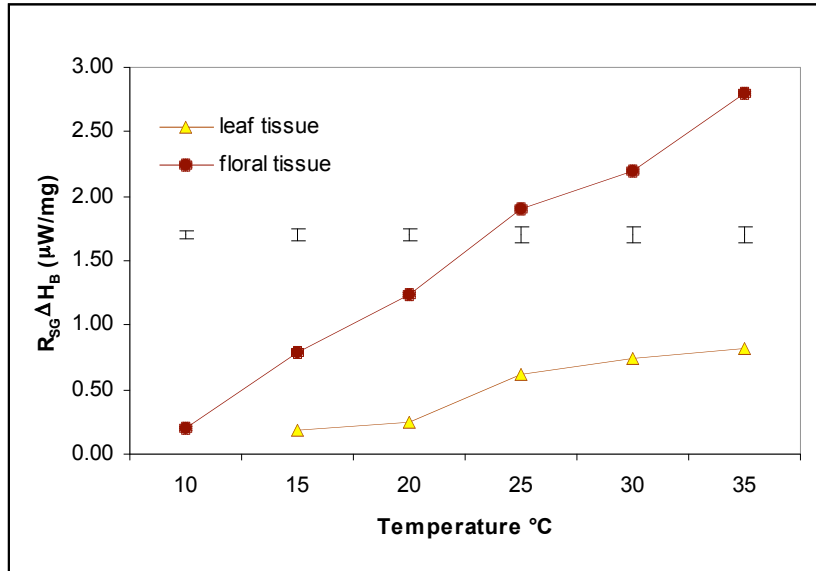
Figure 7. R_q/R_{CO_2} values as a function of temperature for blackbrush from lower elevations (Winchester Hills, 1189m, and Kyle Canyon, 1280m) and higher elevations (Island in the Sky, 1866m; Little Rockies, 1646m; and Beaver Dam Summit, 1450m). The bars indicate the standard error [SE=√(MSE*2/r)] that applies to data points at each temperature.