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Comparison of respiratory and growth characteristics of two co-occurring shrubs from a cold desert, *Coleogyne ramosissima* (blackbrush) and *Atriplex confertifolia* (shadscale)

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ABSTRACT

Coleogyne ramosissima Torr. (blackbrush) and *Atriplex confertifolia* [Torr. & Frem.] Wats. (shadscale) are cold desert shrubs from different families. Despite very different life histories they often grow in close geographic proximity in the Great Basin and the Colorado Plateau between 800 and 2000 m elevation. The purpose of this study is to compare the ecophysiology of slow growing and reproducing blackbrush with the ecophysiology of faster growing and reproducing shadscale. Metabolic heat and carbon dioxide production rates were measured on leaf tissue from wild plants and on lab-grown seedlings at temperatures from 10 to 35 °C at 5 °C intervals. Heat of combustion, ash content, and carbon and nitrogen contents were also measured. Substrate carbon conversion efficiencies and anabolic (or growth) rates were calculated from the respiration data. The growth rate of blackbrush was found to be approximately half that of shadscale because of lower respiration rate, but blackbrush begins growing earlier in the spring and can grow at higher temperatures when water is available. Blackbrush was observed to reproduce heavily when winter and spring precipitation is abundant.

1. Introduction

This study examines two species that grow in close geographic proximity for similarities and differences in their respiratory and growth characteristics. The study focuses on respiration and not on photosynthesis because growth rate and fecundity are directly related to respiratory characteristics. The anabolic rate, which can be calculated from simultaneous measurements of respiratory CO_2 rate and either O_2 uptake or metabolic heat production rate, is a surrogate for growth and development rate. Measurements of respiration rates as a function of temperature thus allow calculation of growth rates as a function of temperature. This study focuses on temperature as the environmental variable because in desert climates water availability generally dictates the growth-season, and thus determines the temperature pattern to which plants must be adapted to successfully grow and reproduce in a given locale. Adaptation of respiratory characteristics to the local temperature pattern thus determines the success of a species within a given ecosystem, but other environmental factors such as salt, water, soil type and mineral availability may affect where plants grow within that locale.

Previous studies we have done on crop plants grown in different seasons and locations (Taylor et al., 1998; Criddle and Hansen, 1999; Matheson, 2000) and on wild plants adapted to different locations (Criddle et al., 1994; Hemming et al., 1999; Criddle and Hansen, 1999; Anekonda et al., 2004; Keller et al., 2004) show regular changes in respiratory properties with latitude and altitude. Many of the studies on wild plants were done on plants grown in common gardens, thus showing the differences in respiratory properties are genetic adaptations, not acclimation. These previous studies examined differences in respiratory properties within a species, between congeneric species, and between closely related species adapted to differing latitudes, elevations, and growth-season. Taken together, the results of these studies imply that differential adaptation of respiratory metabolism to temperature may explain how unrelated, but representative, species can coexist. This study examines the respiration and growth responses to temperature of two unrelated species that grow in close proximity over a large area. So far as we can determine, this is the first in-depth study of the respiratory and growth characteristics of unrelated, autochthonous species that occur in close proximity.

Blackbrush grows in the southwestern United States in the transitional zone between the warm Mojave and Sonoran deserts to the south and the northern cold deserts of the Great Basin and Colorado Plateau at elevations between 760 and 1980 m (Bradley, 1964; Ackerman and Bamberg, 1974; Ackerman et al., 1980; Lei and

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Walker, 1997; Pendleton and Meyer, 2004). Shadscale does well in alkaline and saline soils, allowing growth at lower elevations than blackbrush, and is found from Canada to Mexico (Ackerman and Bamberg, 1974; Ackerman et al., 1980). While the ranges of blackbrush and shadscale overlap and the species are often found growing in close proximity, they occupy different niches defined by soil type. Blackbrush is almost completely confined to shallow, coarse-textured soils, while shadscale is a specialist on deep, fine textured soils. Blackbrush is not found on soils with excess solutes, whereas shadscale, while not found on highly saline sites, is often found on soils that contain moderate levels of solutes. The two species are thus not competitors, but where they grow in close proximity, must be adapted to the same patterns of temperature and water.

There are significant differences in the biology, life histories, and phylogenies of Blackbrush (*Coleogyne ramosissima* Torr.), which is a shrub in Rosaceae, and of shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.) which is a shrub in Chenopodiaceae. The mechanisms of adaptation of the two species are exceedingly different. Blackbrush is very slow growing and very long-lived, some individuals reaching 400 years of age (Callison and Brotherson, 1985). In good years, blackbrush produces perfect flowers for two to three weeks from late March to early May but only when winter and spring precipitation is abundant. Blackbrush exists only as a diploid with a chromosome count of $2n = 16$ (McArthur and Sanderson, 1985). Blackbrush is an ecotonal species and can be upset by frequent large fires, road building and mining, and invasion by exotic species (Callison et al., 1985; Pendleton et al., 1995). 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). In shadscale, male and female flowers appear annually in the spring on separate plants (Welsh et al., 1987). The species consists of five ploidy races from diploid to decaploid. Shadscale plants of different ploidy races are autoploid (Stutz and Sanderson, 1983) and ecological differences exist among the races (Stutz and Sanderson, 1983; Sanderson et al., 1989), indicating rapid adaptation to new, or changed, environments (Sanderson et al., 1990). Thus, blackbrush apparently is adapted for a slow growth strategy for long-term survival in an environment with little fluctuation of resources and few rewards for rapid growth or a plastic growth response. On the other hand, shadscale grows faster, reaches reproductive maturity quickly, and produces long-lived seeds, a strategy that makes it drought prone and short-lived relative to blackbrush, but successful at the population level.

2. Materials and methods

The objective of this research is to measure respiration rates, and from those data, calculate respiration efficiency and growth rates as functions of temperature, and then to compare these characteristics for blackbrush and shadscale. Metabolic and growth responses to environmental temperatures can be determined by calorespirometric measurements of metabolic heat and CO_2 rates (Criddle et al., 1997, Criddle and Hansen, 1999; Smith et al., 1999; Hansen et al., 2004, 2005). Catabolism and anabolism can be separately characterized by this method (Hansen et al., 2002, 2004). The rate of respiration multiplied by the efficiency (i.e. the ratio of anabolic rate to total respiration rate) equals the anabolic or growth rate; therefore determination of respiration rate and efficiency as functions of temperature can be used to demonstrate adaptation of growth rate to environmental temperatures at a particular locale (Hansen et al., 2002).

Seeds were gathered from different populations of blackbrush (Appendix 1, electronic version only), 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 wild populations near Moab, Utah (Appendix 1, electronic version only); branches were cut from 2 to 6 representative plants, placed in a plastic bag in a cooler with ice, transported to the lab and placed in a 5 °C refrigerator until the measurements were made, usually within 48 h of harvest. Although seeds were gathered from different populations of shadscale, germinated, and planted in a greenhouse, the seedlings all died from fungal infection. Thus, shadscale data are for leaf tissue collected in the same way as above from established populations (Appendix 1, electronic version only) in the wild only. Where possible, shadscale accessions of different ploidy levels were also compared.

Young, growing leaves were cut from the branches with a razor blade and about 100 mg fresh weight placed in an ampule of an isothermal calorimeter (Hart Scientific Model 7707 or Calorimetry Sciences Corporation Model 4100) and the heat rate (R_q) and the rate of CO_2 production (R_{CO_2}) measured by the methods described in Criddle et al. (1997), Criddle and Hansen (1999), and Hansen et al. (2005). 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. Replicates of tissue samples were sometimes limited by the amount of young tissue available, but were run as often as possible and range from two to six. Dry weights were obtained after samples were dried in a vacuum oven at 70–80 °C for at least 24 h. Appendix 2 (electronic version only) gives representative R_q and R_{CO_2} data. The dried samples from metabolic measurement were used to determine heats of combustion with a model 1425 Parr oxygen bomb calorimeter calibrated with benzoic acid. Samples were ground and combined to give 0.2 g samples for each combustion; four to ten replicates were run. Ash content was determined as the mass remaining in the combustion boat. Carbon and nitrogen contents were determined on the combined material with an elemental analyzer (Costech, Model ECS 4010); five replicates were run.

Predicted growth rate is calculated as

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

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

$$C_{sub} + (N, P, K, \text{etc.}) \rightarrow C_{bio} + xO_2 \quad (2)$$

which can be estimated from the difference in the heats of combustion per C-mole of biomass (C_{bio}) and photosynthate (C_{sub}) (Hansen et al., 2002; Ellingson et al., 2003). γ_s is the oxidation number of carbon in the respiratory substrate, and ΔH_{O_2} is Thornton's constant (Thornton, 1917), in general -455 ± 15 kJ mol^{-1} O_2, or more exactly, the heat of combustion of the substrate per mole of O_2. Eq. (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 the conversion factor between R_{CO_2} and R_q that depends on substrate carbon oxidation state. In this study the substrate is assumed to be carbohydrate, with $\gamma_s = 0$ and $\Delta H_{O_2} = -470$ kJ mol^{-1} O_2, yielding $-470 R_{CO_2}$ in μW mg^{-1} dw for the first term in Eq. (1). An example of $R_{SG}\Delta H_B$ data is shown in Appendix 2 (electronic version only). Several previous studies (Criddle et al., 1997; Criddle and Hansen, 1999; Ellingson et al., 2003) show that $R_{SG}\Delta H_B$ is directly proportional to the relative growth rate of young vegetative tissues measured by traditional methods.

The calorespirometric ratio R_q/R_{CO_2} is a measure of efficiency for growth driven by aerobic respiration. Eq. (3)

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

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. An example of R_q/R_{CO_2} data is shown in Appendix 2 (electronic version only).

3. Results

Composition and heat of combustion data are given in Appendix 3 (electronic version only). Carbon content is higher in blackbrush than in shadscale because of the lower ash content in blackbrush. Ash content of shadscale is 4–5 times higher than that of blackbrush. Nitrogen content of shadscale is twice that of blackbrush; the N/C mass ratios are 0.081 ± 0.012 and 0.041 ± 0.002 for shadscale and blackbrush, respectively where the uncertainty is the standard error of the mean. Heats of combustion per C-mole of blackbrush (497 ± 9 kJ Cmol^{-1}) and shadscale (492 ± 9 kJ Cmol^{-1}) are within the standard of error in the data, indicating there is no difference between the species, and therefore an average carbon oxidation number, $\gamma_B = -0.21 \pm 0.07$ and $\Delta H_B = +25 \pm 9$ kJ Cmol^{-1} for both species. None of the variables in Appendix 3 (electronic version only) correlate with ploidy of shadscale.

Figs. 1 and 2 show the rate of CO_2 production plotted against metabolic heat rate for all the individual data points for shadscale and blackbrush, respectively. The scatter around the least squares line is largely due to variation in the ratio R_{CO_2}/R_q with measurement temperature. The average substrate carbon conversion efficiencies, calculated from the least squares slopes with zero intercept, (70 ± 7)% and (74 ± 5)% for blackbrush and shadscale, respectively, do not differ significantly as shown by the standard deviation. However, the maximum rates for blackbrush are less than half those of shadscale (note the difference in scale in Figs. 1 and 2). This lower respiration rate is the primary reason that blackbrush grows more slowly than shadscale. There is no apparent effect of seed source on the respiratory properties of blackbrush in Fig. 2. However, for shadscale, although ploidy appears to have little or no effect on the metabolic efficiency (i.e. the slope in Fig. 1), the

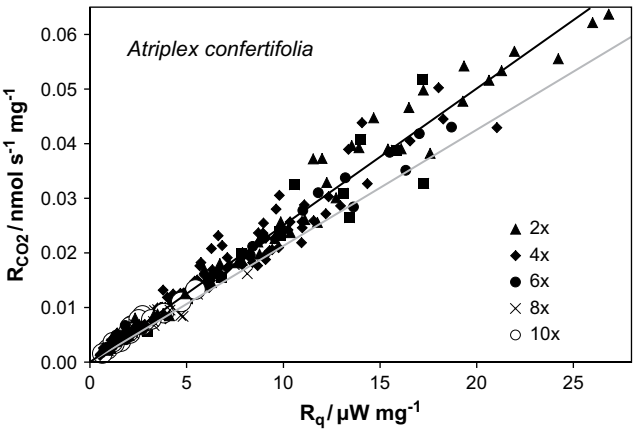

Fig. 1. Rate of CO_2 evolution (R_{CO_2}) plotted against metabolic heat rate (R_q) for leaf tissue from the different ploidy races of shadscale as indicated by different symbols. The lower, gray line represents the heat of combustion of carbohydrate, $y = (1/470)x$, and the upper, solid line is the least squares fit to the data with a forced zero intercept, $y = (0.00251 \pm 0.00019)x$, $r^2 = 0.962$. Measurement temperature ranges from 10 to 35 °C.

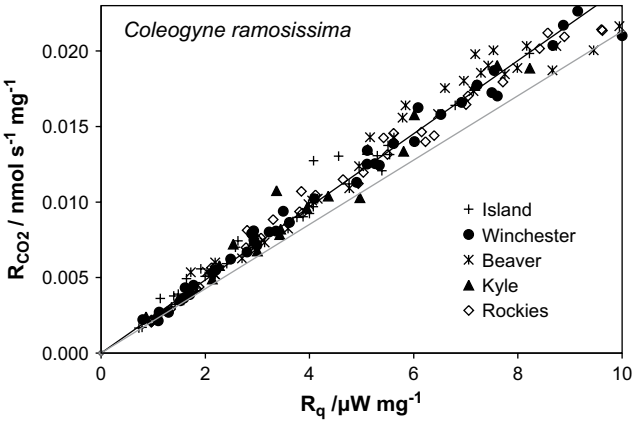

Fig. 2. Rate of CO_2 evolution (R_{CO_2}) against metabolic heat rate (R_q) for leaf tissue from blackbrush seedlings grown from seed collected from different locations as indicated by different symbols. The lower, gray line represents the heat of combustion of carbohydrate, $y = (1/470)x$, and the upper, solid line is the least squares fit to the data with a forced zero intercept, $y = (0.00242 \pm 0.00015)x$, $r^2 = 0.977$. Measurement temperature ranges from 10 to 35 °C.

respiratory heat and CO_2 production rates decrease and thus growth rates decrease as ploidy increases. Appendix 4 (electronic version only) shows anabolic rates ($R_{SG}\Delta H_B$) within shadscale populations at a given location decrease systematically with increasing ploidy. However, quantitation of the effect of ploidy is not possible from these data because tissue samples were collected from the different populations at different times in the season. Since the metabolic rates change with time of season (see Fig. 3), anabolic rates cannot be compared between populations. Fig. 4 shows that blackbrush tissue collected from wild plants shows a similar change in metabolic rate with time of season.

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 (Fig. 3). The difference in these rates between May and June is quite marked, with rates in June about half those in May. Although the optimum temperature (25–30 °C) changes little through the season, $R_{SG}\Delta H_B$ suddenly drops off at 35 °C for tissue collected in April but not tissue collected later in the season, indicating increasing tolerance for higher temperatures as the season progresses.

Blackbrush leaf tissue collected from Moab showed a shift in the optimum temperature for growth ($R_{SG}\Delta H_B$) over the three-month period (Fig. 4). In March, optimum growth occurred between 25

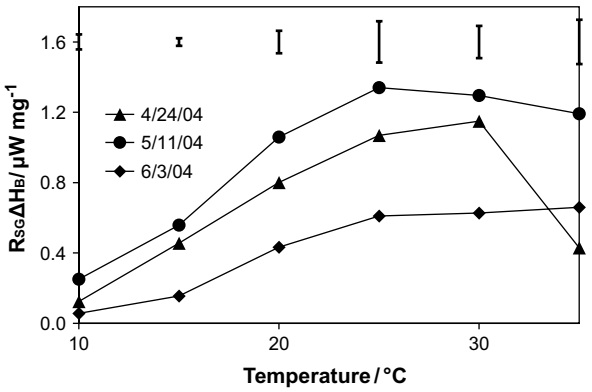

Fig. 3. Specific growth rate ($R_{SG}\Delta H_B$) as a function of temperature, calculated from metabolic heat and CO_2 rates, in microwatts (µW) per mg dry weight for shadscale leaf tissue collected from Moab in late April to early June. The bars indicate the standard error [SE = $\sqrt{(MSE \times 2/r)}$] that applies to data points at each temperature.

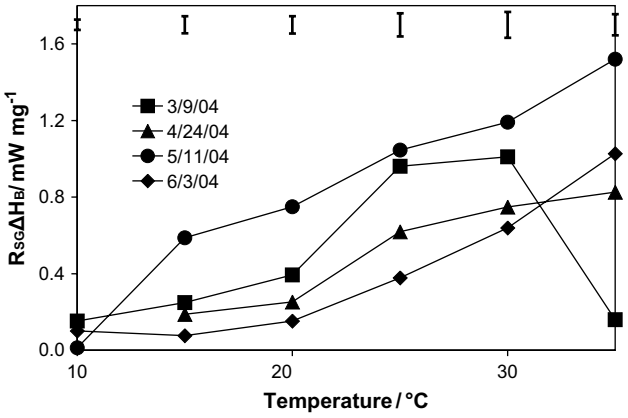

Fig. 4. Specific growth rate ($R_{SG}\Delta H_B$) as a function of temperature, calculated from metabolic heat and CO_2 rates, in microwatts (μW) per mg dry weight for blackbrush leaf tissue collected from Moab 3/9/2004 (not in flower), 4/24/2004 (flowering), 5/11/2004 (near end of flowering), and 6/3/2004 (past flowering—in fruit). The bars indicate the standard error [SE = √(MSE × 2/r)] that applies to data points at each temperature.

and 30 °C and by May shifted to 35 °C, apparently in response to rising average temperatures. In blackbrush, the highest anabolic rates were in tissue collected in May, while leaf tissue collected in April showed rates almost as low as leaf tissue collected in June (Fig. 4). The anomalously high rates measured in March compared with April probably relate to flowering, which occurred from mid-April to mid-May. 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 (Fig. 5) indicating that during early flowering the plants' resources were diverted from leaf growth to reproduction.

More detailed examination of the data in Figs. 1 and 2 shows the temperature response of metabolism differs with the elevation of the seed source for blackbrush and of the wild shadscale plants sampled. Fig. 6A 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 minimum R_q/R_{CO_2} near 20 °C, while blackbrush from lower elevations had the minimum near 25 °C. Note that a lower R_q/R_{CO_2} ratio indicates a higher efficiency, see Eq. (3). Fig. 6B shows that the R_q/R_{CO_2} ratio for shadscale responds similarly to temperature and elevation. The

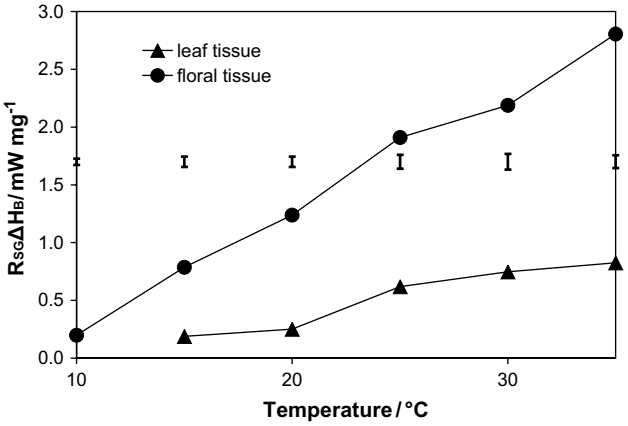

Fig. 5. Specific growth rate $R_{SG}\Delta H_B$ as a function of temperature, calculated from metabolic heat and CO_2 rates, in microwatts (μW) per mg dry weight for blackbrush floral and leaf tissue collected 4/24/2004 from Moab. The bars indicate the standard error [SE = √(MSE × 2/r)] that applies to data points at each temperature.

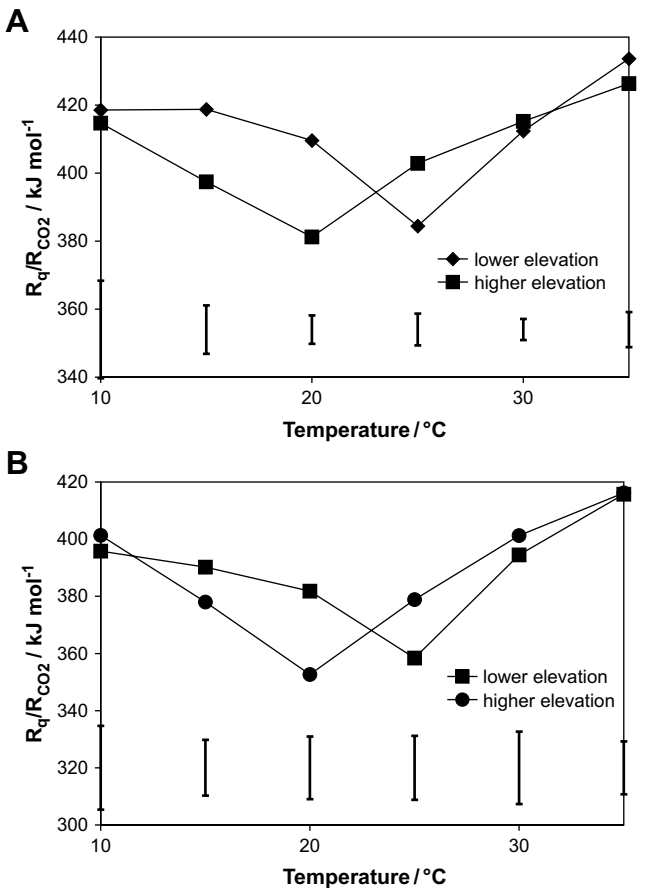

Fig. 6. R_q/R_{CO_2} values as a function of temperature [A] for blackbrush seedlings grown from seed from lower elevations (Winchester Hills, and Kyle Canyon) and higher elevations (Island in the Sky, Little Rockies, Beaver Dam, Veyo Road, and South of Bluff), and [B] for shadscale leaf tissue from wild plants from lower (Lake Mead and Moab) and higher (Millard, Smokey Mtn, Smokey Hollow, Rush Valley, Four Corners, Bigwater, and Cliff Dwellers) elevations. The bars indicate the standard error [SE = √(MSE × 2/r)] that applies to data points at each temperature. Note that the error bars for shadscale include the scatter caused by sampling plants at different times in the season. The significant point to note is the shape of the curve is not affected by this source of scatter.

values of the R_q/R_{CO_2} ratio and the associated uncertainties shown in Fig. 6 show that at the optimum temperature, blackbrush respiration may be slightly less efficient (78 ± 1%) than shadscale (82 ± 1%) ($p < 0.05$). At 10 °C, the differences in substrate carbon conversion efficiency between the species, i.e. $\varepsilon = 69 \pm 7\%$ for blackbrush and 74 ± 5% for shadscale, are within the standard error. At 35 °C shadscale may be slightly more efficient than blackbrush, i.e. $\varepsilon = 62 \pm 2\%$ for blackbrush and 69 ± 2% for shadscale ($p < 0.1$). Because the blackbrush was grown in a common environment, the source of the variation with temperature in this species must be genetic adaptation, not acclimation. The response of this characteristic of respiration to temperature is remarkably consistent between the species.

The figure in Appendix 5 (electronic version only) shows typical examples of Arrhenius plots (i.e. plots of ln(rate) versus reciprocal Kelvin temperature, $\ln(\text{rate}) = (\ln A) + (\mu_{rate}/T)$ where A and μ are constants) of R_{CO_2} and R_q for blackbrush and shadscale. (For reference, $\mu = 6$ corresponds to $Q_{10} = 2$.) The plots for shadscale are linear from 10 to 25 °C above which the plots are curved with decreasing slope. Plots for blackbrush show an abrupt decrease in slope between 20 and 25 °C, but appear to be linear from 10 to 20 °C and from 25 to 35 °C. Above 35 °C the plots are curved with decreasing slope. Appendix 1 (electronic version only) gives the

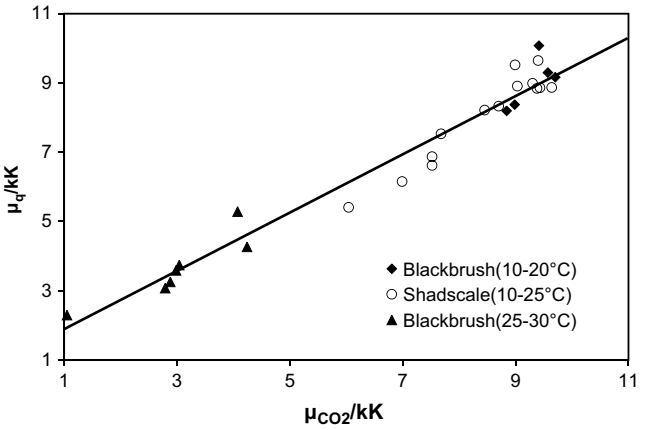

Fig. 7. Correlation between the Arrhenius temperature coefficients for metabolic heat rate (R_q) and CO_2 production rate (R_{CO_2}), see Appendix 1.

Arrhenius temperature coefficients (μ_q and μ_{CO_2}) for all the populations. In the lower temperature range, the μ values are clustered around 9 k K^{-1}, corresponding to $Q_{10} = 3$. The μ values clustered around 3 kK^{-1} in the upper temperature range correspond to $Q_{10} = 1.4$. The values of μ_q and μ_{CO_2} are strongly correlated ($r^2 = 0.961$) as shown in Fig. 7, demonstrating that the catabolic rate (R_q) and the sum of the anabolic and catabolic rates (R_{CO_2}) have similar temperature dependencies. In the lower temperature range, $\mu_{CO_2} > \mu_q$, as required for a growth rate that increases with increasing temperature. In the upper temperature range, $\mu_{CO_2} < \mu_q$, as required for a growth rate that decreases with increasing temperature. The curves of R_q/R_{CO_2} versus temperature in Fig. 6 are a further reflection of the differing temperature dependencies of R_q and R_{CO_2}. The temperature dependence of the growth rate is thus determined by both the temperature dependence of the metabolic rate and the temperature dependence of the efficiency, (see Fig. 6). As indicated by the different temperatures of the minima in Fig. 6A and B, the temperature of maximum efficiency and growth rate is expected to decrease with increasing elevation and latitude, requiring concomitant regular changes in μ values. However, in this study there are too few data points, and not favorably distributed, to determine the correlation between μ and latitude and elevation, but the results do not disagree with the correlation found in a more extensive previous study of three other desert shrub species (Criddle et al., 1994). The previous study examined only the correlation with μ_q, but Fig. 7 shows a similar correlation would hold for μ_{CO_2}.

4. Discussion

The data in Appendix 4 (electronic version only), showing decreasing $R_{SG}\Delta H_B$ with increasing ploidy, agree with previous observations on growth of shadscale. Shadscale plants with higher ploidy numbers are generally smaller, particularly than diploid plants (Stutz and Sanderson, 1983). The increase in ploidy (2×–10×) appears to be the mechanism for physiological adaptation of shadscale to new habitats. Diploid shadscale is found above the level of the Pleistocene lakes, while polyploids grow in valley sides and bottoms. These polyploids probably formed as the lakes disappeared and new habitats appeared (Stutz and Sanderson, 1983). In general, available moisture decreases and salinity increases with decreasing elevation in the shadscale range. Increased ploidy is also correlated with increased osmotic capability (Sanderson et al., 1989), corresponding to increasing salinity from foothills to valley bottom. The large ash content of shadscale leaves reflects the halophilous character of this species.

As a surrogate for environmental temperature, elevation has a clear effect on the temperature of maximum substrate conversion efficiency ($p \leq 0.01$) (Fig. 6) and therefore also on the temperature of maximum growth rate of both blackbrush and shadscale. Blackbrush seed germination requirements also vary with elevation; populations from lower (warmer) elevations have lower primary seed dormancy and shorter chilling requirements than populations from higher elevations (Lei, 1997; Pendleton and Meyer, 2004). Thus, while blackbrush has commonly been assumed to be a paleoendemic species lacking in genetic variation (following the original postulation by Stebbins and Major, 1965), there clearly is genetic variation among blackbrush populations.

Shadscale and blackbrush tissue collected in Moab showed the highest specific anabolic rates in May (Figs. 3 and 4), indicating that they have both adapted to their environment so they grow most when average temperatures are warmer, but when water is still available. In agreement with the hypothesis that adaptation to grow in a common environmental temperature pattern requires similar respiratory responses to temperature, their responses to temperature and elevation are very similar. These similarities in responses of growth and respiration to temperature clearly exist despite large differences in life histories and non-respiratory characteristics. Some quantitative differences in respiratory properties other than temperature responses are present. The most notable differences are that, at optimum growth temperatures and time of season when growth rate is maximum, specific anabolic rates of shadscale are approximately double those of blackbrush. Although the temperature responses of growth and respiration rates in the two species are very similar during the spring and early summer, in mid- to late-summer the temperature responses of R_q and of R_{CO_2} differ. Blackbrush acclimates 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 (Fig. 5), while for shadscale, anabolic rates flatten out or even drop off slightly between 25 and 30 °C (Fig. 3). Blackbrush should therefore be able to carry out anabolic activity in Moab even in the heat of summer as long as there is 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). Metabolic adaptation of blackbrush for slow growth and growth at high temperatures so as to take advantage of summer rain appears to result from natural selection for long-term survival in an environment where resources (e.g. nitrogen and water) are scarce, but relatively stable over the long-term. In comparison, shadscale metabolism is adapted for fast growth and early reproduction in the more variable environment of deep, fine textured soils with a high salt content. These two very different strategies are apparent in the metabolic characteristics and apparently confine these species to their niches as defined by soil type.

Acknowledgments

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Appendix 1. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2008.09.010.

References

Ackerman, T.L., Bamberg, S.A., 1974. Phenological studies in the Mojave Desert at rock valley (Nevada Test Site). In: Lieth, H. (Ed.), Phenology and Seasonality Modeling. Springer-Verlag, New York, pp. 215–226.

Ackerman, T.L., Romney, E.M., Wallace, A., Kinnear, J.E., 1980. Phenology of desert shrubs in southern Nye County, Nevada. In: Nevada Desert Shrub Ecology. The Great Basin Naturalist Memoirs, vol. 4. Brigham Young University, Provo, UT, pp. 4–23.

Anekonda, T., Jones, C., Smith, B.N., Hansen, L.D., 2004. Differences in physiology and growth between coastal and inland varieties of Douglas fir seedlings in a common garden. Thermochimica Acta 422, 75–79.

Bradley, W.G., 1964. The vegetation of the Desert game range with special reference to the Desert Bighorn. Transactions, Desert Bighorn Council, 43–67.

Callison, J., Brotherson, J.D., 1985. Habitat relationships of the blackbrush community (*Coleogyne ramosissima*) of southwestern Utah. Great Basin Naturalist 45, 321–326.

Callison, J., Brotherson, J.D., Bowns, J.E., 1985. The effects of fire on the blackbrush [*Coleogyne ramosissima*] community of southwestern Utah. Journal of Range Management 38, 535–538.

Criddle, R.S., Hopkin, M.S., McArthur, E.D., Hansen, L.D., 1994. Plant distribution and the temperature coefficient of metabolism. Plant, Cell and Environment 17, 233–243.

Criddle, R.S., Smith, B.N., Hansen, L.D., 1997. A respiration based description of plant growth rate responses to temperature. Planta 201, 441–445.

Criddle, R.S., Hansen, L.D., 1999. Calorimetric methods for analysis of plant metabolism. In: Kemp, R.B. (Ed.), Handbook of Thermal Analysis and Calorimetry. Elsevier, Amsterdam, pp. 711–763.

Ellingson, D., Olson, A., Matheson, S., Criddle, R.S., Smith, B.N., Hansen, L.D., 2003. Determination of the enthalpy change for anabolism by four methods. Thermochimical Acta 400, 79–85.

Gebauer, R.L.E., Ehleringer, J.R., 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81, 1415–1424.

Hansen, L.D., Church, J.N., Matheson, S., McCarlie, V.W., Thygerson, T., Criddle, R.S., Smith, B.N., 2002. Kinetics of plant growth and metabolism. Thermochimica Acta 388, 418–425.

Hansen, L.D., Macfarlane, C., Mckinnon, N., Smith, B.N., Criddle, R.S., 2004. Use of calorespirometric ratios, heat per CO_2 and heat per O_2, to quantify metabolic paths and energetics of growing cells. Thermochimica Acta 422, 55–61.

Hansen, L.D., Criddle, R.S., Smith, B.N., 2005. Calorespirometry in plant biology. In: Lambers, H., Ribas-Carbon, M. (Eds.), Plant Respiration, from Cell to Ecosystem. Springer, Dordrecht, pp. 17–30.

Hemming, D.J.B., Meyer, S.E., Smith, B.N., Hansen, L.D., 1999. Respiration characteristics differ among cheatgrass (*Bromus tectorum L.*) populations. Great Basin Naturalist 59, 355–360.

Keller, E.A., Anekonda, T.S., Smith, B.N., Hansen, L.D., St. Clair, J.B., Criddle, R.S., 2004. Stress and respiration traits differ among four geographically distinct *Pinus ponderosa* seed sources. Thermochimica Acta 422, 69–74.

Lei, S.A., 1997. Variation in germination response to temperature and water availability in blackbrush (*Coleogyne ramosissima*) and its ecological significance. Great Basin Naturalist 57, 172–177.

Lei, S.A., Walker, L.R., 1997. Biotic and abiotic factors influencing the distribution of *Coleogyne* communities in southern Nevada. Great Basin Naturalist 57, 163–171.

Lin, G., Phillips, S.L., Ehleringer, J.R., 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. Oecologia 106, 8–17.

Matheson S., 2000. Metabolic adaptation of oats to climatic temperature. Thesis, Brigham Young University, Provo, UT, USA.

McArthur, E.D., Sanderson, S.C., 1985. A cytotaxonomic contribution to the western North American Rosaceous flora. Madroño 32, 24–28.

Pendleton, B.K., Meyer, S.E., 2004. Habitat-correlated variation in blackbrush (*Coleogyne ramosissima*: Rosaceae) seed germination response. Journal of Arid Environments 59, 229–243.

Pendleton, B.K., Meyer, S.E., Pendleton, R.L., 1995. Blackbrush biology: insights after three years of a long-term study. In: Roundy, B.R., McArthur, E.D., Haley, J.S., Mann, D.K. (Eds.), Wildland Shrub and Arid Land Restoration Symposium. Proceedings INT-GTR-315. Ogden, UT. USDA Forest Service, Intermountain Research Station, Provo, UT, pp. 223–227.

Phillips III, A.M., VanDevender, T.R., 1974. Pleistocene packrat middens from the lower Grand Canyon of Arizona. Journal of the Arizona Academy of Science 9, 117–119.

Sanderson, S.C., McArthur, E.D., Stutz, H.C., 1989. A relationship between polyploidy and habitat in western shrub species. In: Wallace, A., McArthur, E.D., Haferkamp, M.R. (Eds.), Symposium on Shrub Ecophysiology and Biotechnology. Proceedings INT-256. Ogden, UT. USDA Forest Service, Intermountain Research Station, Provo, UT, pp. 23–30.

Sanderson, S.C., Stutz, H.C., McArthur, E.D., 1990. Geographic differentiation in *Atriplex confertifolia*. American Journal of Botany 77, 490–498.

Smith, B.N., Jones, A.R., Hansen, L.D., Criddle, R.S., 1999. Growth, respiration rate, and efficiency responses to temperature. In: Pessarakli, M. (Ed.), Handbook of Plant and Crop Stress, second ed. Marcel Dekker, Inc., New York, pp. 417–440.

Spaulding, W.G., 1990. Vegetation dynamics during the last deglaciation, southeastern Great Basin. U.S.A. Quaternary Research 33, 118–203.

Stebbins, G.L., Major, J., 1965. Endemism and speciation in the California flora. Ecological Monographs 35, 1–35.

Stutz, H.C., Sanderson, S.C., 1983. Evolutionary studies of Atriplex: chromosome races of *A. confertifolia* (shadscale). American Journal of Botany 70, 1536–1547.

Taylor, D.K., Rank, D.R., Keiser, D.R., Smith, B.N., Criddle, R.S., Hansen, L.D., 1998. Modelling temperature effects on growth-respiration relations of maize. Plant, Cell and Environment 21, 1143–1151.

Thornton, W.M., 1917. The relation of oxygen to the heat of combustion of organic compounds. Philosophical Magazine 33, 196–203.

Wells, P.V., 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs 53, 341–382.

Welsh, S.L., Atwood, N.D., Goodrich, S., Higgins, L.C., 1987. A Utah Flora. In: Great Basin Naturalist Memoirs, vol. 9. Brigham Young University, Provo, UT, p. 118.