Journal of Arid Environments 72 (2008) 643–651

Journal of Arid Environments

www.elsevier.com/locate/jaridenv

Two subspecies and a hybrid of big sagebrush: Comparison of respiration and growth characteristics

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Received 31 May 2007; received in revised form 30 August 2007; accepted 31 August 2007

Abstract

Environmental temperatures and growth and respiratory characteristics of natural populations of two subspecies and a hybrid of sagebrush (*Artemisia tridentata*) that grow on a single hillside were measured to test a hypothesis that adaptation to microclimate temperature patterns restricts these taxa to their native locations and that plant–endophyte associations are important to temperature adaptation. Reciprocal transplants of plants and soil translocation have previously shown that plants grown outside of their native sites or in non-indigenous soil have different respiratory properties and are less vegetatively and reproductively productive than natural populations. A recent study shows that taxa specific endophytes may be responsible for the differences in respiration characteristics and productivity of transplants growing in non-indigenous soils. In this study, hourly temperatures were measured at the upper and lower sites and the newest leaves from natural populations of each subspecies and hybrid were sampled monthly from mid-February to mid-July 2005. Respiratory heat and CO_2 production rates of the leaves were measured at 5 °C intervals from 10 to 35 °C, as well as heats of combustion and carbon and nitrogen contents. Growth rates and substrate carbon conversion efficiencies were calculated from the respiration data. Monthly mean temperature differences of up to 1 °C were measured at the native sites. Differences between the respiratory and growth characteristics of the three populations may explain the hybrid zone architecture of indigenous populations, but are not large enough to explain the different respiratory characteristics and poor survival and productivity of transplants.

Keywords: *Artemisia tridentata*; Calorespirometry; Endophytes; Substrate Carbon Conversion Efficiency; Temperature adaptation

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1. Introduction

Three populations of big sagebrush (*Artemisia tridentata*) that have been the object of several previous studies grow on the same hillside in Salt Creek Canyon near Nephi, Juab Co., Utah (Miglia, 2003; Smith et al., 2002; Wang, 1996). Mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) grows on a bench at the top of the

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doi:10.1016/j.jaridenv.2007.08.011

hill at an elevation of 1890 m and basin big sagebrush (*A. tridentata* ssp. *tridentata*) grows in the canyon bottom at 1800 m. A hybrid swarm exists between these parental populations. Ssp. *vaseyana* is characteristically small, only growing up to about 50 cm tall, while ssp. *tridentata* grows up to about 250 cm. The hybrid population shows mixed morphology with both short and tall plants, but previous morphological and chemical studies have shown that plants in this hybrid swarm are hybrids of various classes (Byrd et al., 1999; Freeman et al., 1991; McArthur and Sanderson, 1999). Several double reciprocal transplant experiments have been conducted in three fenced gardens established on the hillside at 1890 m in the mountain big sagebrush zone, at 1850 m near the center of the hybrid swarm zone, and at 1800 m in the basin big sagebrush zone. Previous studies show that parental taxa and hybrids are most fit in their native zones, but less fit when transplanted into the other zones or into non-indigenous soils (Graham et al., 1995; McArthur and Sanderson, 1999; Miglia et al., 2005, 2007 and unpublished data; Wang et al., 1997). Earlier studies of respiratory characteristics of plants grown in the gardens (McArthur et al., 1998; Smith et al., 1999, 2002) found that plants growing in non-native zones had low productivity because their respiratory characteristics differed from those of plants growing in the garden in their native zone. However, these earlier studies did not identify the cause of the decreased fitness. The study described in this paper examines the interaction between the environment and respiratory characteristics that might determine plant fitness both in natural populations and in transplants to non-native locations and non-indigenous soils.

The first goal of this study is, by comparing respiratory and growth characteristics of natural populations growing outside the fenced gardens, to test a hypothesis that adaptation to local temperature patterns (i.e. average temperature, diurnal temperature change, maximum and minimum temperatures) restricts these sagebrush taxa to their native locations, thus maintaining a hybrid zone architecture, i.e. a stable separation of the subspecies with a hybrid zone or hybrid swarm in between for an extended period of time (Harrison, 1993; Miglia, 2003). To optimize fitness, plant respiration and growth must be adapted to both diurnal temperature variation as well as to the mean temperature (Criddle et al., 2005). Because of the topography, environmental temperature patterns are expected to differ between the population sites. The slope faces east, and therefore the upper site warms earlier in the day than the lower or middle sites. The sun also sets earlier in the lowest site, leaving the lower sites at a lower temperature for longer than the uppermost site. The uppermost site is thus expected to be the warmest on average. The study was conducted during an entire vegetative growth season (February through July of 2005).

A second goal of the study is, by comparing respiratory and growth characteristics of the natural populations measured in this study to those of transplants measured in previous studies, to determine why transplants growing in non-native zones or in non-indigenous soils at native sites are less fit. Recent studies (Freeman, unpublished data, McArthur, unpublished data) show that plants infected with non-indigenous endophytes growing in non-indigenous soils have reduced vegetative and reproductive production even when planted at their native locations, whereas plants from all three taxa appear to grow well in all three gardens if they are infected with the natural endophyte in indigenous soils. Infection by non-indigenous endophytes thus may explain the differences in respiratory and growth characteristics seen in previous studies of plants grown inside the gardens (McArthur et al., 1998; Smith et al., 1999, 2002). Other work (Marquez et al., 2007) shows that temperature tolerance of plants can be drastically altered by mutualistic association with a fungal endophyte.

The two goals of the study are complementary; together suggesting a general hypothesis that endophyte–plant associations determine the respiratory characteristics, including temperature responses, which in turn determine plant productivity and hence fitness in a given environment. The temperature differences between the three population sites are expected to be of the same order of magnitude as expected from climate change. If the hypothesis tested in this study, i.e. that adaptation to small differences in average temperature or in diurnal temperature variation is a significant determinant of survival and reproductive success, the results would contribute to understanding and thus to predicting the effects of climate change on native plant populations.

2. Materials and methods

Temperature data were collected hourly at the upper (mountain big sagebrush) and lower (basin big sagebrush) reciprocal transplant gardens (Miglia, 2003; Wang, 1996) in Salt Creek Canyon with HOBO

Pro-Temperature Data Loggers (Onset Computer Corp., Pocasset, MA). Branches were cut from 10 to 12 randomly selected native sagebrush plants next to these gardens monthly from mid-February to mid-July 2005. Collected tissue samples were placed in open plastic bags and transported in ice chests back to the lab where they were stored in a 5 °C room.

Respiratory measurements were made during the two days following each collection. The branches' youngest leaves were removed with a razor blade, and approximately 100 mg of tissue placed in an ampule of an isothermal calorimeter (Hart Scientific Model 7707, Calorimetry Sciences Corporation Model 4100 or a similar 16-cell prototype calorimeter built by Calorimetry Sciences Corp., Lindon, Utah, USA). The metabolic heat rate (R_q) and rate of CO_2 production (R_{CO_2}) were measured by the methods described in Criddle and Hansen (1999), Criddle et al. (1997), and Hansen et al. (2005). These measurements were repeated at 5 °C intervals, ranging downward from 20 to 10 °C (4 replicates), and upward from 20 to 30 °C (4 replicates) and 30 to 35 °C (10–12 replicates). Data taken on the second day statistically differed ($p = 0.03$) from data taken on the first day, but the average decrease ($0.2\,\mu W\,mg^{-1}$) was the same for all three populations and the decrease was insignificant compared with the random scatter in the data. Therefore, the data from both days were averaged without adjustment. Dry weights were obtained on the samples used for metabolic measurements after drying in a vacuum oven at 70–80 °C for 24 h.

A model 1425 Parr oxygen bomb calorimeter (Parr Instrument Co., Moline, IL) calibrated with benzoic acid was used to determine the heats of combustion for each of the samples (two to eight replicates). Leaf tissue was removed from the stems, ground with a coffee grinder, dried in a vacuum oven at 70–80 °C, and then pressed into 0.2 g pellets for combustion. Ash content was determined as the mass remaining in the combustion boats following a complete, successful burn.

Carbon and nitrogen contents were determined with an elemental analyzer (Costech, Model ECS 4010, Valencia, CA) on three replicates of the same material used to measure the heats of combustion.

Statistical analyses were done by the Statistics Consultation Center at Brigham Young University.

2.1. Calculating growth rates and efficiencies from respiratory heat and CO_2 rates

A previously published thermodynamic model (Criddle and Hansen, 1999; Criddle et al., 1997; Hansen et al., 2004; Hansen et al., 2005) relating substrate carbon conversion efficiency and growth rate to metabolic heat rate (R_q) and CO_2 production rate (R_{CO_2}) assumes the rate of growth or development is directly proportional to the anabolic rate (R_{AP}):

$$R_{AP} = \frac{[(-R_{CO_2})(\Delta H_{CO_2}) - R_q]}{\Delta H_B} \tag{1}$$

ΔH_{CO_2} is the enthalpy change for combustion of the substrate per C-mole, assumed to be a carbohydrate under the conditions of this study. For oxidation of carbohydrates to CO_2 and water, ΔH_{CO_2} equals $-470\,kJ\,mol^{-1}$ of oxygen consumed or per mole of CO_2 produced. (For other substrates, ΔH_{CO_2} can be approximated as $(-455 \pm 15\,kJ\,mol^{-1}\,O_2)\,[1-(\gamma_s/4)]$ where γ_s is the average chemical oxidation state of carbon in the substrate; $\gamma_s = 0$ for carbohydrates.) ΔH_B is the difference in the enthalpy changes per C-mole for combustion of the substrate and of the anabolic product. If ΔH_B is constant between compared values, $R_{AP}\Delta H_B$ can be used as a relative measure of growth rate.

The equation for substrate carbon conversion efficiency (ε) in terms of R_q, R_{CO_2} and ΔH_B is

$$\frac{R_q}{R_{CO_2}} = -\Delta H_{CO_2} - \Delta H_B \left[\frac{\varepsilon}{1-\varepsilon}\right] \tag{2}$$

As long as ΔH_{CO_2} and ΔH_B are constant, the ratio R_q/R_{CO_2} can be used as a relative measure of efficiency. Essentially all metabolic heat is produced by the oxidative reactions of catabolism, while CO_2 is produced by both catabolism and anabolism. Smaller values of R_q/R_{CO_2} thus indicate greater efficiency of growth because less energy from catabolism is lost to the environment per unit of anabolism, and larger values of R_q/R_{CO_2} indicate that more energy is lost per unit of growth. Note that because $R_{CO_2}/R_{O_2} = R_{CO_2}/(R_q/455\,kJ\,mol^{-1}\,O_2)$, the ratio R_{CO_2}/R_q is proportional to the respiratory quotient.

3. Results

Appendix 1, electronic version, gives the results of determinations of carbon and nitrogen contents and ΔH_B values for the leaf tissue of the three populations. Carbon content does not differ with location ($p = 0.96$), but differs among months ($p = 0.001$). However, the variation shows no systematic pattern or decrease with advancing time in the season. Nitrogen content does not differ among months ($p = 0.15$), but does differ among locations ($p = 0.015$). The difference in leaf nitrogen content between the upper and middle populations is not significant ($p = 0.38$), but plants from the upper and middle populations both have significantly less nitrogen than plants from the lower garden ($p = 0.006$ and 0.03, respectively). ΔH_B values for the upper and middle populations are not significantly different ($p = 0.7$), but both differ from the lower population value ($p = 0.02$ and 0.04 for upper and middle, respectively). Although there are statistically significant differences between the populations, the differences in composition and energy content are small and probably do not contribute to differences in fitness.

Fig. 1 shows monthly average temperatures and temperature variations at the upper and lower gardens for the study period. Short-term temperature variation does not differ between the locations. During the early part of the season the uppermost site is cooler than the lower, but during May and June when most growth occurs, the upper site is up to 1 °C warmer than the lower, Fig. 1b.

Metabolic heat rates (R_q) in Fig. 2 and CO_2 production rates (R_{CO_2}) in Fig. 3 are shown as functions of temperature. For a given population, the heat and CO_2 rates exhibit similar seasonal responses to temperature, but responses of the populations differ in detail. R_q and R_{CO_2} values for the upper population are at a maximum during June; the maximum for the middle population occurs between May and June and the maximum for the lower population occurs during May. Metabolic rates for the middle and lower populations are more similar to each other than to the upper population. Note that the metabolic

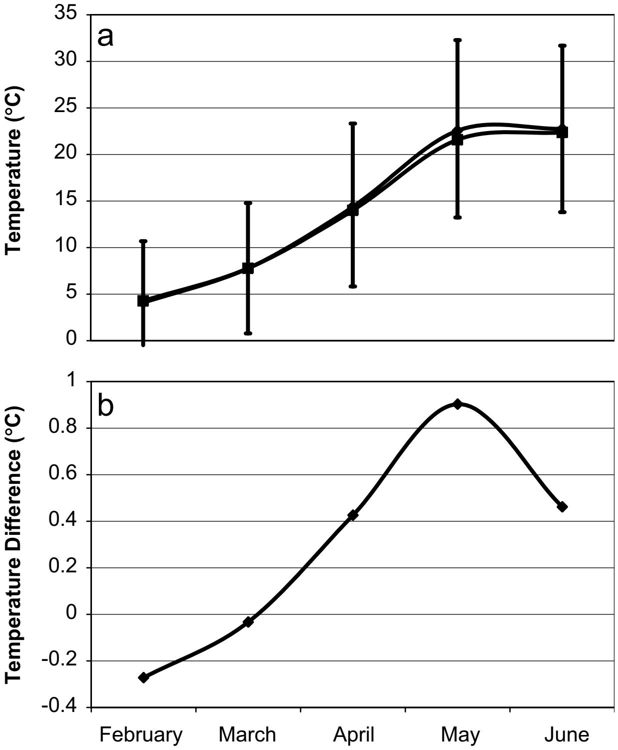

Fig. 1. (a) Monthly average temperatures in the upper (◆) and lower (■) sagebrush gardens and (b) differences in monthly average temperatures; upper minus lower garden. Temperature variations of the upper and lower gardens are plotted as twice the standard deviation which indicates 95% of the values.

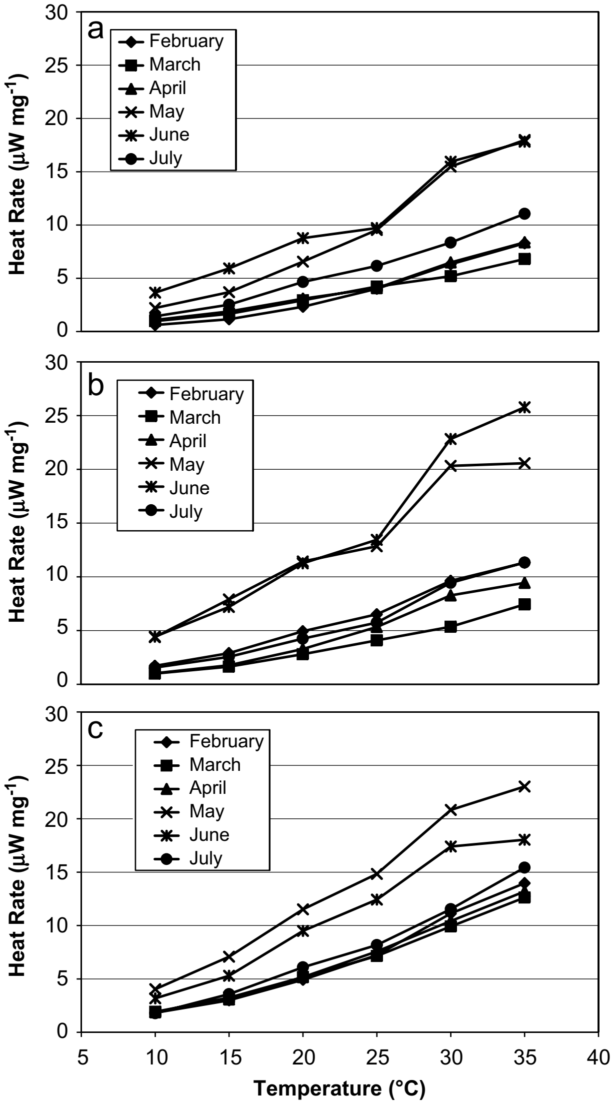

Fig. 2. Specific metabolic heat rates of sagebrush leaf tissue as functions of temperature and month for (a) upper, (b) middle, and (c) lower populations. The average precision of the heat rate is ±9% expressed as the standard error.

heat and CO_2 rates of the upper population are only about two-thirds those of the middle and lower populations.

Plots of R_{CO_2} versus R_q were fit to a linear equation (i.e. $R_{CO_2} = a + bR_q$) by least squares to (a) determine if the substrate carbon conversion efficiency changes with temperature and to (b) obtain values of the ratio R_{CO_2}/R_q. These results are given in Appendix 2, electronic version. No significant differences in the slopes or intercepts were found between the populations. Therefore, there are no significant differences in substrate carbon conversion efficiencies between the populations.

Temperature responses of the heat and CO_2 production rates are summarized in Appendix 3, electronic version, as coefficients of the Arrhenius equation, $\ln R = \ln A - (\mu/T)$, from 10 to 20 °C. These data do not show any significant differences among the three populations. Taken together with the higher temperature data in Figs. 2 and 3, this result shows there are no differences in the temperature responses of respiration rates among the populations.

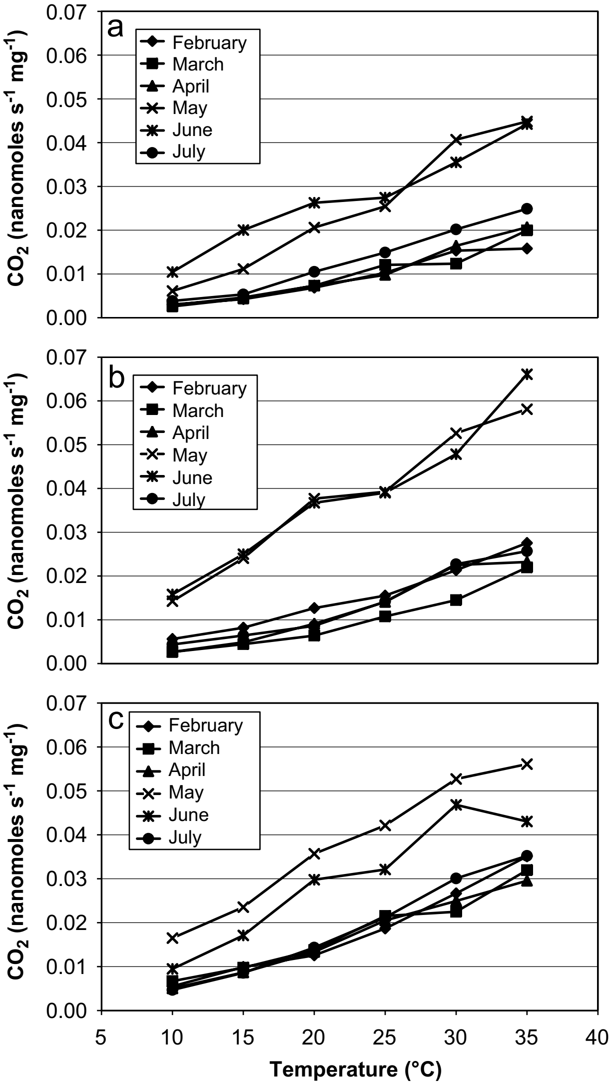

Fig. 3. Carbon dioxide production rates of sagebrush leaf tissue as functions of temperature and month for (a) upper, (b) middle, and (c) lower populations. The average precision of the CO_2 production rate is ±13% expressed as the standard error.

Plots of growth rate of the leaf tissue in Fig. 4 (as $\Delta H_B R_{SG}$, calculated from R_q and R_{CO_2}, see Eq. (1)), as a function of temperature show that growth rates are maximal in May and June and the optimal growth temperature is approximately 20 °C for all three populations. Note that 20 °C is near the average environmental temperature during May and June (≈18 °C, see Fig. 1). Growth rates decrease rapidly above 25 °C. The abrupt changes in direction in the plots of $\Delta H_B R_{SG}$ indicate severe temperature stress above 30 °C. The maximum growth rate at 20 °C of leaf tissue from plants in the upper population ($3.6 \pm 0.6\,\mu W\,mg^{-1}$ with $n = 8$) is significantly lower ($p = 0.86$) than growth rates of leaf tissue from the middle and lower populations, ($6.2 \pm 1.0\,\mu W\,mg^{-1}$ with $n = 8$) and ($5.2 \pm 0.8\,\mu W\,mg^{-1}$ with $n = 8$), respectively.

Although a direct, quantitative comparison is not possible because of differing study designs, the respiratory and growth characteristics found in this study of natural populations clearly differ from those found in previous studies (McArthur et al., 1998; Smith et al., 1999, 2002, and unpublished data) of plants growing in non-native locations or in non-indigenous soils. These transplants had lower carbon substrate conversion efficiencies and poorer tolerance to high temperatures; consistent with poor growth, both calculated from respiration data and directly observed.

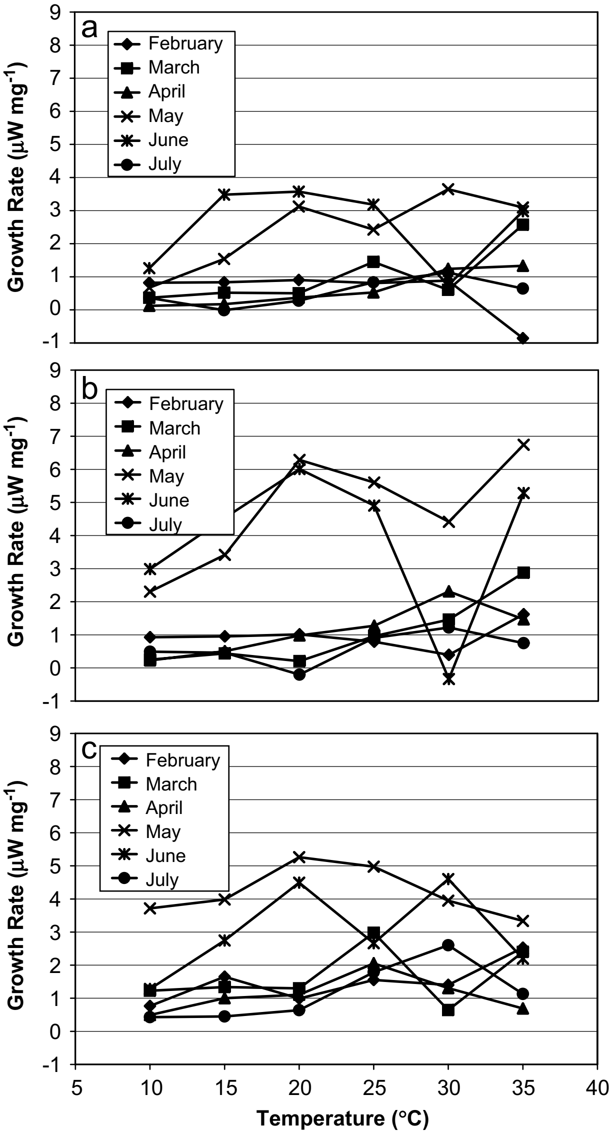

Fig. 4. Relative growth rates of sagebrush leaf tissue as functions of temperature and month for (a) upper, (b) middle, and (c) lower populations; calculated from respiratory heat and carbon dioxide production rates. The average precision of the growth rate is estimated to be ±16% expressed as the standard error.

4. Discussion

The only significant differences in respiration and growth characteristics among the three natural populations are (a) respiration and growth rates of the uppermost population (*vaseyana*) are only about two-thirds those of the middle (hybrid) and lower (*tridentata*) populations, and (b) seasonal maximum respiration and growth rates of *vaseyana* occur approximately two weeks later in the season than for hybrids and approximately a month later than for *tridentata* at the lowest elevation. This latter result is surprising since the uppermost site is the warmest during the season of maximum growth. If the shift from slow to rapid growth as seen in Fig. 4 of the plants at the upper site was triggered by the same temperature as for plants at lower sites, the upper site plants would exhibit their maximum growth rate earlier in the season than plants at the lower, cooler sites, but exactly the opposite is observed. The delay in maximum growth period at the uppermost site increases the temperature difference at which most of the growth occurs. We thus posit that cumulatively, over the decades-long life spans of big sagebrush plants, these differences contribute to differential fitness of the subspecies in their respective habitats. We thus conclude that temperature differences of the order of 1 °C and differences in timing of changes in growth rate are important in restricting these taxa to their native locations. Responses of the plants to temperature differences between the sites thus partially answer the question of why the hybrid architecture is stable and the much more vigorous hybrid and ssp. *tridentata* plants have not displaced the slower-growing ssp. *vaseyana* under current, natural and competitive conditions.

Since climate change is expected to cause temperature changes of the order of 1 °C, this result supports the idea that small changes in temperature and seasonality will cause significant changes in the distribution of native plants (Criddle et al., 2005). Specifically, considering only the effects of temperature, if a uniform 1 °C rise in temperature occurs at this study site, the hybrid swarm would be replaced by ssp. *vaseyana* and ssp. *tridentata* at the bottom of the hillside would be replaced by the hybrid, i.e. the upper and middle taxa would move down the hillside and replace the current taxa. However, if plant–endophyte association controls temperature adaptation as suggested by the data on transplants (Freeman, unpublished data, McArthur, unpublished data), both subspecies would go extinct and the hybrid would move to the lower site, leaving the upper and middle zones devoid of sagebrush.

The respiratory and growth characteristics of the natural populations included in this study show large differences from these characteristics measured in previous studies (Miglia, 2003; Smith et al., 1999, 2002) on plants from the same populations, but grown in the gardens at non-indigenous locations. These differences are sufficiently large to explain the rapid decline in productivity of plants growing at non-indigenous locations, but raise the question of how growth at a non-indigenous location or in a non-indigenous soil changes the respiratory characteristics. Because only plants growing in indigenous soil were included in this study, and thus assumed to be infected with the indigenous endophyte, and because other studies at this site (Freeman, unpublished data, McArthur, unpublished data) show reduced fitness when plants are infected with a non-native endophyte, we conclude the differences in respiratory and growth properties observed in this and the earlier studies is probably a consequence of plant–endophyte associations. Thus, the ultimate reason why mountain big sagebrush (ssp. *vaseyana*) has not been displaced is because the soil at the upper location contains the wrong endophyte to support rapid growth and fecund reproduction of the hybrid or basin big sagebrush (ssp. *tridentata*), and further, because these endophyte–plant associations have the wrong temperature responses. This further suggests, in agreement with a recent report (Marquez et al., 2007), that plant–endophyte associations may be a determinant of the temperature responses of plant respiration and thus of growth characteristics.

Acknowledgments

We gratefully acknowledge support from BYU for this work. We appreciate our colleagues, Carl Freeman, Rusty Rodriguez, Regina Redman and Kathy Miglia sharing unpublished data with us and Rusty Russell's help with graphics.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2007.08.011.

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