Respiration characteristics differ among cheatgrass (Bromus tectorum L.) populations

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The annual grass *Bromus tectorum* was introduced into western North America in the late 19th century and is now a dominant plant in many areas including the Great Basin (Mack 1981). Alteration of the wildfire cycle has contributed to this invasion. Before European settlement, areas of the Great Basin experienced wildfires once each 32–70 yr, but now, because of cheatgrass, many areas have wildfires every 3–5 yr (Whisenant 1990). More frequent burns accelerate conversion of vegetation from shrubs to annual grasses.

Because frequent burning is counterproductive and areas of cheatgrass are too extensive for mechanical or chemical control, the best possibility for controlling cheatgrass is to find plants that can compete effectively with this weed (Pellent 1990). Cheatgrass is a predominantly self-pollinating winter annual. Seeds ripen and disperse in early summer but do not germinate until autumn (Beckstead et al. 1996). Germinated seedlings overwinter and continue growth in the very early spring, then flower and set seed by early June. Because most precipitation in the Great Basin is winter snow, cheatgrass can effectively use winter–spring moisture to outcompete rival summer-active species.

Seed maturation and germination differences among populations of cheatgrass are known adaptations to particular sites (Beckstead et al. 1996), and such differences have a genetic basis (Novak et al. 1991). Among populations of other species, differences in photosynthesis, water-use efficiency, and respiration have been documented ( Tilman 1993). This study shows that respiratory characteristics differ among populations of cheatgrass. Two measures of respiration rate, CO$_2$ evolution rate and metabolic heat rate, and their temperature dependencies were determined and used to calculate growth rate and efficiency of converting photosynthate to structural carbon, both as functions of temperature (Hansen et al. 1994).

Increased understanding of adaptation of cheatgrass metabolism to environmental temperature may provide a basis from which to begin selecting populations of other species that can compete effectively with cheatgrass early in the growing season. Other properties of the environment, e.g., growth season, water availability, soil type, and mineral exchange...
TABLE 1. Origin of Bromus tectorum used in this study.

<table>
<thead>
<tr>
<th>Location</th>
<th>Community type</th>
<th>Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) St. George, UT</td>
<td>creosote bush scrub</td>
<td>ca 850 m</td>
</tr>
<tr>
<td>(2) Hobble Creek Canyon,</td>
<td>mountain brush</td>
<td>ca 1250 m</td>
</tr>
<tr>
<td>Springville, UT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(3) Potosi Pass, near Las Vegas</td>
<td>blackbrush</td>
<td>ca 1250 m</td>
</tr>
<tr>
<td>NV</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(4) Whiterocks Rd, near</td>
<td>shadscale, Wyoming big sagebrush</td>
<td>ca 1450 m</td>
</tr>
<tr>
<td>Dugway, UT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(5) Strawberry Reservoir, UT</td>
<td>mountain meadow</td>
<td>ca 2290 m</td>
</tr>
<tr>
<td>(6) Fairview Rd., Manti-LaSal</td>
<td>aspen/fir</td>
<td>ca 2520 m</td>
</tr>
<tr>
<td>National Forest, UT</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

capacity, and physiological parameters other than those included in this study are also important but are not considered here.

MATERIALS AND METHODS

Cheatgrass seed from 6 different populations (Table 1) was provided by the USDA Forest Service Shrub Sciences Laboratory in Provo, Utah. Seed used in the 1st part of this study was harvested from all 6 populations immediately following the 1992 growing season. Seed was also collected in 1995 from greenhouse-grown progeny of 10 maternal lines of 3 populations and used for a more extensive 2nd set of measurements.

Cheatgrass seed was germinated at room temperature in normal room light on wet filter paper in petri dishes. Measurements were made on whole seedlings, 5–8 d old. Several previous studies have shown data on seedlings predict vegetative growth rates of older plants (Anekonda, Criddle, and Hansen 1994, Anekonda, Criddle, Libby et al. 1994, Criddle et al. 1995, Monaco et al. 1994, Smith et al. 1996, Taylor et al. 1998).

All data were collected with Hart Scientific model 7707 differential, heat conduction, temperature-scanning calorimeters operated in the isothermal mode according to published procedures (Criddle et al. 1991, Hansen et al. 1996). Baseline corrections were made with data taken on empty ampules. Specific metabolic heat rates, q (μJ s⁻¹ mg dry wt⁻¹ or μW mg dry wt⁻¹), and dark respiratory CO₂ rates, R_CO₂ (pmol s⁻¹ mg dry wt⁻¹), were calculated from the measurements. Tissue was dried overnight at 70°C in a vacuum oven for dry weight. Measurements of q and R_CO₂ were made at 15°C and 25°C on 6 populations from seed collected in 1992 and at 5, 10, 15, 20, 25, 30, and 35°C on 3 populations from seed collected in 1995. Three or 4 (typically 3) seedlings were used for each measurement, and several replicates were performed and averaged at each temperature.

Heat rate (q) for each sample was first obtained at a given temperature; then a 50-μL vial containing 40 μL of 0.4M NaOH was placed in the 1-mL calorimeter ampule and total heat rate measured. This was followed by another measurement of q for the sample. The difference between heat rates with and without NaOH, divided by the enthalpy change for the reaction of CO₂ with NaOH(aq) to produce HCO₃⁻ (−108.5 kJ mol⁻¹), gives R_CO₂ (Criddle et al. 1991, Hansen et al. 1996). The ratio of q/R_CO₂ was calculated for individual samples and then averaged for replicate experiments on a population. Slope of an Arrhenius plot (ln q vs. T⁻¹ in reciprocal kilo-Kelvins) of averaged q data is equal to μₚₐ temperature dependence of q. Temperature dependence of R_CO₂, μ_R_CO₂, is the slope of the Arrhenius plot (ln R_CO₂ vs. T⁻¹) for the averaged R_CO₂ data.

Model

The model proposed by Hansen et al. (1994, 1996) is used to interpret the data obtained. Specific growth rate R_SG (pmol C s⁻¹ mg dry wt⁻¹), i.e., rate of conversion of substrate carbon to biomass carbon, as given by this model is equation

$$R_{SG} = \frac{[-q - R_{CO₂} (1 - T²/4) \Delta H_{O₂}] \Delta H_B}{R_{CO₂} [1 - \varepsilon(1 - \varepsilon) - \varepsilon]}$$  (1)
where \( q \) is specific metabolic heat rate, \( R_{CO2} \) is specific CO\(_2\) rate, \( \gamma_p \) is mean oxidation state of the substrate carbon, \( \Delta H_{CO2} \) is a constant equal to \(-455 \pm 15 \text{ kJ mol}^{-1}\), \( \Delta H_B \) is enthalpy change for conversion of substrate to biomass, and \( \epsilon \) is substrate carbon conversion efficiency. In the calculations done in this study, \( \gamma_p \) was assumed equal to zero (i.e., substrate C was assumed to be carbohydrate). \( \Delta H_B \) was assumed to be constant, but no value was assumed because \( \Delta H_B \) was not separated from \( R_{SC} \) or the \( \epsilon \) function. Thus,

\[
R_{SG} \Delta H_B = 455R_{CO2} - q \quad (2)
\]

In the range of temperatures where the Arrhenius equation describes temperature dependence of respiration rates, substitution of the Arrhenius equation \( R = Ae^{-\mu q/T} \), where \( A \) is a constant, \( \mu \) is Arrhenius temperature coefficient, and \( T \) is absolute temperature) for the temperature-dependent variables in equation 2 gives

\[
R_{SG} \Delta H_B = [-Aq e^{-\mu q/T} + 455A_{CO2} e^{-\mu CO2/T}] \quad (3)
\]

where \( \mu_q \) is temperature coefficient for metabolic heat rate, \( \mu_{CO2} \) is temperature coefficient for CO\(_2\) rate, and temperature is absolute temperature in Kelvins. Equation 3 thus predicts how temperature affects \( R_{SG} \) from short-term, rapid measurements.

The product \( R_{SG} \Delta H_B \) is the predicted specific growth rate in terms of energy storage in new structural biomass with substrate as reference. Ratio of metabolic heat rate to CO\(_2\) rate is related to \( \epsilon \), substrate carbon conversion efficiency, by the model as

\[
\frac{q}{R_{CO2}} = 455 - \left[ \epsilon/(1 - \epsilon) \right] \Delta H_B \quad (4)
\]

Temperature dependence of \( q/R_{CO2} \) and thus of \( \epsilon \) (assuming \( \epsilon \) is the only temperature-dependent quantity on the right side of equation 4) is given by

\[
\frac{q}{R_{CO2}} = \left[ -A_q e^{-\mu q/T} \right]/[A_{CO2} e^{-\mu CO2/T}] \quad (5)
\]

**RESULTS**

Values of \( q \) and \( R_{CO2} \) measured at 15° and 25°C on seedlings grown from seed collected in 1992 are presented in Table 2. Because of within-population (genetic) biodiversity, standard deviations of mean values in Table 2 are larger than in other studies we have done with clones and cultivars, where relative uncertainties are generally <10%. Therefore, several (~10) replicates were run to properly characterize the population; i.e., each mean is the average for 30–40 seedlings.

Figure 1 represents extrapolations of \( q \) and \( R_{CO2} \) data at 15° and 25°C according to the Arrhenius equation. Slopes of lines shown in Figure 1 are \(-\mu_q \) and \(-\mu_{CO2} \) values. Temperature effect on \( q \) is much greater than for \( R_{CO2} \) in all cases. The ratio \( q/R_{CO2} \) thus increases rapidly with temperature, predicting a rapid decline in substrate carbon conversion efficiency as temperature increases (Fig. 2). While \( \mu_q \) varies among populations, it is less variable than \( \mu_{CO2} \).

Figure 2 shows curves of \( R_{SG} \Delta H_B \) values as a function of temperature as calculated from equation 3. In agreement with directly observed growth characteristics, Figure 2 predicts rapid growth of cheatgrass at cool temperatures and decreasing growth rate as temperatures rise. Based on predicted behavior at temperatures

<table>
<thead>
<tr>
<th>Accession</th>
<th>q at 15°C (µW/mgDW)(^{-1})</th>
<th>q at 25°C (µW/mgDW)(^{-1})</th>
<th>( R_{CO2} ) at 15°C (pmol/mgDW)(^{-1}))(^{1})</th>
<th>( R_{CO2} ) at 25°C (pmol/mgDW)(^{-1}))(^{1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. George</td>
<td>5.1 ± 2.2 (12)</td>
<td>11.7 ± 4.1 (14)</td>
<td>18.8 ± 13.9 (12)</td>
<td>24.8 ± 10.1 (14)</td>
</tr>
<tr>
<td>Hobble Creek</td>
<td>6.7 ± 2.5 (11)</td>
<td>12.7 ± 4.6 (13)</td>
<td>23.4 ± 10.9 (11)</td>
<td>36.1 ± 14.6 (13)</td>
</tr>
<tr>
<td>Potosi Pass</td>
<td>4.6 ± 3.3 (11)</td>
<td>10.2 ± 4.3 (11)</td>
<td>24.4 ± 32.2 (11)</td>
<td>24.7 ± 14.0 (11)</td>
</tr>
<tr>
<td>Whiterocks</td>
<td>5.6 ± 1.3 (9)</td>
<td>12.7 ± 4.2 (12)</td>
<td>21.5 ± 11.8 (9)</td>
<td>25.4 ± 6.0 (12)</td>
</tr>
<tr>
<td>Strawberry</td>
<td>5.6 ± 1.8 (14)</td>
<td>10.5 ± 3.9 (10)</td>
<td>25.4 ± 19.2 (14)</td>
<td>26.4 ± 11.6 (10)</td>
</tr>
<tr>
<td>Fairview</td>
<td>5.8 ± 1.5 (8)</td>
<td>12.3 ± 4.4 (10)</td>
<td>24.4 ± 7.0 (8)</td>
<td>30.3 ± 11.7 (10)</td>
</tr>
</tbody>
</table>

\( \Delta H_B \) is the enthalpy change for conversion of substrate to biomass.
Efficiency curves given in Figure 4 exhibit much the same temperature dependence as growth rate curves shown in Figure 3, thus showing that temperature dependence of efficiency is the major determinant of temperature dependence of growth rate; that is, even though metabolic rate increases with temperature, efficiency decreases even faster.

**DISCUSSION**

Results shown in Figures 2 and 3 correlate with cheatgrass growth strategy which, in general, is to germinate in fall, overwinter in a vegetative state, and then grow rapidly in early spring when temperatures are still cold. Figure 2 indicates the Hobble Creek population from 1992 seed had a growth response to temperature significantly different from other populations. Cheatgrass grows very well in the mouth of Hobble Creek Canyon during late winter and early spring when below-freezing nighttime temperatures are common. However, 30–35°C daytime temperatures can also occur during the same time period. Seedlings from the Hobble Creek population grown from more genetically uniform seed collected in 1995 were not as different from the other populations.
populations (Fig. 3). These results may reflect a climatic selection of annual selfed seeds.

Our results indicate that cheatgrass populations are distinguished from one another by metabolic phenotypes defined by temperature dependencies of \( q \) and \( R_{\text{CO}_2} \). Earlier, Novak et al. (1991) reported genetic differences between populations of cheatgrass. Temperature dependencies of growth rate and substrate carbon conversion efficiency, and thus site fitness of a population, are determined by the difference between \( \mu_g \) and \( \mu_{\text{CO}_2} \), which in turn is related to the biochemistry of metabolism (Taylor et al. 1998). These data on seedlings should be representative of metabolism in field plants because, during measurement, seedlings were metabolizing stored substrate with normal dark respiratory pathways at temperatures not damaging to tissues. Under these conditions about 90% of metabolic heat is generated from reduction of oxygen in mitochondria (Hansen et al. 1997) by carbohydrate from stored substrates. \( \text{CO}_2 \) is generated mostly in mitochondria, but some comes from the pentose phosphate shunt. For \( q \) and \( R_{\text{CO}_2} \) to have different temperature dependencies, reactions producing heat and \( \text{CO}_2 \) cannot be stoichiometrically linked. This in turn requires a change in the coupling of ATP synthesis to oxidative reactions with temperature. Therefore, differences in temperature dependencies of \( q \) and \( R_{\text{CO}_2} \) between populations are genetically determined and do not represent acclimation.

Application of techniques used in this study to other species could be used to rapidly determine if another species has the potential to outgrow cheatgrass at temperatures similar to those conducive to cheatgrass growth. If potential competitor species can be identified, then field tests and competition trials could be used much more efficiently.

**Literature Cited**


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