

Respiratory and Physiological Characteristics in Subpopulations of Great Basin Cheatgrass

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Abstract—Cheatgrass (*Bromus tectorum* L.) is a dominant weed that has increased the frequency of wildfire in the Great Basin since its introduction approximately 106 years ago. Characteristics of respiratory metabolism were examined in eleven subpopulations from different habitats. Seeds from each subpopulation were germinated (4mm radicle) and metabolic heat rates (q) and respiration rates (R_{CO_2}) determined calorimetrically at 5 °C intervals from 5 to 30 °C or from 5 to 45 °C. From the experimental data, growth rates and ratios of q/R_{CO_2} (a measure of efficiency) were calculated. In general, growth rate increases from a low temperature limit of 3 to 7 °C to an upper temperature limit between 27 to 31 °C. Beyond these limits growth ceases. These limits differ among subpopulations, and are related to the native microclimate.

Introduction

Since its Eurasian origins—introduced from the eastern Mediterranean area of Europe into the United States—cheatgrass (*Bromus tectorum* L.) has become one of the most troublesome weeds in the western United States (Upadhyaya and others 1986). Furthermore, cheatgrass—more than any other plant—has transformed the vegetative landscape in the Great Basin and Columbia Basin areas since its introduction approximately 106 years ago (Upadhyaya and others 1986; Klemmedson and Smith 1964). Despite a few advantageous characteristics, such as being high-quality forage in the early spring for grazing animals, and the fact that its dense root growth and expansive top growth prevent erosion, the disadvantages of cheatgrass—in relation to the environment and other native perennial plants—far outweigh the advantages (Morrow and Stahlman 1984).

Cheatgrass appears to have an extraordinary ability to adapt to a variety of microclimates. Some studies suggest that cheatgrass grows well, even under low-nitrogen situations (Klemmedson and Smith 1964). Additional studies suggest that, though water is a limiting factor in the growth of cheatgrass, its ability to thrive under relatively

low-water conditions is superior to perennial grasses. If moisture levels allow seed production, the germination rate of stressed seed is unchanged relative to seed produced under normal conditions (Richardson and others 1989). As early as 1955, striking phenotypic variation was observed in cheatgrass (Klemmedson and Smith 1964). Moreover, a few studies conducted during the 1990s provide evidence for not only phenotypic variation (Meyer and Allen 1999), but also genetic variation within populations (Hemming and others 1999), and more robustly between populations (Novak and others 1991, 1993; Novak and Mack 1993; Mack and Pyke 1983, 1984). According to Novak and Mack (1993) genetic differentiation is greater between populations because cheatgrass has very high levels of inbreeding, which reduces the chance for recombination of the genome. Nevertheless, cheatgrass appears to be capable of adapting to a variety of climates and can do so even with low levels of water, relative to other native species.

Throughout the western United States, cheatgrass has invaded crop plants such as winter wheat (*Triticum aestivum* L.) and alfalfa (*Medicago sativa* L.) (Morrow and Stahlman 1984). A number of factors have contributed to this invasion—both in crop plants and undeveloped habitats. Wild fires and soil-nutrient depletion have been suggested, yet overall it becomes apparent that no matter how cheatgrass initially gained a foothold in the western United States, its ability to adapt and take over native habitats has increased. As Nasri and Doescher (1995) point out in their study of Idaho fescue, increased competition from cheatgrass depleted soil moisture available for the fescue and consequently reduced Idaho fescue's growth substantially. Further validating this claim, Evans and Young (1984) argue that cheatgrass was one of three alien grasses that established, dominated, and revolutionized plant succession in the sagebrush grasslands in the western United States. Even during the 1960s Klemmedson and Smith (1964) observed that cheatgrass' physiological responses were much quicker than their native perennial grass counterparts.

Fire, growth periods, and its physiological characteristics give cheatgrass a competitive advantage. The caryopses of cheatgrass are essentially fireproof and as it ends its growth cycle the extremely high flammability of the grass permits fires to start and spread with unusual rapidity. Cheatgrass seeds are protected while other perennial grass seeds are made impotent. Cheatgrass has added to the fire cycle: over a century ago, fire-return intervals on the sagebrush-steppe in Idaho's Snake River Plains fluctuated anywhere from 35 to 100 years. Now, because cheatgrass creates a more continuous fuelbed, the fire-return interval is very

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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short—anywhere from 2 to 4 years (Whisenant 1990). Furthermore, native plants, such as sagebrush do not have a quick capability to regenerate after a fire has devoured native habitats. Fire enhances the establishment of cheatgrass: while everything else is trying to regenerate—slowly—cheatgrass is back the next spring taking over the decimated lands. Since its growth season includes germination in the fall after autumn rains (Beckstead and others 1995), overwintering in the vegetative stage, and completing growth in the early spring, cheatgrass gets first track on available water and nutrients in the soil. Additionally, following rapid germination in the fall, cheatgrass quickly establishes an extensive fibrous root system that continues to grow through the winter (Thill and others 1984). Finally, even under drought conditions cheatgrass will mature sufficient seed to ensure plants for the following year (Klemmedson and Smith 1964).

From its Eurasian origins cheatgrass has adapted to the Great Basin remarkably quickly. If the restoration of native ecosystems is a primary goal, cheatgrass is one of the primary culprits in impoverishing native ecosystems of their natural species (Billings 1990; D'Antonio and Vitousek 1992); therefore, the physiology of cheatgrass must be understood. This study reflects an effort to understand the respiratory physiology of cheatgrass and its adaptation to the Great Basin.

In this study, the respiratory characteristics of cheatgrass subpopulations are determined by calorimetric techniques and analyzed with a model of plant growth first introduced nearly a decade ago (Criddle and others 1991, 1994, 1996, 1997; Criddle and Hansen 1999; Hansen and others 1994, 1997, 1998a, 1998b; Smith and others 1999, 2000). Since growth rates are functions of energy metabolism, calorimetry is necessary to understand plant metabolic physiology (Hansen and others 1994). Plant metabolic calorimetry might be defined as the thermodynamic study of physiological processes.

Materials and Methods

Caryopes from eleven subpopulations of cheatgrass in the Great Basin were used in this study. Nine of the eleven subpopulations came from Utah; the other two originate in Colorado and Nevada (table 1). The United States Department of Agriculture, Forest Service Shrub Sciences Laboratory, at Provo, Utah, provided the caryopes for this analysis. The caryopes were greenhouse-grown progeny of a number of maternal lines. The original seeds were collected in 1995 and this study conducted on seeds produced in 1998 and 1999. Seeds from each subpopulation were placed on petri dishes, dampened with distilled water, and germinated at 20 °C. Germinated seedlings' respiratory characteristics were measured when 2 to 5 days old.

Data were collected with calorimeters: Calorimetry Sciences Corporation model 4100 and Hart Scientific model 7707. R_{CO_2} and q were determined at temperatures from 5 to 45 °C. These determinations came from (a) placing 80 to 150 mg (15 to 30 seeds) of germinated caryopes into 1-ml calorimeter ampules; (b) setting a desired temperature and waiting approximately 20 minutes for a steady-state heat rate; (c) placing a 40 μ l vial of 0.4M NaOH in the ampule and again

Table 1—Eleven subpopulations of cheatgrass (*Bromus tectorum* L.) in the Great Basin: classified by sites of origin.

Subpopulation	County	State	Altitude
St. George	Washington	Utah	850 m
Green River	Emery	Utah	1,280 m
Whiterocks	Tooele	Utah	1,450 m
Ephraim	Sanpete	Utah	1,740 m
Hobble Creek	Utah	Utah	1,800 m
Potosi	Clark	Nevada	1,850 m
Castle Rock	Douglas	Colorado	1,980 m
Salina	Sevier	Utah	2,040 m
Strawberry	Wasatch	Utah	2,400 m
Fairview	Sanpete	Utah	2,770 m
Nebo Summit	Utah	Utah	2,850 m

waiting for a steady-state heat rate, which now includes both metabolic heat and heat from the reaction of carbon dioxide and sodium hydroxide to produce carbonate; (d) removing the vial of NaOH and again waiting for a steady-state; and (e) repeating the process at another temperature. Measurements were done in the order of 20, 15, 10, and 5 °C on one sample and at 25, 30, 35, 40, and 45 °C on another. Data were analyzed by averaging the heat rates directly measured in steps b and d, to obtain the metabolic heat rate q , subtracting this from the heat rate measured in step c, and dividing this difference by the enthalpy change for the reaction, $-108.5 \text{ kJ mol}^{-1}$, which gives R_{CO_2} . The ratio of q/R_{CO_2} was calculated from average values of q and R_{CO_2} obtained in approximately 5 replicates.

Thermodynamic Model

Growth rates were calculated from equation 1

$$R_{SG}\Delta H_B = 455R_{CO_2} - q \quad (1)$$

where R_{SG} is the specific growth rate in moles of carbon per gram of tissue per second, and ΔH_B is the enthalpy change for formation of structural biomass from substrate in kilojoules per mole of carbon. The constant, $455 \text{ kJ mol}^{-1} \text{ CO}_2$, comes from Thornton's rule by assuming carbohydrate is the substrate. Note that under conditions where q is greater than $455R_{CO_2}$, $R_{SG}\Delta H_B$ will be negative, indicating conditions of no growth.

Results

After replicating the experiment several times on each subpopulation and thereby providing mean data from about 100 caryopes per temperature, the data were analyzed for distinct differences in the physiological responses to temperature. Figures 1, 2 and 3 show plots of metabolism of subpopulations that, in general, are indicative of the response of other subpopulations to temperature. Figure 4 shows q/R_{CO_2} averaged over the subpopulations as a function of temperature. Figure 5 depicts the calculated growth rate as a function of temperature averaged over the 11 subpopulations. Table 2 provides Arrhenius slopes for q and R_{CO_2} (Criddle and Hansen 1999).

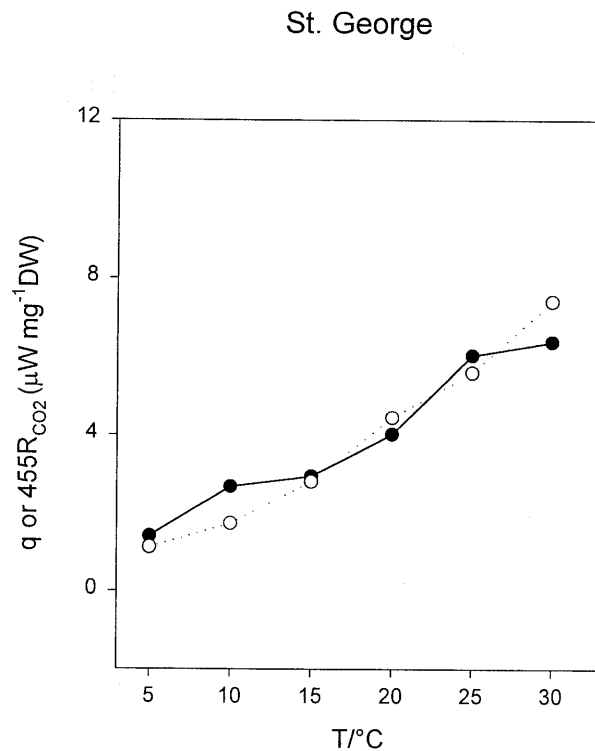


Figure 1—Metabolic heat rate (open circle) and R_{CO_2} production rate (closed circle) as function of temperature for the St. George subpopulation.

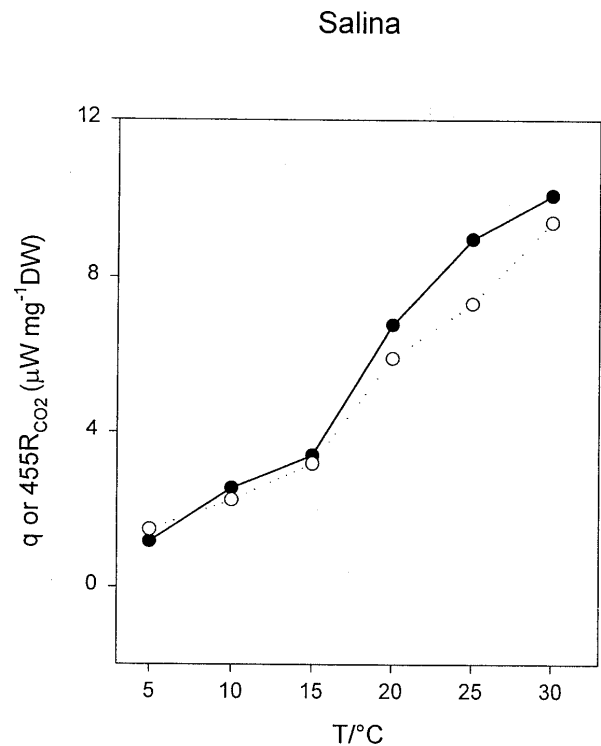


Figure 3—Metabolic heat rate (open circle) and R_{CO_2} production rate (closed circle) as function of temperature for the Salina subpopulation.

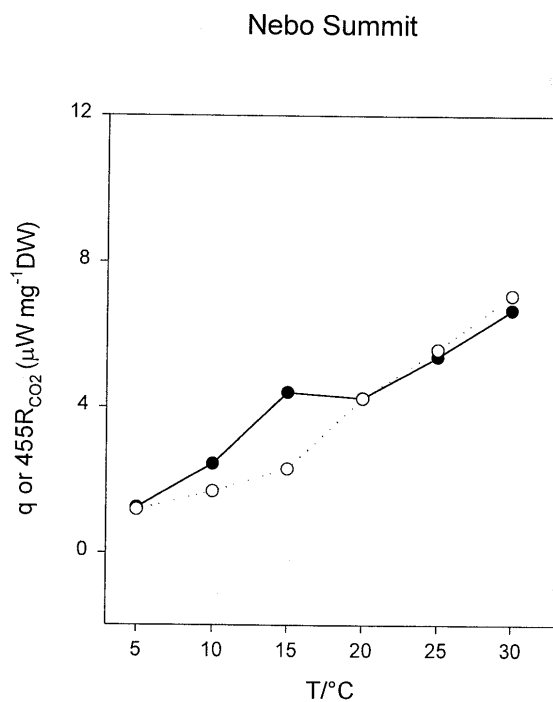


Figure 2—Metabolic heat rate (open circle) and R_{CO_2} production rate (closed circle) as function of temperature for the Nebo Summit subpopulation.

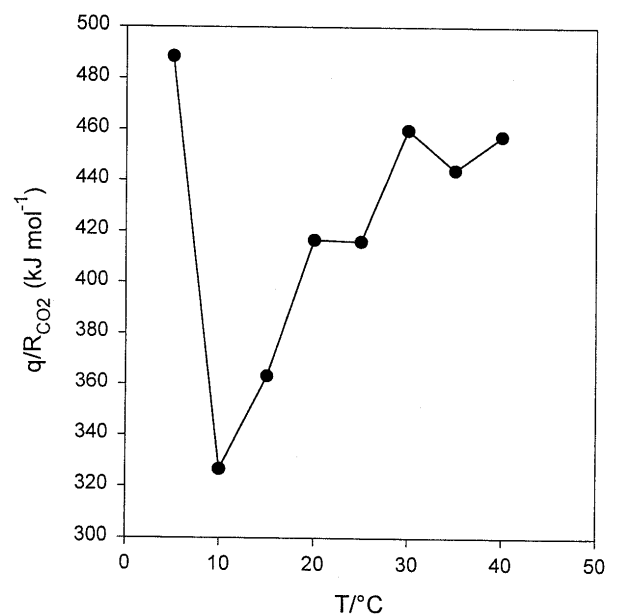


Figure 4—Averaged q/R_{CO_2} ratios for eleven subpopulations of cheatgrass as functions of temperature. This ratio demonstrates, in general, the efficiency of cheatgrass throughout the Great Basin in converting substrate into biomass. Lower values translate into greater efficiency.

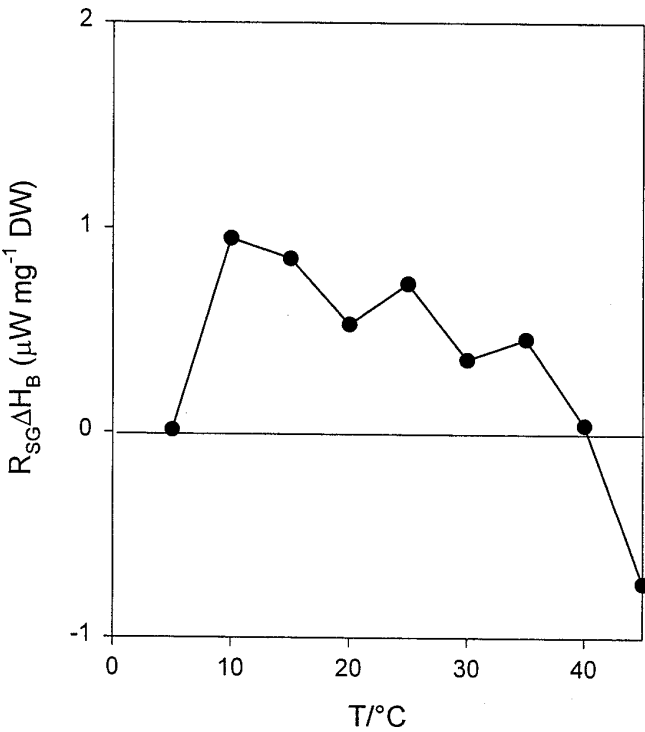


Figure 5—Calculated growth rate as a function of temperature averaged across eleven subpopulations. Depicts, in general, both low and high extreme temperature limits to growth.

Discussion

In this study, it has become apparent that although the subpopulations are different from one another in terms of temperature response (table 2), there are also some general conclusions. Cheatgrass barely grows at 5 °C (fig. 5), and is very inefficient in doing so (fig. 4). Furthermore, the optimum growth temperature is between 10 and 20 °C. Moreover, cheatgrass' growth rate is apparently a bi-phasic

function, that is, at lower temperatures cheatgrass has a different physiological response or combination of responses, than at higher temperatures (figs. 1-3; table 2). Cheatgrass stops growing between 30 and 40 °C.

Another interesting finding is that, at very low temperatures (in other words around 5 °C) cheatgrass appears to waste a lot of energy in burning lipid as an energy substrate for growth as shown by the value of q/R_{CO_2} greater than 455 at 5 °C (figure 4). Carbohydrate is a free fuel, in terms of energy expended, to an autotrophe; whereas lipid costs a substantial amount of energy to produce energy that could theoretically be used to produce more biomass. The drop in q/R_{CO_2} from 5 to 10 °C indicates a switch to carbohydrate by 10 °C.

Cheatgrass has adapted (or adapts) to grow at temperatures extant when water is available. For example, St. George (fig. 1) cheatgrass is adapted to grow at some of the lowest temperatures relative to the other subpopulations. Thus, instead of growing in April, May, and June, the St. George growth temperatures loosely correlate with environmental temperatures in February, March, and April when rainfall occurs at this site, where by May available water is reduced by 65 percent. This means then, in general, that subpopulations, which experience the hottest climates, are adapted to the coldest temperatures. Therefore, we see that cheatgrass' respiratory metabolism is closely aligned with its environment.

Now, though we have said that cheatgrass has adapted to its specific environment, individuals cannot adapt to transplanted environments—we must remember that cheatgrass was only introduced approximately 106 years ago, and in many areas less. Nevertheless, cheatgrass grouped-progeny (stands) appear to have the capability to adapt rapidly to microclimates. The response to climate is clearly not a short-term acclimation or even acclimation of first or second-generation progeny or the subpopulation differences observed would not be present in the greenhouse-grown seed used in this study. A full analysis of temperatures at each site during the growth season for cheatgrass is expected to show that the Arrhenius slopes for each population are correlated with site temperature and temperature variability.

Table 2—Arrhenius slopes μ_q and μ_{CO_2} that represent physiological responses to temperature, along with temperature range. Differences between slopes are related to the different microclimates at the site of origin.

Subpopulations	μ_q, kK^{-1}	ΔT	μ_{CO_2}, kK^{-1}	ΔT	μ_q, kK^{-1}	ΔT	μ_{CO_2}, kK^{-1}	ΔT
St. George	7.5	5 to 20 °C	10.1	5 to 10 °C	5.0	25 to 30 °C	5.3	15 to 20 °C
Green River	6.4	5 to 30 °C	17.0	5 to 10 °C	-0.8	35 to 40 °C	4.7	15 to 30 °C
Whiterocks	7.0	5 to 10 °C	13.1	5 to 15 °C	14.1	15 to 20 °C	-1.2	20 to 25 °C
Ephraim	7.2	5 to 15 °C	3.1	5 to 15 °C	4.6	20 to 30 °C	4.4	20 to 30 °C
Hobble Creek	7.8	5 to 15 °C	7.4	5 to 20 °C	4.3	20 to 30 °C	0.7	25 to 30 °C
Potosi	7.8	5 to 15 °C	6.6	5 to 20 °C	4.3	20 to 30 °C	3.0	25 to 30 °C
Castle Rock	7.4	5 to 20 °C	22.4	5 to 10 °C	3.5	25 to 35 °C	3.6	15 to 35 °C
Salina	6.1	5 to 15 °C	8.9	5 to 20 °C	4.1	20 to 30 °C	2.1	25 to 30 °C
Strawberry	7.2	5 to 30 °C	2.0	5 to 10 °C	-1.4	35 to 40 °C	6.4	15 to 30 °C
Fairview	5.4	5 to 30 °C	10.2	5 to 10 °C	0.3	35 to 40 °C	3.1	15 to 25 °C
Nebo Summit	5.3	5 to 15 °C	10.0	5 to 15 °C	4.5	20 to 30 °C	4.0	20 to 30 °C

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