

Mechanisms controlling the distribution of two invasive *Bromus* species

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Abstract. In order to predict future range shifts for invasive species it is important to explore their ability to acclimate to the new environment and understand physiological and reproductive constraints controlling their distribution. My dissertation studied mechanisms by which temperature may affect the distribution of two aggressive plant invaders in North America, *Bromus tectorum* and *Bromus rubens*. I first evaluated winter freezing tolerance of *Bromus* species and demonstrated that the mechanism explaining their distinct northern range limits is different acquisition time of freezing tolerance. While *B. rubens* has a slower rate of freezing acclimation that leads to intolerance of sudden, late-autumn drops in temperature below -12°C , *B. tectorum* rapidly hardens and so is not impacted by the sudden onset of severe late-autumn cold. In addition, the analysis of male reproductive development and seed production showed that neither species produces seed at or above 36°C , due to complete pollen sterility, which might trigger climate-mediated range contractions at *B. tectorum* and *B. rubens* southern margins. Finally, a detailed gas-exchange analysis combined with biochemical modelling demonstrated that both species acclimate to a broad range of temperatures and photosynthetic response to temperature does not explain their current range separation.

Keywords. freezing tolerance, grasses, invasive species, photosynthesis, reproduction, temperature

Introduction

The role of physiological processes and their tolerance limits in species range formation was first formulated by Ronald Good in his “Theory of Tolerance” (Good 1931). Good suggested that a species’ distribution is closely linked to its physiological responses to climate and implied that even closely related sister species can have distinct tolerance ranges. Species’ tolerance, according to Good (1931) is comprised of many tolerance parameters, but only one of them limits its distribution. In reality, however, a single species might be limited by more than one factor and process since the nature of geographical ranges and niches is multi-dimensional (Hutchinson 1957). In order to predict changes in vegetative cover, one has to look at a large number of proximal variables and understand their effect on major physiological and reproductive processes (Bykova et al. 2012, Higgins et al. 2012, Schurr et al. 2012). My thesis contributes to this area by looking at the effects of temperature on range formation of two closely-related grass invaders, *B. tectorum* and *B. rubens*,

through the assessment of their freezing tolerance, male reproductive development and photosynthetic performance under varying temperatures. I hypothesized that temperature plays an important role in their range formation through its effect on major physiological and reproductive processes and that differences in species physiological responses may drive their range separation. The major results of my PhD thesis are presented in three chapters (I. “Winter cold tolerance and the geographic range separation of *Bromus tectorum* and *Bromus rubens*, two severe invasive species in North America” (Bykova and Sage 2012); II. “Heat sterility of reproduction in a changing global climate: Implications for the pernicious invaders *Bromus tectorum* and *Bromus rubens* in North America”; III. “Thermal acclimation of photosynthesis in two winter annual grass invaders from semi-arid regions of North America”).

Bromus tectorum and *Bromus rubens* were of particular interest to me because of their critical role in North American semi-arid biomes and

the allopatric character of their geographical ranges. Existing ecological reports conclude temperature somehow influences the distribution of *Bromus* species, possibly due to a physiological mechanism (Hulbert 1955, Chambers et al. 2007, Leger et al. 2009). Despite morphological and life-history similarities (Fortune et al. 2008), *Bromus* species tend to occupy distinct thermal habitats. In North America, *B. tectorum* and *B. rubens* are usually geographically separated along latitudinal and altitudinal gradients (Beatley 1966). While *B. tectorum* grows primarily at high elevation sites above 1500m, *B. rubens* is present at low and mid elevations below 1500m (Beatley 1966). Moreover, while the northern limit of *B. tectorum* distribution is 65° N (Valliant et al. 2007), *B. rubens* is mainly found only up to 48°N latitude (Kartesz and BONAP 2011). Dense stands of these species are also separated. *Bromus rubens* is a severe invader in the Mojave desert region of southwestern North America; its sister species, *B. tectorum* is dominant in the colder Intermountain Region of western North America (Figure 1, Salo 2004, 2005, Pavlick and Anderton 2007).

Methods

I took a diversified approach by including both reproductive and physiological variables in the analysis of mechanisms controlling species distribution. I first looked at the development of cold tolerance, frost resistance and minimum cold tolerance levels in *Bromus* species using electrolyte leakage, leaf fluorescence and whole-plant mortality tests. In this study I examined distinct northern range limits of *B. tectorum* and *B. rubens* and investigated possible physiological mechanisms responsible for their range separation. I also explored the capacity of each species to acclimate to rapid freezing events at the beginning of the cold season and examined differences in their responses at young and mature developmental stages. Identification of any winter cold dependence controlling northern range limits of *Bromus* species can provide insights into their future invasive potential at higher latitudes and elevations.

I evaluated possible reasons for distinct southern ranges of *Bromus* species and compared

responses of their male reproductive development and tillering to elevated temperatures. This is the first study on the effect of climate change on the reproductive development of invasive grasses. It is also the first to look at heat induced male sterility in plants as an important contributor to species distributions. The experimental manipulations used microscopic observations to evaluate changes in anther development, pollen production and cell division. By comparing closely related species that segregate along a thermal cline I also evaluated natural variability in the sterility threshold. Finally, in the last chapter I examined the effect of distinct growth temperatures on the photosynthetic performance of *B. tectorum* and *B. rubens*. This combined experimental gas-exchange measurements with biochemical modelling in order to understand major processes limiting photosynthesis over the entire temperature range and to examine the effect of growth temperatures on photosynthetic performance. Growing *B. tectorum* and *B. rubens* under four temperature regimes provided one of the most comprehensive pictures of photosynthetic acclimation over the growing season.

Results and Discussion

I demonstrated that the mechanism explaining the distinct northern range limits of *Bromus* species was different acquisition time of freezing tolerance. While *B. rubens* has a slower rate of freezing acclimation that leads to intolerance of sudden, late-autumn drops in temperature below -12°C, its colder-adapted sister species, *B. tectorum*, rapidly hardens and so is not impacted by the sudden onset of severe late-autumn cold. *Bromus tectorum* rapidly acclimates to sub-zero temperatures and reaches its maximum cold tolerance level of -30°C when minimum air temperature falls below -10°C. These results establish a mechanistic means for modelling the impact of future climate on invasive species. Instead of modelling distribution based on winter minimums, severe cold events in autumn appear to be the more critical predictor. With anthropogenic warming, isoclines for minimum winter temperature and the range limits of many species will progressively shift to

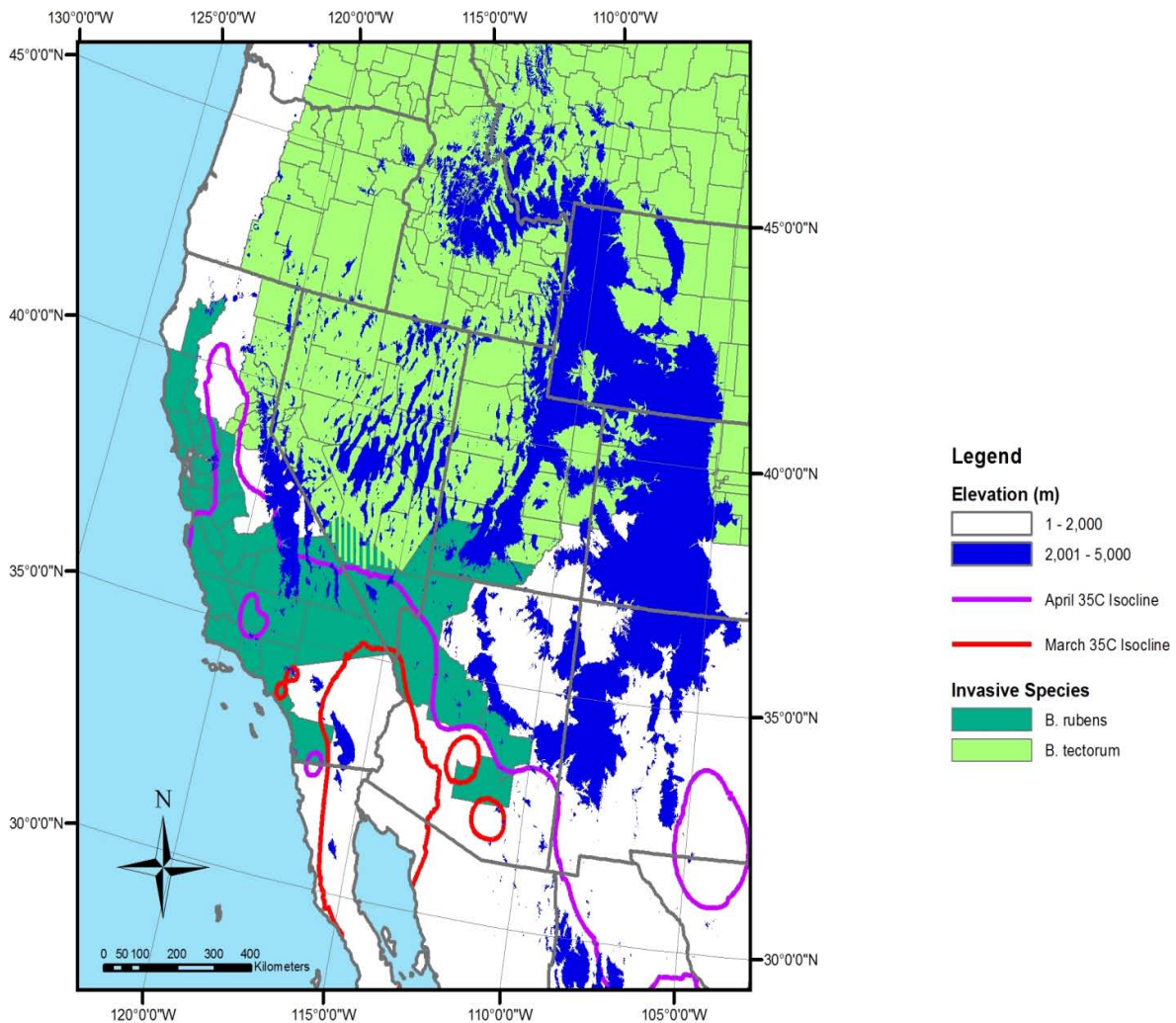


Figure 1 The current ranges where *Bromus tectorum* (light green) and *Bromus rubens* (blue-green) are invasive in relation to the isoclines of the 35°C maximum temperature during March (red) and April (purple) in the western US. The temperature data were obtained from the Western Regional Climate Center¹. Information on *B. tectorum* and *B. rubens* invasion was obtained from Mack (1981) and Salo (2004, 2005), respectively, as well as this author's personal observations. 35°C temperature isoclines were generated in ArcGIS, using maximum temperature data over the ten-year period, 1998–2008, from 212 cities in the Western US, extracted from the 'Local Climate Data Summaries for Western US' (Western Regional Climate Center²). This data set shows temperature highs (variable: Extreme Max Temp) during the last ten-year period based on unedited daily ASOS data. Elevation map layers used for the map construction were obtained from the National Atlas of the United States Raw Data³. Blue color indicates areas of higher elevation (>2,000 m). Slashed light green and blue-green lines represent regions where *Bromus tectorum* and *Bromus rubens* co-occur (Bykova 2012).

higher latitudes and altitudes. If so, *Bromus rubens* should follow the modulation of the -12°C minimum autumn isocline and potentially infest areas currently occupied by *B. tectorum* (Bykova and Sage 2012). Once the likelihood of early frost events $\leq -12^\circ\text{C}$ in the regions currently occupied by *B. tectorum* decreases, *B. rubens* should heavily

invade new habitats and potentially replace *B. tectorum* (Bykova and Sage 2012).

In addition, I detected that, along with excellent freezing tolerance capacity, *Bromus* species exhibit high photosynthetic rates at chilling temperatures. Both species can alter relative investments into their photosynthetic components

¹ <http://www.wrcc.dri.edu/>

² <http://www.wrcc.dri.edu>

³ <http://www.nationalatlas.gov/atlasftp.html>

and rapidly acclimate to growth under the sub-optimal temperatures. Low-temperature acclimation ameliorates inorganic phosphate regeneration limitation in these species and increases net CO₂ assimilation rate at sub-optimal temperatures. Overall, I found that *B. tectorum* and *B. rubens* acclimate to broad thermal ranges, and are also able to grow and photosynthesise under temperature conditions (36°C) close to temperature extremes encountered during flowering in their natural environment (Bykova 2012, R.F. Sage and T.L. Sage unpubl. data). Growth under higher temperatures improved their carboxylation capacity (capacity of enzyme Rubisco to catalyze the irreversible carboxylation of RuBP) above the thermal optimum which probably resulted from increased thermostability of Rubisco activase. I found no difference in their photosynthetic responses nor acclimation capacity which indicates that photosynthesis-related traits do not explain current range separation of *Bromus* species (Bykova 2012).

Finally, I found the threshold of heat sterility in *B. tectorum* and *B. rubens* is 36°C. Exposure to 36°/24°C (day/night) during the flowering triggered complete pollen abortion and a subsequent seed set failure in all populations of *B. tectorum* and *B. rubens* (Bykova 2012). During the flowering period, both *Bromus* species already experience temperatures close to their reproductive threshold (Figure 1). This indicates that in a warmer world *B. tectorum* and *B. rubens* might undergo severe contraction of their southern range limits. Yet, lethal heat events are episodic by nature and therefore their effect on species fecundity will depend on a number of factors, such as the timing, extent and frequency of heat events. If they are to impact on *B. tectorum* and *B. rubens* distribution, they must either occur frequently enough to have a long-term impact on a population, or should be severe enough to reduce the population to low levels from which recovery is slow. Because both *Bromus* species are annuals and their seed bank is short lived (Holm et al. 1977, Wu and Jain 1978, Smith et al. 2008), they appear to be particularly vulnerable to heat effects on reproduction. Temperatures $\geq 36^\circ\text{C}$ during flowering in back

-to-back years may reduce seed banks of *Bromus* species and diminish their cover in the semi-desert biomes. As a result, the shift of *Bromus* species towards higher latitudes and elevations described above will likely be offset by a contraction of the distribution at the southern and lower end of their ranges (Bykova and Sage 2012). Patterns of heat-induced sterility in *Bromus* species demonstrate that their reproductive threshold is similar to the ones reported for crops and might be an important factor controlling the distribution of warm-climate grasses (Bykova 2012). Exposure to 34°C to 36°C during anthesis decreases pollen viability in numerous agronomic species, such as wheat, rice and sorghum, thereby leading to floret sterility (Saini and Aspinall 1982, Sakata et al. 2000, Vara Prasad et al. 2006, Jagadish et al. 2010). If the 34–36°C threshold for heat sterility is widespread in the plant kingdom, then climate warming could potentially have a massive impact on the reproductive ability of the world's flora, particularly at low latitude, and in short-lived species that do not form long-term seed banks. Even species active in cool conditions, such as the winter-active *Bromus* species studied here, can experience heat sterility and thus may have evolved developmental mechanisms to avoid it. The apparent lack of variation in heat sterility between species and populations of different climate zones indicates evolutionary adaptation is unlikely, particularly given the rapid rate of anthropogenic climate change. For species living in climates that approach the thermal threshold for heat sterility, large losses in fecundity are probable with increasing frequency of heat events, as demonstrated by the *Bromus* example.

Overall, the results of my thesis suggest that climatic changes will cause northward range expansion of *Bromus* species due to less severe autumn and winter conditions, while reproductive failure could cause range contraction at their southern margins. They also demonstrate that physiological and reproductive processes could be important determinants of species distribution and therefore should be considered in species distribution models. Despite postulates of Good's "Theory of Tolerance" (Good 1931), these results

show that the distribution of a single species can be limited by more than one physiological parameter suggesting the importance of Hutchinsonian multidimensional approach (Hutchinson 1957). Moreover, the similarity between the freezing tolerance of *B. tectorum* and *B. rubens* and minimum winter/autumn temperature isoclines corresponding to their northern-most distributions supports the hypothesis that aggressive weedy invaders expand their realized niche to correspond to their fundamental niche. Yet, the presence of distinct tolerance thresholds in *Bromus* species indicates that distribution models should take into account a larger suite of temperature variables when predicting ecosystem responses to climatic changes.

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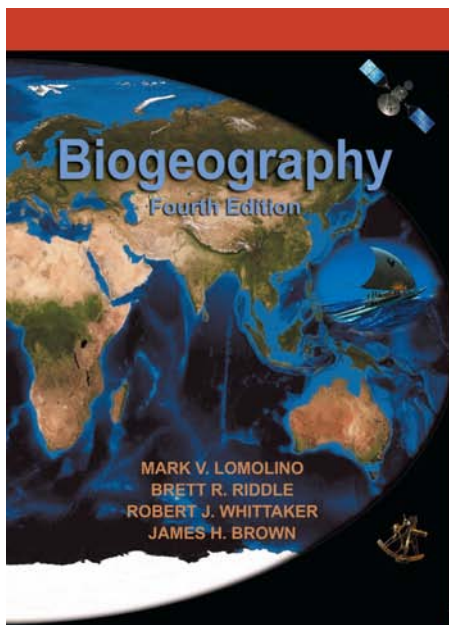
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