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Testing invasion filters for the alpine: the roles of temperature, nitrogen deposition and soil

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Abstract Alpine areas will likely experience an increase in non-native plant species invasions. Increased human activity and environmental changes are expected to lower the environmental constraints for their establishment and spread. To understand and prepare for high elevation plant invasions it is necessary to evaluate the changes in environmental factors that make alpine regions susceptible to potential invaders. The alpine of the Rocky Mountains has very few occurrences of non-native species to date, but anthropogenic environmental changes may facilitate invasion. We tested whether *Bromus tectorum* (cheatgrass or downy brome) invasion in the Rocky Mountain alpine could be facilitated by increases in mean and minimum growing season temperatures. We also tested whether nitrogen (N) deposition and alpine soil may modify *B. tectorum*'s responses to climate warming. Our findings suggest that alpine soils inhibited growth of *B. tectorum* regardless of temperature or simulated N deposition. These results indicate that local alpine invasion by *B. tectorum* is unlikely in the near future. However, higher minimum growing temperatures and increased N addition did enhance *B. tectorum* growth for plants grown in upper montane soils. Such changes may promote population growth of *B. tectorum* within montane elevations.

Keywords Cheatgrass · *Bromus tectorum* · Alpine · Invasion filters · Freeze · Soil

Introduction

Alpine ecosystems are some of the least invaded environments due both to low seed dispersal and environmental constraints such as low temperatures (Lonsdale 1999; Alexander et al. 2016). Increasing human activity, such as road building and recreation, in alpine regions is resulting in the movement of invasive species' propagules to high elevation ecosystems (Marini et al. 2009; Rundel and Keeley 2016). Concurrent increases in nitrogen (N) deposition and climate warming have the potential to facilitate invasions in high mountain ecosystems (Dukes and Mooney 1999; Pauchard and Alaback 2004; Concilio et al. 2013; Petitpierre et al. 2015; Lembrechts et al. 2016). Invasive species are now established and spreading along alpine roadsides in the Andes

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(Cavieres et al. 2005), the Northern Calcareous Alps (Dullinger et al. 2003), and the Australian Alps (Johnston and Pickering 2001), demonstrating that the alpine is not immune to invasive species establishment (reviewed by Alexander et al. 2016).

To successfully establish in a new habitat such as the alpine, non-native species must overcome multiple barriers (i.e. ecological filters). Seed availability is the initial filter (i.e. dispersal limitation), which is followed by multiple site-level filters including abiotic conditions and biotic interactions that determine whether individuals establish a population (Theoharides and Dukes 2007). Multiple site-level filters have been hypothesized to confer invasion resistance to alpine ecosystems. A long-standing hypothesis posits that alpine ecosystems are too cold for invasive species to establish (Pauchard et al. 2009). However, anthropogenic climate warming is increasing growing season temperatures which may benefit non-native species that are adapted to the climate at lower elevations (Dukes and Mooney 1999; Hellmann et al. 2008; Walther et al. 2009; Najberek et al. 2017). Both increases in growing season air temperatures as well as an increase in minimum (subfreezing) growing season air temperatures could allow non-native species with established populations in montane and subalpine ecosystems to colonize the alpine. Haider et al. (2011) found that upper elevation limits of non-native species' populations in the Alps was not related to how the same nine non-native species responded to a gradient of temperature treatments, suggesting that climate extremes or other site-level conditions determine upper elevation limits. A leading hypothesis for non-native species' elevation limits is that cold temperatures impose physiological constraints (Dukes and Mooney 1999; Pauchard et al. 2009; Alexander et al. 2016). Several studies have demonstrated that increasing air temperatures determine or predict non-native species' range expansions in low elevation ecosystems (Jarnevich and Stohlgren 2009; Bradley et al. 2010; Verlinden and Nijs 2010; Hou et al. 2014). Yet, few studies have addressed temperature constraints of non-native species in montane ecosystems (Haider et al. 2011; Barni et al. 2012). Additional experiments are needed to isolate the unique effects of temperature and other site-level filters on non-native species' abilities to germinate, survive, grow, and reproduce because causation cannot be assessed using a correlational or modeling approach.

Elevated N availability has also been implicated in enhanced growth and reproduction of non-native species (Dukes and Mooney 1999). Invasive, non-native species often grow best in nutrient rich soils and compete well for limiting nutrients relative to native species (Davis et al. 2000; Levine et al. 2003; Funk and Vitousek 2007; Rao and Allen 2010). While native alpine plant species grow slowly and exhibit conservative changes in N use with increasing N availability (Bowman and Bilbrough 2001), the opposite is generally true for non-native species in their invaded ranges (Milberg et al. 1999; Vasquez et al. 2008). Given that N is a limiting nutrient for plant growth, anthropogenic N deposition could benefit non-native species that are able to overcome both dispersal and environmental constraints (Davis et al. 2000; Gross et al. 2005; Flores-Moreno et al. 2016; Liu and van Kleunen 2017).

While air temperature and N deposition may operate as independent invasion filters, shifts in *multiple* site-level factors in the alpine (i.e. increases in propagule pressure, N availability, and air temperatures) may be necessary to increase the likelihood of invasions. This idea has been examined in the context of community assembly with some evidence supporting it (Myers and Harms 2009; Pinto et al. 2014), but only recently have multiple, potentially interacting factors been tested in invasion biology (Maron et al. 2014; Eskelinen et al. 2017; Lembrechts et al. 2018). In the southern Rocky Mountains, a continued trend toward earlier spring snowmelt (Schwartz et al. 2006; Clow 2010), higher minimum temperatures (McGuire et al. 2012), and increased N availability from N deposition (Sievering 2001) in alpine ecosystems may operate together to make suitable conditions for some non-native plant species (i.e. species that are not dispersal limited and are able to grow in alpine soils).

Bromus tectorum L. (cheatgrass or downy brome) is an invasive, self-pollinating, winter annual grass that is likely to benefit from anthropogenic changes occurring in alpine ecosystems of the Rocky Mountains (Kao et al. 2008; Bromberg et al. 2011). *Bromus tectorum* is a widespread invasive species in the western United States which does not occur above treeline in the Rocky Mountains (Mack 1981; Chapin et al. 2000). *Bromus tectorum* is a facultative winter annual and thus pre-adapted to spend the seedling stage under snow and grow quickly in early spring. This species exhibits high phenotypic variability across growing conditions, which includes an ability to produce seed when plants are quite small (Chambers et al. 2007; Griffith et al. 2014). We expect that these traits make *B. tectorum* well suited for short, cold growing seasons (Leger et al. 2009; Concilio et al. 2013), and thus a candidate species for alpine invasion. While *B. tectorum* has been predicted to be temperature limited at its upper elevation range on the Colorado Plateau (Chambers et al. 2007), experimental evidence for this assertion is lacking. Additionally, Colorado's mountain ecosystems are expected to experience an increase in mean air temperatures between 3 and 5 °C between 2035 and 2064 (Lukas et al. 2014). Evidence from N addition studies also demonstrates that *B. tectorum* is a strong competitor for N in its invaded range compared to native and agricultural plant species (Ball et al. 1996; Vasquez et al. 2008; He et al. 2011).

We experimentally test how environmental conditions may affect *B. tectorum* invasion in the alpine using growth chamber experiments in which we manipulate temperature, nitrogen (N) availability, and soil type. We hypothesized that cold growing season temperatures or spring subfreezing temperatures, or both, currently inhibit *B. tectorum* establishment in the alpine. Thus, warmer temperatures should enhance growth and reproduction of *B. tectorum*. Two experiments were conducted to address how increases in mean growing season temperature and increases in minimum (subfreezing) growing season temperatures affect *B. tectorum* growth and spikelet production. We also hypothesized that increased N availability from N deposition could promote invasive species establishment when temperature is not the primary constraint on growth, which we tested in both *B. tectorum* experiments. We additionally expected that alpine soils would be suitable for *B. tectorum* growth, especially under warmer temperatures and enhanced N availability. Montane soils were used to compare the relative suitability of alpine soils for *B. tectorum* growth.

Methods

Study species

Bromus tectorum was introduced to the western United States in the late nineteenth century. Populations were established throughout the Intermountain West by 1930 (Mack 1981). In its native range, which includes most of Europe, the northern edge of Africa, and western Asia, it is found at upper montane elevations below 3000 m (Upadhyaya et al. 1986; Novak and Mack 2001). There is no evidence of *B. tectorum* occurring above treeline in the Rocky Mountains at this time. Treeline occurs at 3400–3800 m in the southern Rocky Mountains (Peet 1978). Verified locations of *B. tectorum* populations at high elevations are rare, however, the Rocky Mountain Herbarium currently has 19 accessions of *B. tectorum* collected from 2743 to 3048 m throughout the southern Rocky Mountains (2019). Germination studies have shown that *B. tectorum* can germinate and grow in 5 °C nighttime and 10 °C daytime temperatures (Aguirre and Johnson 1991; Meyer et al. 1997), and root growth persists below this range and ceases around 3 °C (Harris 1967). *Bromus tectorum* is also adapted to a relatively wide range of physical soil properties (i.e. soil texture) (Norton et al. 2004; Reisner et al. 2013) and has been shown to respond positively to N when temperature and water availability are not limiting (Uresk et al. 1979; Concilio and Loik 2013).

Growing season experiment

To explore the effect of N availability on *B. tectorum* growth in alpine growing season temperatures, we conducted a pot experiment in two temperature and light-controlled growth chambers. We recorded establishment (survival to the end of the experiment) and *B. tectorum* growth in two trials, a current mean growing season temperature (hereafter, current temperature trial) and expected future alpine growing season temperatures (hereafter, warmer temperature trial) for Niwot Ridge, a long-term alpine study site. The 4 °C temperature increase we used for our warmer temperature trial is consistent with estimates for Colorado's mountain regions, which are predicted to experience an increase in temperatures of 3–5 °C between 2035 and 2064 (Lukas et al. 2014). We tested whether simulated increases in N deposition would enhance the growth of *B. tectorum* with or without increases in temperature. In this experiment we collected *B. tectorum* seeds from a single montane population (elevation 1780 m, 40.1262° N, − 105.3078° W). Seeds were sown in a fine sandy loam alpine soil collected from a road cut at a dry meadow site on Niwot Ridge, CO (elevation 3466 m, lat 40.052486° N, long 105.582467° W). This soil type is classified as Moran family-Cryothent Series according to the Web Soil Survey (NRCS 2019). Additional soil characteristics are provided in Table 1 (Eilers et al. 2012). The top 20 cm of soil was collected from the road cut. This included soil from both the A and B horizons and therefore our growing media was a mixture of mineral and organic soil. The soil was mixed and sieved to 2 mm to homogenize and remove rocks and coarse organic material. Then the soil was placed in 164 ml 3.8 × 21 cm conical pots.

We germinated *B. tectorum* seeds on filter paper in petri dishes in both temperature trials to determine whether temperature influenced germination success. Seedlings were then transplanted into the prepared conical pots. The temperatures for the current growing season temperature trial was set to 12 °C daytime and 8 °C nighttime to simulate average July growing season temperature in the alpine (elevation 3,739 m) on Niwot Ridge (Greenland and Losleben 2001). The warmer summer growing season trial was set to 16 °C daytime and 12 °C nighttime temperatures. Both temperature trials were applied by growing plants in growth chambers, where plants received 14 h of daylight at 400 mmol photons m^{-2} s^{-1}. These conditions were maintained throughout the germination and growth phases of the experiment.

Half of the pots began receiving the N addition treatment 40 days after transplanting, resulting in a total of 40 pots with 10 replicates for each temperature and N level combination. The N addition treatment of 20 kg N ha^{-1} $year^{-1}$ was applied as $NH_4{}^+NO_3{}^-$ dissolved in tap water at a concentration of 1 mmol N L^{-1} applied at 30 ml increments. Niwot Ridge receives approximately 8–9 kg N ha^{-1} $year^{-1}$ (wet + dry) (NADP 2018). Given that alpine soils in the Front Range have been receiving N deposition at nearly this rate for many years, we added a higher rate of N above ambient N deposition in order to determine whether increases in the quantity or further accumulation of N would increase *B. tectorum* growth or reproduction compared to ambient N availability. The control treatment (ambient N) received the same volume of tap water without N addition. Pots were randomized in the growth chambers and we allowed the plants to grow for 78 days total to simulate the short alpine growing season. We then measured establishment, shoot length (longest leaf), dry shoot mass, and dry root mass.

Freeze recovery experiment

The goal of the freezing experiment was to determine whether frost events influence establishment and reproduction of *B. tectorum*, and whether soil type and N addition influence *B. tectorum*'s responses to simulated frost events. For this experiment, seeds from a different (higher elevation) montane population of *B. tectorum* (elevation 2632 m, lat 40.0024° N, long 105.5013° W) were collected in August of 2015. The alpine soils used in this experiment were from the same source as the soils used for the growing season experiment. Two additional gravely, sandy loam montane soils were collected from within a population of *B. tectorum* (elevation 2611 m, location 40.0481° N, 105.4671° W) and just outside of that population (elevation 2,611 m, 40.0481° N, 105.4665° W). These soils are classified as Ratake-Cathedral families-Rock outcrop complex according to Web Soil Survey (NRCS 2019). Additional soil characteristics are provided in Table 1 (Eilers et al. 2012). A primary goal of the study was to determine whether alpine conditions could be suitable for *B. tectorum*'s growth including both alpine soil properties and abiotic

Table 1 Soil characteristics of the montane and alpine soils

	Elevation (m)	pH	Texture (%)			C:N	Bulk density (g cm^{-3})
			Sand	Silt	Clay		
Montane	2730[a]	5.35	38	10	52	26.9[a]	1.14[a]
Alpine	3450	5.00	52	29	19	15.6[b]	0.44[b]

[a] Data are from Eilers et al. 2012

[b] Data are from Seastedt, Timothy. 2018. Krummholz island soil C and N data for East of Tvan, 1994–1996. http://niwot.colorado.edu

conditions. With this goal in mind, results from the growing season experiment indicated that a non-alpine soil treatment could be useful for interpreting growth results in alpine soil. The addition of the soil treatment for which soil from within the *B. tectorum* population allowed for comparing alpine soil to a soil known to be suitable for growth of *B. tectorum*. Addition of the non-conditioned, uninvaded soil, on the other hand, allowed for comparison of two uninvaded soils. These two soil types will be referred to as 'conditioned' and 'non-conditioned' hereafter. Each soil type was sieved and placed in conical pots (see growing season experiment section above). Seeds were germinated on filter paper and seedlings were planted in the prepared pots of all three soil types which were then randomly arranged to achieve a completely randomized experimental design.

Both temperature treatments were applied using a growth chamber where plants received 12 h of daylight at 400 mmol photons m^{-2} s^{-1}. Seedlings were grown in 10 °C daytime and 5 °C nighttime temperatures for 50 days to mimic early growing season alpine temperatures. Watering and N additions were performed in the same manner as the growing season experiment (N addition was equivalent to 20 kg N ha^{-1} $year^{-1}$). We measured plant height as length of inflorescence or length of longest leaf, whichever was longer.

Plants were then subjected to one of four subfreezing treatments. Plants were randomly assigned to a subfreezing temperature, − 8 °C, − 6 °C, − 4 °C or control (5 °C nighttime temperature). This range of temperatures were centered around the annual minimum June temperature at a high alpine weather station (3,739 m elevation) on Niwot Ridge, averaged across 1994–2014 minimums (mean = − 6 °C, median = − 6.5 °C) (Losleben 1994). The range of temperatures was intended to reveal whether a specific temperature threshold exists for survival or growth of *B. tectorum* or whether growth response is linear with increasing temperature. Freezing events occurred in an incubator for 3 h between 3:00 am and 6:00 am to simulate a realistic time period when minimum diurnal temperatures would naturally occur. Pots were randomly arranged within the incubator during freezing events.

After freezing events were conducted, pot locations in pot racks were re-randomized across all treatments and plants were allowed to recover from the freezing event in growth chambers with the same watering frequency for an additional 37 ± 3 days to determine whether soil type or N addition affected plants' recovery from freezing. For this growth period, plants experienced 14 h per day with lights on to simulate lengthening daylight in the growing season. At the end of the experiment, establishment was recorded as survival from the freezing event to the end of the experiment. Plant heights were measured and plants were harvested to measure dry shoot mass and dry root mass. Additionally, reproduction potential was estimated as the number of fully emerged spikelets per plant. This estimate has been used previously (Griffith and Loik 2010; Concilio et al. 2013), and was used for this experiment because, while many plants matured to this flowering stage, none produced fruit over this time interval. For each treatment, between 13 and 16 plants survived for a total of 349 total plants that were included in analysis.

Data analyses

Total plant mass (root + shoot) was used as a response variable in ANOVAs for both experiments. A two-way ANOVA was conducted to determine the effects of N treatment in the two temperature trials on plant mass in the growing season experiment. The two temperature trials were not replicated and therefore we only report p-values for the N treatment effect. For the freeze recovery experiment, a three-way ANOVA was used to assess the response of plant mass to N, temperature, and soil. This ANOVA was performed using type III sum of squares (car package in R, Fox and Sanford 2011). Type III sum of squares is justified because of unbalanced sample sizes after a few plants died in various treatment groups as well as the presence of significant interactions in the model. Omega squared was calculated for the effect sizes (sjstats package in R, Lüdecke 2018; Yigit and Mendes 2018). The effects of freezing temperature and N addition were also assessed *within* the alpine soil treatment using a two-way ANOVA because a main objective of the experiment was to test for conditions that would allow alpine conditions to be suitable for *B. tectorum* establishment. We examined residuals for normality and sample sizes within treatments were sufficiently large for ANOVAs. All statistical analyses were performed using R statistical software (R Core Team 2016).

An additional test was conducted on spikelet number data in the freeze recovery experiment to assess treatment effects on potential reproduction. A zero-inflated negative binomial general linear model with a logit link function was used for these zero inflated count data (pscl package in R, Jackman 2017).

Results

Growing season experiment

Under the current growing season temperature treatment, 46% of seeds germinated, while 88% of seeds germinated in the warmer temperature treatment. Establishment, which we defined as survival to the end of experiment, was 100%. At the end of the experiment, plant dry mass was greater for plants in the warmer temperature trial compared to the current temperature trial (Fig. 1), however we were unable to statistically separate the temperature affect from a potential growth chamber affect as a consequence of conducting the experiment one time in two different growth chambers. Plants in both temperature trials were small at the end of the experiment (mean height, 4.7 ± 0.15 cm; mean total mass, 0.015 ± 0.001 g) relative to individuals grown in the field from the populations where the seeds were collected (> 20 cm). The N addition treatment did not influence plant mass in either temperature trial (Table 2, Fig. 1). None of the plants in the experiment produced flowers.

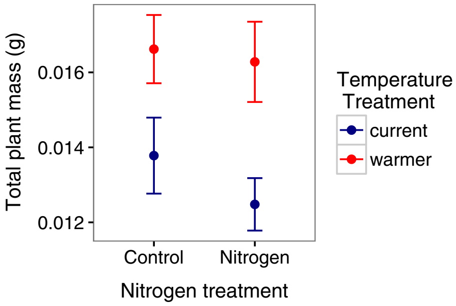

Fig. 1 Means and standard errors of *B. tectorum* total dry plant mass from the growing season experiment. The N addition treatment pots received the equivalent of 20 kg N ha^{-1} year^{-1}. The current growing season treatment was set to 12 °C daytime, 8 °C nighttime, and the warmer growing season treatment was set to 16 °C daytime, 12 °C nighttime

Freeze recovery experiment

Two plants died within the first 10 days after the freezing events, and subtle changes in leaf coloration immediately following the freezing event returned to pre-freezing appearance within this time period. Post-freezing treatment establishment (survival) was 99% for the whole experiment. Subfreezing temperatures significantly affected total dry mass per plant (Table 2, Fig. 2). However, the effect of freezing temperature on plant dry mass differed depending on the soil type in which plants were grown (Table 2, Fig. 2). The model with all predictor variables (temperature, N, and soil) resulted in a significant effect of soil type on plant mass (Table 2, Fig. 2), with significant interactions between soil type and N level (Table 2, Fig. 2), as well as a three-way interaction among temperature, N, and soil type (Table 2, Fig. 2). Total plant mass was 38% lower in alpine soil compared to upper montane soil (Fig. 2).

The different treatments did not influence potential reproduction in the same way as total plant mass for all predictor variables. Subfreezing temperatures did not influence the number of spikelets produced per plant (Table 2, Fig. 3). Spikelet production was, however, significantly greater in the N addition treatment relative to ambient N (Table 2, Fig. 3), and there was a significant interaction between soil type and N in the full model (Table 2, Fig. 3) despite soil types not having unique effects on spikelet production ($F_{2,325} = 1.3$, $p = 0.273$).

Because the effect of temperature differed depending on the soil type (Fig. 2), and an objective for this experiment was to determine the suitability of alpine soils for *B. tectorum*, we conducted ANOVAs with the subset of plants grown in alpine soil. Within the alpine soil treatment, N addition decreased total plant mass ($F_{1,106} = 13.1$, $p < 0.001$) and the warmer temperatures resulted in marginally non-significant lower biomass than colder subfreezing temperatures ($F_{3,106} = 2.5$, $p = 0.061$). There was no significant interaction between N treatment and subfreezing temperature ($F_{3,106} = 0.5$, $p = 0.678$). For plants grown in the non-conditioned soil, there was a significant decrease in plant mass after exposure to lower subfreezing temperatures ($F_{3,109} = 45.5$, $p < 0.001$). Nitrogen addition also increased total mass in the non-conditioned soil type ($F_{1,109} = 23.1$, $p < 0.001$), and the magnitude of the effect of the

Table 2 Full model results for growing season and freeze recovery greenhouse experiments

Response	Source	Effect size	MS	df	F	*p*
Growing season experiment						
Dry mass (g)	N	< 0.001	0	1	0.771	0.386
	Residuals		0	36		
Freeze recovery experiment						
Dry mass (g)	Temp	0.009	0.053	1	50.62	**< 0.001**
	N	0.013	0.071	1	47.10	**< 0.001**
	Soil	0.162	0.445	2	386.56	**< 0.001**
	Temp*N	0.002	0.013	1	10.39	**0.001**
	Temp*soil	0.025	0.071	2	65.10	**< 0.001**
	N*soil	0.014	0.040	2	50.02	**< 0.001**
	Temp*N*soil	0.006	0.017	2	15.68	**< 0.001**
	Residuals		0.001	337		

Response	Source	Effect size	Beta SE	Z	*p*
Potential reproduction (number of spikelets)	Temp	0.031	0.179	0.172	0.864
	N	− 0.657	0.310	− 2.118	**0.034**
	Conditioned soil	− 0.346	0.310	− 0.848	0.396
	Non-conditioned soil	− 0.299	0.337	− 0.889	0.374
	Temp*N	− 0.329	0.357	− 0.921	0.357
	Temp*conditioned soil	0.187	0.320	0.583	0.560
	Temp*non-conditioned soil	− 0.216	0.409	− 0.529	0.597
	N*conditioned soil	1.579	0.495	3.188	**0.001**
	N*non-conditioned soil	1.327	0.440	3.016	**0.003**
	Temp*N*conditioned soil	0.041	0.477	0.086	0.931
	Temp*N non-conditioned soil	0.367	0.537	0.684	0.494

Effect size for ANOVAs with dry mass as the response variable = ω^2. Effect size for the zero-inflated negative binomial general linear model = Beta coefficients. $p < 0.05$ are in bold text. Values reported for the zero-inflated negative binomial general linear model are relative to alpine soil treatment

MS mean squares

different subfreezing temperatures on mass was greater in the N addition treatment ($F_{3,109} = 13.6$, $p < 0.001$) with the control and least cold freezing treatment (− 4 °C) showing increased biomass with N addition (Fig. 2). For plants grown in the conditioned soil from the upper montane *B. tectorum* population, N addition again significantly enhanced total mass ($F_{1,110} = 166.2$, $p < 0.001$), but exposure to subfreezing temperatures did not impact mass accumulation during the recovery period ($F_{3,110} = 0.6$, $p = 0.63$).

Discussion

The goal of this study was to evaluate multiple alpine invasion filters which we hypothesized may fail to prevent establishment of non-native species' populations in the future as alpine regions experience more environmental changes. We found that alpine growing season temperatures, exposure to subfreezing temperatures, and N addition conditionally increased plant mass and reproduction of *B. tectorum* grown in montane soils, while alpine soil inhibited growth regardless of the other treatments.

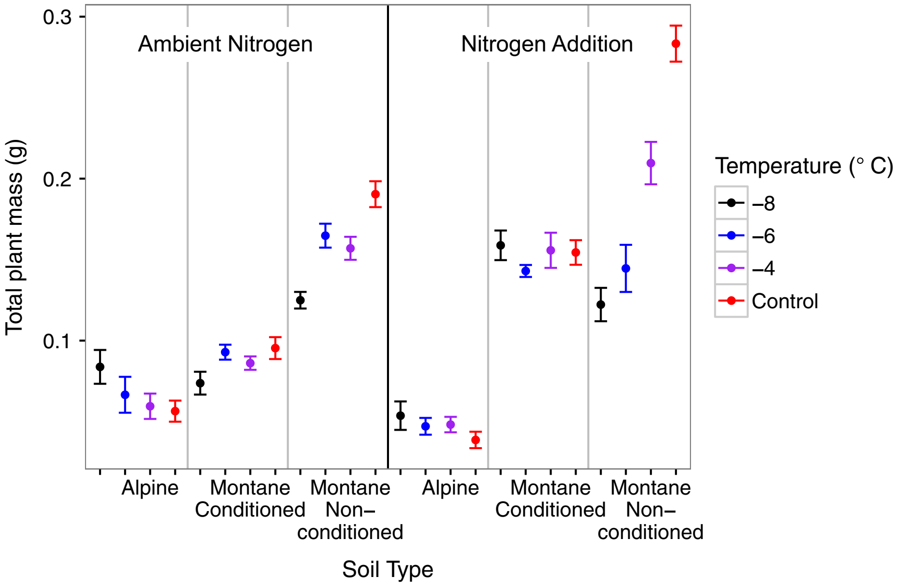

Fig. 2 Means and standard errors of *B. tectorum* total dry plant mass at the end of the freeze recovery experiment. The N addition treatment pots received the equivalent of 20 kg N ha^{-1} year^{-1}. The control freezing temperature was 5 °C which was the nighttime temperature experienced by all plants during the growing and recover phases of the experiment

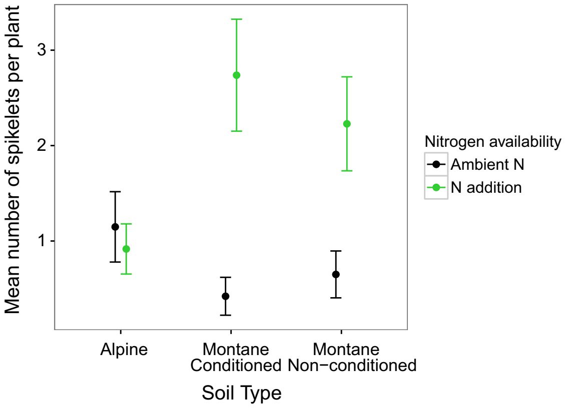

Fig. 3 Means and standard errors of *B. tectorum* spikelet production per plant (including plants with zero spikelets). We pooled freezing temperature treatments because we did not detect an effect of freezing temperature on spikelet production. The N addition treatment pots received the equivalent of 20 kg N ha^{-1} year^{-1}

Alpine soils inhibit mass and reproduction

Evidence from both experiments indicates that the alpine soil used in this experiment would be the most effective site-level invasion filter for inhibiting *B. tectorum* establishment. In the freezing experiment, we found that total biomass of plants grown in montane soils was more than 2.5 times greater than plants grown in alpine soil. Nitrogen addition and freezing treatments had no effect on this difference. In the growing season experiment, where all plants were grown in alpine soil, plant height and plant mass were small (plants were < 7 cm tall) and the plants did not produce flowers. *Bromus tectorum* is generally thought to be well adapted to a wide range of soil conditions (Bradford and Lauenroth 2006; Blank 2008), and yet our results suggest that the transition between upper montane and alpine soil may be an effective invasion barrier. Soil characteristics of the alpine soil source used in this study are on the periphery of soil characteristics for what is typically reported for *B. tectorum* populations in the invaded range (Bradford and Lauenroth 2006; Miller et al. 2006; Concilio et al. 2013). However, we note that the vast majority of studies reporting soil characteristics in *B. tectorum* populations were conducted in low elevation, arid ecosystems of the Great Basin. In comparison, the alpine soil used in our study is lower in pH and higher in organic matter than cool desert soils, and this may have contributed to poorer growth (mass) of *B. tectorum* in this study (Miller et al. 2006; Perkins et al. 2011).

The two montane soils were used in the freeze recovery experiment to provide both invaded soil and uninvaded soil as points of reference for the ability of *B. tectorum* to grow in alpine soil. Because *B. tectorum* performed worse in alpine soil compared to both montane soils, the inclusion of both non-conditioned and conditioned montane soil types in this study cannot help us determine whether a microbial mechanism may be involved in the inhibitory effect of alpine soils. Comparing *B. tectorum* mass in unconditioned montane and conditioned montane soils does suggest that negative microbial feedback loops may occur within the montane ecosystem (Evans et al. 2001; Concilio et al. 2015). Further investigations are necessary to determine whether alpine soil inhibits growth of invasives across different alpine soils in the Rocky Mountains and determine whether soil microbes or other attributes of alpine soil inhibit *B. tectorum* growth (North 2019). To our knowledge, soil characteristics that are not suitable for *B. tectorum* growth have not been assessed and therefore a number of potential characteristics including soil texture, bulk density, pH, and C:N may contribute to the inhibitory effect of the alpine soil (Table 1).

Interacting effects of nitrogen, soil, and temperature

Contrary to our hypothesis, N did not enhance the growth of *B. tectorum* in alpine soils. Thus, it is unlikely that N deposition would improve establishment or spread, or both, of *B. tectorum* into the alpine. In the growing season experiment, plants did not respond to N addition, even in the warmer than average growing season trial. The amount of N added (20 kg N ha^{-1} $year^{-1}$) is near the upper end of the range of forecasted rates near urban and agricultural centers in the western United States for the middle of the twentyfirst century (Dentener et al. 2006). Thus, we interpret this result as evidence that N deposition will not facilitate *B. tectorum* establishment in this alpine ecosystem, even if rates of N deposition increase locally. This finding differs from lower elevations biomes in *B. tectorum*'s invaded range wherein *B. tectorum* often responds positively to high N availability, alters N cycling and changes competitive outcomes in invaded communities (Sperry et al. 2006; He et al. 2011; Concilio and Loik 2013). For example, Uresk et al. (1979) showed that soil temperature constrained growth (measured as dry mass) of *B. tectorum* below 11 °C, and that above this temperature, N availability influenced mass (Uresk et al. 1979).

Although N addition had no effect on *B. tectorum* grown in alpine soils, N addition did have a significant positive effect on total biomass accumulation and spikelet production for plants grown in the two montane soil treatments. For plants grown in the non-conditioned soil treatment, N increased plant mass in the control treatment (no freeze) and the least cold subfreezing treatment (− 4 °C), whereas temperature appeared to impede a response to N in the colder subfreezing treatments (− 6 °C and − 8 °C). These results show some similarities to an experiment with *B. tectorum* in the eastern Sierra Nevada, California, USA where N addition enhanced biomass accumulation but not spikelet production when water availability was not limiting (Concilio and Loik 2013). The positive response of *B. tectorum* to higher minimum temperatures and N addition in our study may suggest that increased N deposition and increased minimum temperatures during growing seasons could promote persistence and spread of current populations *within* montane ecosystems. This response would depend partly on current genetic variation among montane populations and differences in abilities of populations to adapt to montane conditions (Kao et al. 2008; Leger et al. 2009; Germino et al. 2016). Larger, persistent populations in the montane are cause for concern because they may provide more opportunities for adaptation to alpine conditions over time (Haider et al. 2010).

We originally hypothesized that cold alpine temperatures currently prevent establishment of non-native species in the alpine, as has been proposed previously (Pauchard et al. 2009). We found that the variation in growing season and extreme minimum temperatures had different effects on *B. tectorum*'s growth and reproduction respectively. This implies that there are multiple ways in which temperature could act as an invasion filter (Haider et al. 2011). First, no *B. tectorum* plants reached reproductive maturity under current or warmer growing season temperatures, which may be due to the inhibiting effect of the alpine soil and less to do with growing season temperature. Concilio et al. (2013) found that late melting snowpack delayed phenology but did not ultimately limit spikelet production compared to plots with earlier snow melt. In the context of climate warming, a shift in plant phenology with early spring snowmelt would also increase plants' exposure to subfreezing temperatures, which is the second way temperature may act as an invasion filter (Synder and de Melo-Abreu 2005). However, none of the subfreezing temperature treatments resulted in *B. tectorum* mortality and 25% of plants produced flowers, suggesting that spring freezing events may not prevent

B. tectorum from establishing in the alpine. This outcome differs from a transplant experiment where high rates of *B. tectorum* mortality occurred at a montane site but not at a lower elevation site. Abiotic constraints were not tested to determine the cause of mortality in the experiment (Leger et al. 2009).

Conclusion

Our study of plants grown from seed originating from a single population of *B. tectorum* suggests that locally the alpine in the Colorado Front Range is not at immediate risk of invasion by *B. tectorum*. Alpine soil was also associated with significantly lower plant biomass compared to montane soils in a related experiment that assessed *B. tectorum* growth in additional montane and alpine soils in the Front Range (North 2019). Warmer growing season temperatures that are expected with climate warming as well as anthropogenic N deposition may have little impact on non-native species' establishment if site-level factors like soil strongly inhibit growth and reproduction. Further research is needed to determine the mechanism or mechanisms of soil inhibition and whether this inhibition may occur in other alpine soils from different geographic locations beyond the Front Range. The spread of *B. tectorum* populations at lower elevations *within* montane ecosystems is also a concern, and our results suggest that fewer freezing events, warmer freezing temperatures, or both, could enhance growth and reproduction of *B. tectorum* within montane populations. Haider et al. (2010, 2011) demonstrated that upslope range expansion of non-native plant species relies on genetic changes for species to become adapted to high elevation conditions, indicating that adaptation within current montane *B. tectorum* populations may be necessary for alpine invasions to occur. Acquiring beneficial genetic changes could be a slow process given that outcrossing is quite rare for *B. tectorum* (Leger et al. 2009; Haider et al. 2011). However, the discovery of relatively high genetic variability and outcrossing frequency (compared to other selfing plant species) within some montane populations of *B. tectorum* in the Rocky Mountains (Kao et al. 2008; Leger et al. 2009) indicates that adaptation to alpine conditions is a feasible trajectory for some populations.

Low temperatures and resource availability have been hypothesized as potentially important invasion filters in high elevation systems (Pauchard et al. 2009), but to our knowledge, this is the first time they have been experimentally tested together. Contrary to our expectations, warmer growing season temperatures, warmer minimum temperatures and increased N availability did not lower constraints on growth and reproduction when plants are grown in alpine soil. Our results demonstrate that alpine soil could be an effective invasion barrier for *B. tectorum* if the inhibitory attributes of the alpine soil we used are widespread.

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