THE UNWELCOME ARRIVAL OF BROMUS TECTORUM TO HIGH ELEVATIONS

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ABSTRACT

Cheatgrass (*Bromus tectorum*) is an early-season, annual invasive grass that has great impacts on plant communities and ecosystems through altered fire regimes, competition with native plants and interactions with microbial communities. Cheatgrass has spread to high elevations in the western U.S. over the last 10 to 15 years, raising concerns about the negative effects it will have on the newly invaded habitats. This range expansion may be due to (1) local adaptation, (2) phenotypic plasticity of all-purpose genotypes, (3) changes in climate, (4) increased local disturbance, (5) nutrient enrichment, (6) seed dispersal, or some combination of one or more of these mechanisms. There have been climate and N deposition changes that may facilitate the success of cheatgrass at high elevations. Genetic factors may also be at work. Cheatgrass seeds from populations along an elevation gradient germinated differently over time in response to pre-chilling and light, patterns which may suggest selection for dormancy at low elevations and release from this selection at high elevations. Successional theory is being applied and the addition of carbon (to reduce N availability) and mycorrhizal inoculum (to reestablish mutualistic relationships with native plants) are being tested for restoration of cheatgrass invaded plant communities at high elevations.

INTRODUCTION

Cheatgrass or downy brome (*Bromus tectorum* L.) is a winter annual C_3 grass that is self-pollinating (McKone 1985, Allen & Meyer 2002). Cheatgrass normally germinates in the fall, but seeds germinate at other times of year as well (Mack 1981). Seedlings that emerge in the fall develop a rudimentary root and shoot system that remains quiescent during the winter. Cheatgrass begins rapidly growing in late winter and early spring with warmer night and daytime temperatures and reaches full vegetative and reproductive maturity over a period of 6 to 8 weeks (Mack & Pyke 1983, Pierson & Mack 1990). These life history traits, especially rapid growth and corresponding depletion of soil water and N, which results in lower resource availability for perennial neighbors (Gordon et al. 1989, Welker et al. 1991), have contributed to the success of cheatgrass.

Cheatgrass has large impacts on plant communities and ecosystems. It has been implicated in increasing fire frequencies and intensities (Klemmedson & Smith 1964, Stewart & Hull 1949, Knick & Rotenberry 1997), which has led to its replacement of shrubs and perennial grasses (DiTomaso 2000). It is the most ubiquitous weed in steppe vegetation in Western North America (Mack 1981). Cheatgrass is known to have negative effects on native species through competition, reducing establishment and growth of native perennial grasses (Harris 1967, Young & Evans 1985, Svejcar 1990, Rafferty and Young 2002). Cheatgrass can change N dynamics in ecosystems (Paschke et al. 2000, Evans et al. 2001) and its dominance can alter the composition of microbial communities (Belnap and Phillips 2001, Al-Qarawi 2002, Kuske et al. 2002), which can result in loss of plant species diversity (van der Heijden et al. 1998).

Land managers report that cheatgrass now occurs at elevations where it was not found in the past. Jeff Connor, Natural Resource Specialist at Rocky Mountain National Park, Colorado, reports that he has observed the advance of cheatgrass to high elevations over the past 10 to 15 years (personal communication 2003). Similar changes in distribution have been noted in Mesa Verde National Park (Bill Romme, Professor, Colorado State University, personal communication 2003), rangeland in

Wyoming (Stephen Enloe, Extension Weed Specialist, University of Wyoming, personal communication 2003) and throughout the Colorado Rockies (meeting of the Colorado Weed Network, personal communications, July 16, 2003). Managers are concerned about losing valuable winter habitat for wildlife due to the invasion of cheatgrass and its ability to out-compete native perennial grasses (Harris 1967, Rafferty and Young 2002) and to increase fire frequency and intensity (Klemmendson & Smith 1964, Stewart & Hull, 1949, Knick & Rotenberry 1997).

There are many possible explanations for the expansion of cheatgrass to high elevations including (1) local adaptation (2) phenotypic plasticity of all-purpose genotypes, (3) changes in climate that create conditions at high elevations that are more favorable for cheatgrass than they were in the past, (4) increased local disturbance, e.g. extremely high grazing pressure due to over-population of elk, (5) regional nutrient enrichment, e.g. increased N deposition due to upslope air pollution (Bowman 1992), (6) seed dispersal, i.e. the seed only arrived at high elevations sites in the last 10 to 15 years, or some combination of one or more of these mechanisms. Here I begin to explore the potential roles of local adaptation, plasticity of all-purpose genotypes, N deposition and climate change in the range expansion of cheatgrass.

Genetic factors

Local adaptation is the superior performance of a genotype in its home environment compared to a new environment. Genetic differentiation may have resulted in adaptation of cheatgrass to high elevation environments, which may be a mechanism responsible for the observed expansion. Genetic differentiation that corresponds to environmental differences has been demonstrated in cheatgrass (Rice et al. 1991a, b, c, Rice et al. 1992, Meyer et al. 1997, Allen & Meyer 2002, McCarlie et al. 2003). Survival (Rice et al. 1991b, c), phenotypic plasticity (Rice et al. 1991b), growth rates (McCarlie et al. 2003) biomass allocation (Rice et al. 1991b, Rice et al. 1992), phenology (Rice et al. 1992, Rice et al. 1991a, b, c), plant size (Rice et al. 1991b) and seed production (Rice et al. 1991b, c), have all been demonstrated to be related to environments from which populations originated. Rice et al. (1992) found that populations of cheatgrass from arid steppe flowered earlier, set seed earlier and allocated less biomass to root growth than populations from mesic steppe or forest habitat. These traits correspond to adaptation to environments with short growing seasons due to limited water availability.

Previous work has shown that cheatgrass was introduced into the U.S. from multiple sources. Some of the genetic evidence for this is that there is more genetic variation within naturalized populations than native populations (Novak & Mack 2001). However, this species has reduced overall (i.e. among population) genetic variation in the naturalized range compared to native range, probably due to founder effects at the time of introduction (Novak & Mack 2001). The plant is very nearly always self-pollinating with little or no heterozygosity (Bartlett et al. 2002). Dick Mack, in his many years of working with the plant, has never found any anthers exerted from the inflorescences, thus precluding out-crossing. However, Novak & Mack (2001) reported some evidence of "novel recombinant genotypes (p 120)." The ecological significance of these patterns of genetic variability has not yet been thoroughly explored.

Nitrogen deposition

Nitrogen deposition has increased in the Rocky Mountains, most notably in areas influenced by the Colorado Front Range (Bowman and Seastedt 2001). At least half of the annual 6 kg N ha^{-1} deposition at Niwot Ridge, Colorado is anthropogenic in origin and subalpine forest, the areas most recently invaded by cheatgrass, is more influenced by air from the Colorado Front Range than the alpine tundra (Sievering 2001).

Cheatgrass may benefit from increased N deposition like that experienced by Niwot Ridge over the past several decades (1950-1996) (Welker et al. 2001). Elevated N levels can inhibit establishment of native late-successional plant species (Cherfas 1991). Increased N availability has been shown to affect successional processes in semiarid ecosystems, slowing the replacement of weedy annuals by native herbaceous perennials (McLendon & Redente 1991; Paschke et al. 2000; McLendon & Redente 1992; Trent et al. 1994). Conversely, decreased N availability has been correlated with the replacement of early-successional species by mid-successional species in a variety of systems (McLendon & Redente 1994; Paschke et al. 2000; Wedin & Tilman 1990; Tilman & Wedin 1991; McLendon & Redente 1992; Trent et al. 1994; Young et al. 1998), and competitive success of shrubs over grasses is increased by lower N availability in semiarid (Vanauken & Bush 1989) and arid ecosystems (Ettershank et al. 1978). Cheatgrass biomass and community dominance can be greatly affected through manipulation of soil N availability with sucrose amendments (McLendon & Redente 1994; McLendon & Redente 1992; Paschke et al. 2000). Given this evidence, cheatgrass may benefit much more from increased N deposition than native perennial species at high elevations.

Climate change

One possible driver of the continuing expansion of the range of cheatgrass may be climate changes that are occurring at an unprecedented rate in the western U. S. (Kittel et al. 2002). Warmer or wetter conditions in higher elevations (Kittel et al. 2002), or both, could provide new habitats for cheatgrass expansion, especially if temperatures in spring become warmer, which would facilitate early season growth, photosynthesis, and soil water extraction (Harris 1967). In addition, if snow-melt dates become earlier because of reduced snowfall and increasing spring temperatures (Kittel et al. 2002), cheatgrass may have a competitive advantage because it typically germinates in the fall and over-winters under snow. It is able to grow rapidly under the cooler temperatures of spring compared to native forbs and grasses that often reach peak growth in mid-summer. Pierson and Mack (1990) found that the growing season was too short in the forest community zones on an elevation gradient they studied for cheatgrass to be highly successful. They identified the abbreviated period suitable for cheatgrass growth as the cause for these habitats being the edge of the range for this species. With warmer and wetter climates, performance of cheatgrass in these habitats may improve.

We have initiated studies of the relationship between seed dormancy and germination response of cheatgrass populations collected from an elevation gradient that may indicate that local adaptation has occurred. We hypothesized that populations from lower elevations on the eastern plains of Colorado would be more likely to require chilling or short day lengths, indicating fall conditions, to break dormancy than populations from high elevations. The risk of premature germination may differ among habitats at different elevations, as suggested by previous work (Beckstead et al. 1996, Meyer et al. 1997). Cheatgrass that germinates in the summer on low-elevation plains, where summer precipitation is not predictable, may be less likely to reach maturity than in the mountains, where it rains most afternoons. This may exert a significant selection pressure for seed dormancy among low elevation populations.

METHODS AND RESULTS

A study investigating germination characteristics of seeds collected from 12 cheatgrass populations along an elevation gradient (1414 m – 2682 m) (Table 1) in Colorado indicates that germination response to environmental conditions differ among populations, which hints at genetic differentiation and local adaptation.

Table 1. *Bromus tectorum* populations

Location	Elevation (m)
Akron	1,414
Fort Morgan	1,385
Greeley	1,406
Loveland	1,557
Sylvandale	1,639
Drake	1,962
Crosier Mountain	2,135
Estes Park	2,350
Lower-Deer Mountain	2,460
Mid-Deer Mountain	2,581
Upper-Deer Mountain	2,670
Golden Gate Canyon	2,682

To test the hypothesis, we conducted two experiments. First, ten seeds from 11 of the 12 cheatgrass populations were planted in 15 cm diameter pots filled with commercial potting soil in a cooled greenhouse at Colorado State University in Fort Collins, Colorado in August 2003. Seed germination was monitored to evaluate differences among populations in germination percentage. Data were evaluated with analysis of variance using JMP version 5.0.1.2 (SAS Inst. Inc., Cary NC).

We expected populations from low elevations to have higher dormancy than those from high elevations. This pattern was followed in general, but the populations from the highest elevation and one of the low-elevation populations had low and high germination rates, respectively, contrary to our expectations (ANOVA $P < 0.0001$, $F_{10, 99} = 15.97$; linear regression $P = 0.0006$, df $= 1,108$) (Figure 1).

Figure 1. Number of seedlings produced from ten seeds of each of 11 cheatgrass populations along an elevation gradient. The line is the least squares linear regression. Bars are means of 10 pots $\pm$ 1 standard error of the mean. Means with different letters are significantly different at $\alpha = 0.05$ based on Tukey's HSD.

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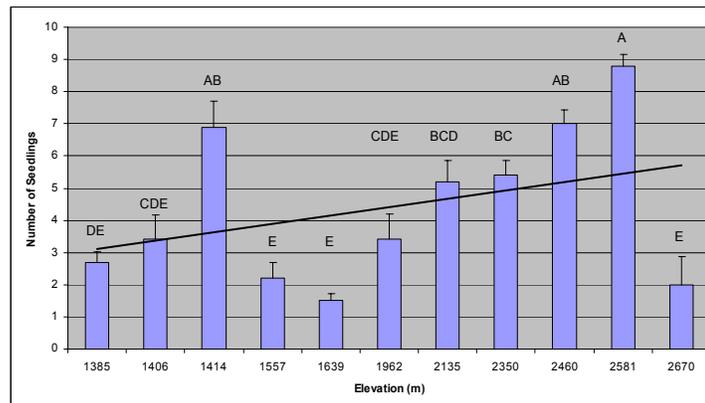
In a second experiment, seeds of four populations (1385 m, 1406 m, 2670 m and 2682 m) were placed on moist germination paper and either subjected to 10 days of 2 °C before initiation of tests (pre-chilled) or placed directly into incubation chambers (not-chilled). Chilled and not-chilled treatments were held at 25 °C and exposed either to 8 hours of light (+light) or no light (-light) during each 24-hour cycle. Data were evaluated with repeated measures analysis of variance using JMP version 5.0.1.2 (SAS Inst. Inc., Cary NC).

Populations germinated at different rates based on a significant population by time interactions ($P <$ 0.0001) (Figure 2). The population from the highest elevation germinated most quickly, reaching greater than 80% germination at the fourth day of evaluation while the next highest germination rate was the population from the lowest elevation site with 60% germination.

Figure 2. Percent germination over time of seeds from four populations of cheatgrass from an elevation gradient. Means of four replicates ± 1 standard error of the mean are presesnted.
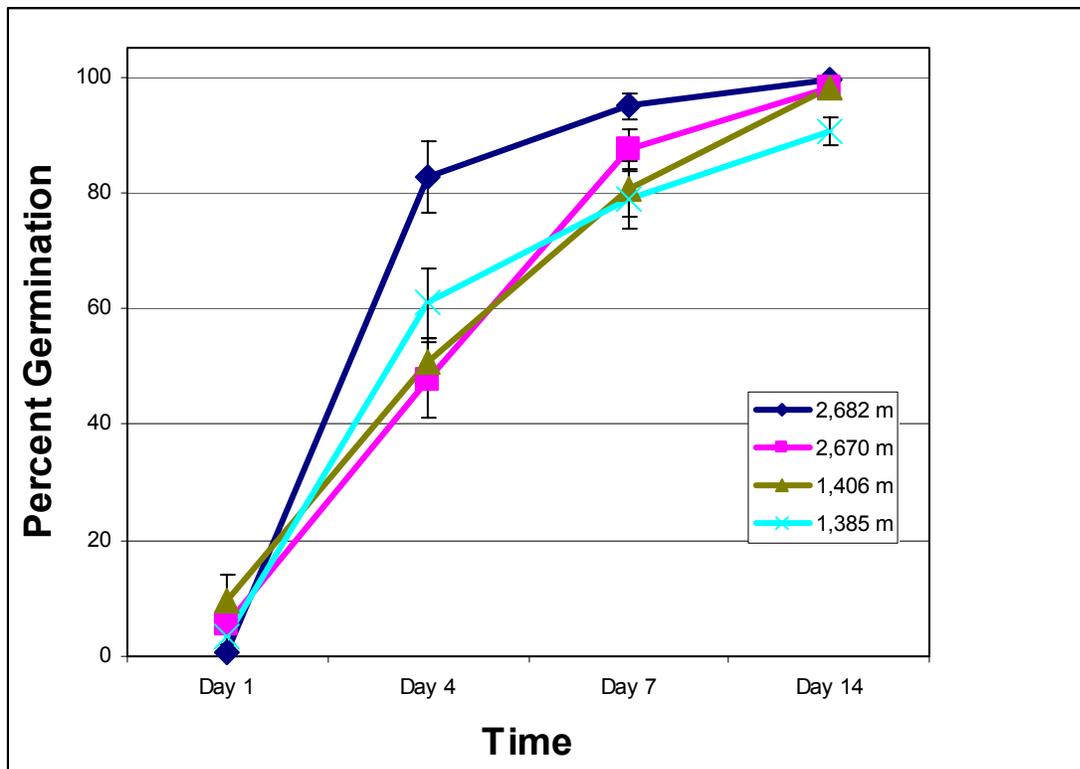

The patterns of germination over time for the populations depended on whether or not they had been pre-chilled (time x population x chilling treatment interaction, $P <$ 0.0001) (Figure 3). The germination of seeds from the 2,682 m and 1,385 m populations slowed down with chilling, while germination of seeds from the 2,670 m population occurred more rapidly with chilling.

Figure 3. Percent germination over fourteen days of seeds from four populations of cheatgrass from an elevation gradient (a) with and (b) without pre-chilling. Means of four replicates ± 1 standard error of the mean are presented.
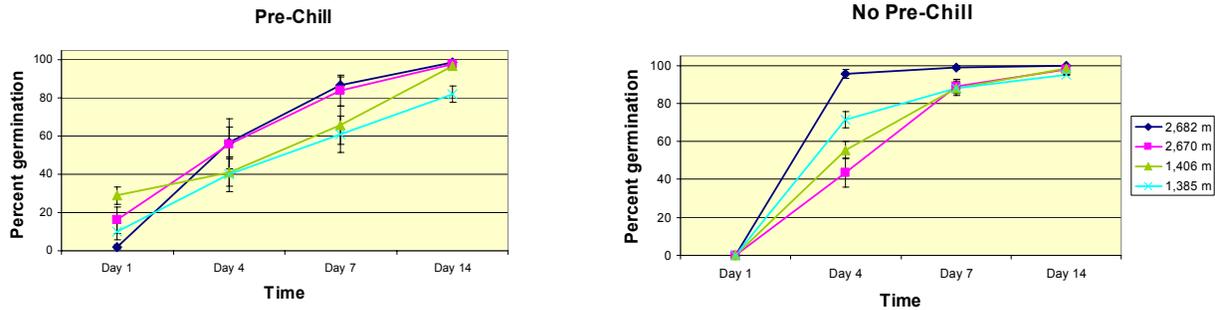
The pattern of germination over time for the populations also depended on whether or not the seeds were exposed to light during the tests (time x population x light interaction $P = 0.02$). Light increased the speed of germination of the 2670 m and 1385 m populations, while germination rates of the 2682 m and 1406 m populations were similar with and without light.

Figure 4. Percent germination over fourteen days of seeds from four populations of cheatgrass from an elevation gradient (a) with 8 hours of light and (b) without light. Means of four replicates ± 1 standard error of the mean are presented.
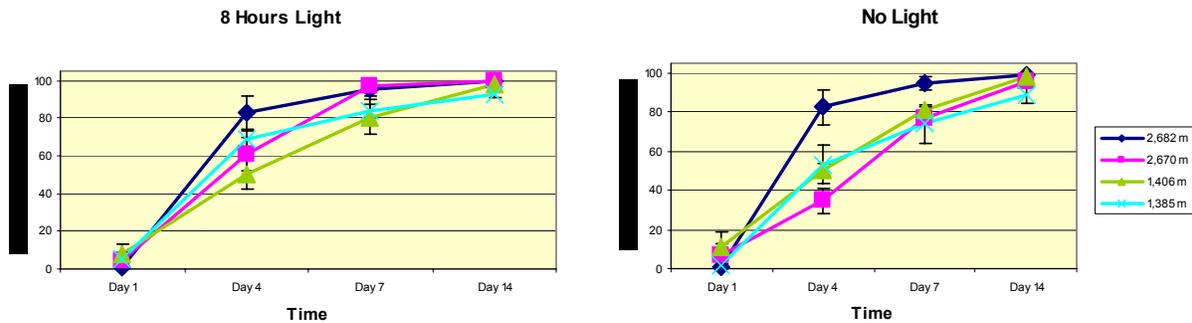
DISCUSSION

Potential for local adaptation

Some of the results show that patterns of cheatgrass seed dormancy correspond, on average, to seed source elevation and suggest that there may be selection for seed dormancy among low-elevation populations and release from this selection pressure at high-elevations (Figure 1). However, the patterns were not strictly followed and germination response to pre-chilling and light did not suggest that dormancy was related to seed source elevation (Figure 2, 3 and 4). Despite this, the strong differences among populations indicate potential for local adaptation. Our results are consistent with those of previous authors who found that germination responses can be of adaptive importance, but that the patterns were not always consistent (Beckstead et al. 1996, Meyer et al. 1997, Meyer & Allen 1999 a, b).

It should also be noted that the germination responses we detected may be affected by the environments in which the parent plants grew. To minimize the effects of maternal environment, tests should be conducted on seeds that come from plants grown under identical environmental conditions, which there was insufficient time to do for the experiments reported here.

Cheatgrass control and restoration of cheatgrass invaded communities

The control of cheatgrass once it has become established and restoration of plant communities that it invades continue to be major challenges for land managers. Furthermore, approaches that are most effective at high elevations may differ from those that are successful at low elevations. We have begun to test several approaches to address these problems. The use of intermediate, early-successional species as a "bridge" to ameliorate site conditions for late-successional species has been recently applied to the restoration of weed dominated landscapes (Hardy and Palazzo 2002). This research project seeks to test this "bridge" approach by applying facilitation, tolerance and inhibition models of succession (Connell and Slatyer 1977). In all models, disturbance opens a space and colonizers with early-successional traits establish on the site. The models differ in how late-successional species become established. With facilitation, early-successional species create conditions favorable for establishment of late-successional species. In the tolerance model, late-successional species establish subsequent to early species because of their life history traits but will eventually dominate due to their superior competitive abilities. The inhibition model describes conditions by which the early colonizers inhibit establishment of other species (Connell & Slatyer 1977). Integtral to this "bridge" concept is that planting intermediate species will result in facilitation or tolerance models of succession. Testing whether restoration techniques can achieve these effects will allow us to evaluate the success of the methods and target modifications necessary for future applications.

We have established an experiment to test whether the facilitation, tolerance, or inhibition model of succession is supported by results from seeding techniques for cheatgrass infested sites. The study will evaluate the performance of early-succession (ES) and late-succession (LS) species mixtures grown alone, planted simultaneously (LE), or planted sequentially (LSES), with the ES seed mixture planted in the first year and the LS mixture added in the second year. In the second year, the LS mixture will also be added to plots that were not seeded in the first year (NS) to create the LSNS treatment. The following tables describe alternative hypotheses for testing the two stages of succession, establishment (Table 2) and growth (Table 3) (Connell and Slatyer 1977). The hypotheses will be tested by comparing the success of the seeded species in each of the treatments.

Table 2: Test emergence and establishment of late-successional species

Hypothesis	Interpretation	Restoration implications
LS>LE, LSNS>LSES	Inhibition	Plant LS seeds alone
LS=LE	Tolerance	Plant LS seeds with ES species or alone.
LSNS=LSES	Tolerance	Plant LS seeds alone or into established ES communities.
LS<LE	Same year facilitation	Plant LS seeds with ES species.
LSNS<LSES	Next year facilitation	Better to plant LS seeds into established ES community than into bare soil.

Table 3: Test growth in later stages of succession

Hypothesis	Interpretation	Restoration implications
LS>LE, LSNS>LSES	Inhibition	Death/damage of ES species necessary for LS establishment
LS=LE, LSNS=LSES	Tolerance	Presence of ES plants does not affect LS species
LS<LE, LSNS<LSES	Facilitation	Presence of ES plants on the site enhance LS plants.

In low nutrient environments, late-successional species with greater dependence on abuscular mycorrhizal fungi (AMF) can take advantage of mycorrhizal associations to extract scarce resources and gain a competitive edge over early-successional species (Doerr et al. 1984, Reeves 1985, Miller 1987). Sucrose addition (N-) has been an effective treatment to reduce N and other nutrient levels in soils and shift community composition from annual to perennial species (McLendon and Redente 1994, Paschke et al. 2000, McLendon and Redente 1992). Mycorrhizal fungi are ubiquitous and easily colonize sites, thus

the addition of mycorrhizal inoculum is generally not required and has not been tested in combination with the sucrose treatments. However, in the case of cheatgrass, where AMF communities have been shown to be depressed (Al-Qarawi 2002), supplementation of naturally occurring AMF spores may be necessary for optimal establishment and growth of native plant species. Mycorrhizal inoculation may increase the competitive ability of highly mycorriza dependent, late-successional plants in the low nutrient environment created by sucrose addition.

An experiment is being conducted to evaluate the efficacy of carbon addition to reduce available N, and mycorrhizal inoculation to ensure important biotic mutualists to promote the establishment of native perennial vegetation. The hypotheses this experiment will test are outlined in Table 4.

Table 4: Test whether mycorrhizal inoculation (M+) in combination with sucrose (N-) has greater effect in shifting the composition of a community towards a late-successional species compared with sucrose treatments alone (N-).

Hypotheses	Test	Restortion implicatns
H1: AMF in cheatgrass dominated soils < AMF in desired community soils	Compare MIP[1] for cheatgrass dominated and native communities	Restore AMF for desired plant establishment
H2: High RMD[2] species establish better in M+ relative to NM	(1) Determine RMD for each species and cheatgrass. (2) Compare species biomass in M+ and NM plots.	Add AMF with high-RMD plants
H3: Cheatgrass hosts fewer/different AMF taxa, or both, relative to the desired species	(1) Inoculate cheatgrass and desired dominant species with AMF morphotypes[3]. (2) Evaluate levels of infection and plant responses with each AMF morphotype.	Need specific AMF taxa to re-establish native plants
H4: Native plants increase and cheatgrass decrease in N- relative to N	Compare establishment and biomass of seeded species in N- and N plots.	Perennial species performance > cheatgrass in N-
H5: Native plants > cheatgrass in N-M+ relative to N-NM	Compare establishment and biomass of seeded species in N-M+ and N-NM plots.	AMF increases effectiveness of N-

[1] Mycorrhizal inoculation potential (MIP) is a measure of AMF infection induced in a host plant by inoculant.

[2] Relative mycorrhizal dependency (RMD) is the degree of response of a plant species to mycorrhizal infection at a given nutrient level.

[3] Follow established procedures (INVAM).

These experiments will provide land managers with valuable information to assist in the control of cheatgrass and restoration of plant communities at high elevations. First, the results will indicate which models of succession may be most successfully applied to restore native vegetation in high elevation habitats. Second, the results will inform us about the strength and importance of interactions between N availability and mycorrhizal symbionts for the successful establishment of native species.

The invasion of high altitude habitats by cheatgrass is relatively recent and has the potential for causing dramatic environmental change. Developing an understanding of the mechanisms underlying this range expansion will allow us to determine what approaches will be most effective at controlling its spread, reversing its effects and restoring native plant communities after its invasion.

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