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Effects of soil amendments on germination and emergence of downy brome (*Bromus tectorum*) and *Hilaria jamesii*

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Downy brome is an introduced Mediterranean annual grass that now dominates millions of hectares of western U.S. rangelands. The presence of this grass has eliminated many native species and accelerated wildfire cycles. The objective of this study was to identify soil additives that allowed germination but inhibited emergence of downy brome, while not affecting germination or emergence of the native perennial grass *Hilaria jamesii.* On the basis of data from previous studies, we focused on additives that altered the availability of soil nitrogen (N), phosphorus (P), and potassium (K). Most water-soluble treatments inhibited downy brome germination and emergence. We attribute the inhibitory effects of these treatments to excessive salinity and ion-specific effects of the additives themselves. An exception to this was oxalic acid, which showed no effect. Most water-insoluble treatments had no effect in soils with high P but did have an effect in soils with low P. Zeolite was effective regardless of P level, probably due to the high amounts of Na^+ it added to the soil solution. Most treatments at higher concentrations resulted in lower downy brome emergence rates in soils currently dominated by downy brome than in uninvaded (but theoretically invadable) *Hilaria* soils. This difference is possibly attributable to inherent differences in labile soil P. In *Stipa* soils, where *Stipa* spp. grow, but which are generally considered to be uninvadable by downy brome, additions of high amounts of N resulted in lower emergence. This may have been an effect of NH_4^+ interference with uptake of K or other cations or toxicity of high N. We also saw a positive relationship between downy brome emergence and pH in *Stipa* soils. *Hilaria* development parameters were not as susceptible to the treatments, regardless of concentration, as downy brome. Our results suggest that there are additions that may be effective management tools for inhibiting downy brome in calcareous soils, including (1) high salt applications, (2) K-reducing additions (e.g., Mg), and (3) P-reducing additions.

Nomenclature: Downy brome, *Bromus tectorum* L. BROTE; *Hilaria jamesii* L., galleta grass; *Stipa* spp.

Key words: Annual invasive grass, desert grasslands, semiarid, soil amendments.

Native North American ecosystems that have been invaded by the Eurasian–Mediterranean annual grass downy brome show critical alterations in ecosystem structure and function (see reviews in Mack 1981; Upadhyaya et al. 1986). Replacement of native vegetation and elevated wildfire frequency have reduced native plant and animal biodiversity, deteriorated agricultural and range lands, and required large expenditures for fire suppression (Vail 1994; Whisenant 1990). Downy brome invasion also has transformed soils, including food web structure, biogeochemical characteristics, and nutrient cycles (Belnap and Phillips 2001; Evans and Belnap 1999; Wilson et al. 1966). Continued downy brome dominance is encouraged through the positive feedback between this species and associated ecosystem alterations (Belnap and Phillips 2001; Evans et al. 2001). Consequently, land managers throughout the western United States need ways to prevent downy brome invasion or to restore invaded landscapes.

Semiarid grasslands in southeastern Utah, United States, that are dominated by *Hilaria jamesii* appear particularly susceptible to downy brome invasion. However, those dominated by needle-and-thread (*Stipa comata* Trin. & Rupr.) or *Stipa hymenoides* (Welsh et al. 1993) exhibit little, if any, invasion by downy brome (Belnap and Phillips 2001). Both downy brome and *Hilaria* occur in soils with higher exchangeable potassium (K) and silt than in areas where *Stipa* spp. dominate, suggesting that low K or water may limit this annual grass (Hansen 1999; Howell 1998). Downy brome growth in the field is also positively associated with the high ratio of soil K or phosphorus (P) relative to calcium carbonate ($CaCO_3$) and magnesium (Mg) or iron (Fe) oxides (Belnap and Phillips 2001; Miller 2000). These latter compounds can bind with P, rendering it unavailable to plants. In addition, Mg can inhibit K uptake (Haynes and Goh 1978; Thompson and Troeh 1978). Mg, Fe, and calcium (Ca) can also increase soil acid–neutralizing potential (ANP) or buffering capacity, which through sorption reactions may inhibit the availability of carbonate-related nutrients such as P, manganese (Mn), and copper (Cu) (Miller 2000). Combined, these data suggest downy brome is limited by K or P (or both) in these soils.

Howell (1998) and Morrison (1999) added magnesium oxide (MgO) and K to soils seeded with downy brome in greenhouse experiments and observed that Mg additions depressed and K additions stimulated downy brome emergence and biomass. Miller (2000) also observed that MgO additions in the field diminished downy brome establishment. Nitrate (NO_3^-) and ammonium (NH_4^+) have also been ob-

TABLE 1. Characteristics of soils from three different plant communities in southeastern Utah.

	Soil type		
	Stipa	*Hilaria*	*Bromus*
P (ppm)	7.3	9.1	17.1
Available K^+ (ppm)	70.4	179.2	198.4
Exchangeable Ca^{2+} (ppm)	2820.0	3174.0	2568.0
Exchangeable K^+ (ppm)	95.9	293.2	295.0
Exchangeable Mg^{2+} (ppm)	54.6	132.3	129.4
Exchangeable K^+/Mg^{2+}	1.5	2.2	2.2
Exchangeable Na^+ (ppm)	51.0	60.9	40.0
Organic matter (%)	0.3	0.3	0.4
Electrical conductivity (dS/M)	0.5	0.5	1.1
pH	8.0	8.2	7.8
Sand (%)	72.0	65.3	71.6
Silt (%)	18.1	17.4	14.1
Clay (%)	9.9	17.3	14.3
Total N (ppm)	89.3	87.4	73.9
NH_4-N (ppm)	4.1	6.5	7.4
NO_3-N (ppm)	1.6	1.6	19.6
$CaCO_3$ (%)	6.8	5.2	3.2
Cu^{2+} (ppm)	0.2	0.7	0.6
Fe^{2+} (ppm)	2.9	3.5	3.7
Mn^{2+} (ppm)	2.5	6.1	4.6
Zn^{2+} (ppm)	0.2	0.3	0.3

served to stimulate seed germination of many species (Egley and Duke 1985; Karssen and Hilhorst 1992).

The effects of pH on germination potential differ among plant species. Some species benefit from more acidic conditions, others prefer neutral or alkaline pH, and some show no response to pH manipulations (Justice and Reece 1954; Pierce et al. 1999; Susko et al. 1999). Data addressing the effects of pH on the germination of species on calcareous soils are generally lacking (Baskin and Baskin 1998), although one study demonstrated that acidic soils inhibit both germination and seedling growth of species that prefer calcium-rich soils (Okusanya 1978).

One managerial approach to diminishing the ecological success of invasive downy brome is to apply soil treatments that allow downy brome seeds to germinate but reduce or eliminate their emergence without also suppressing the germination and emergence of the native perennial grass *Hilaria*. Based on the literature reviewed above, we manipulated the availability of soil P, K, and nitrogen (N) and pH to determine if soil amendments could achieve this objective.

Materials and Methods

We collected downy brome seed in September 1997 from Canyonlands National Park (CNP), Needles District, southeastern Utah, United States (~1,500 m elevation; average annual precipitation and temperature 216 mm and 12 C, respectively; Miller 2000). In January 2000 we obtained *Hilaria* seed[1] that was grown nearby in Dolores, CO. Three sandy loam soils (Typic Torripsamments from the Begay series) dominated by different plant communities were collected at the Squaw Flat site of CNP (Table 1). "Downy brome soils" are previously *Hilaria*-dominated soils that have been dominated by downy brome for over 50 yr. "*Hilaria* soils" are uninvaded soils dominated by *Hilaria*, and "*Stipa* soils" are uninvaded soils dominated by *S. hymenoides* and needle-and-thread. Although *Hilaria* soils are considered invadable by downy brome, the soils we used supported no or small downy brome populations. To date, *Stipa* soils have been observed to be mostly noninvadable by downy brome.

The following methods were employed for soil analyses: P (Olsen et al. 1954) and available K (Schoenau and Karamonos 1993) were extracted with $NaHCO_3$. All exchangeable nutrients were extracted with ammonium acetate ($NH_4C_2H_3O_2$; Thomas 1982). Organic matter (OM) was determined by the Walkley–Black (1934) procedure. Electrical conductivity (EC) and pH were determined using a saturated paste (Rhoades 1982). Texture was determined by the hydrometer method and total N by Kjeldahl analysis (Bremner 1996). Inorganic N was extracted with KCl and analyzed by steam distillation (Kenney and Nelson 1982). $CaCO_3$ was measured by HCl neutralization (Allison and Moode 1965) and thus includes any soil constituent that neutralizes acid. Cu, Fe, Mn, and zinc (Zn) were extracted with diethyltriaminepentaacetic acid (Lindsay and Norwell 1978).

We applied additives to downy brome and *Hilaria* soils that manipulated availability of soil N, P, and K (Table 2). Because certain treatments could have unforeseen side effects or not fulfill intended goals, we used multiple ways to manipulate the availability of a given soil nutrient. Except for ferric oxide (Fe_2O_3) and zeolite (discussed below), all fertilizers were added at equivalent osmolar rates using Cannon et al. (1995) as a guide for additive levels. The concentrations we used (Table 2) resulted in the following osmotic potentials: 1 ×, 2 ×, 3 ×, 4 ×, and 5 × were the equivalent of − 0.46, − 0.91, − 1.37, − 1.83, and − 2.28 MPa, respectively. For Fe_2O_3 additions, we used levels similar to those of Solis and Torrent (1989), Carreira and Lajtha (1997), Hamad et al. (1992), and Samadi and Gilkes (1999).

To decrease available soil P, we added calcium oxide (CaO), Fe_2O_3, and calcium chloride ($CaCl_2$). CaO and Fe_2O_3 increase the buffering capacity of soil and can thus decrease available P (Hamad et al. 1992; Menon et al. 1990). $CaCl_2$ was used as a water-soluble alternative to CaO, as results from our initial experiments indicated CaO was difficult to dissolve. Also, Carreira and Lajtha (1997) found that addition of soluble $CaCl_2$ to a calcareous entisol resulted in less available P, presumably due to $CaCO_3$ precipitation induced by the added Ca. To increase available soil P, we added oxalic acid to free carbonate-bound P and sodium phosphate (Na_2HPO_4). To decrease available K, we used magnesium chloride ($MgCl_2$), MgO, and zeolite, a high cation-exchange capacity (≈220 $cmol_c$ kg^{-1}), crystalline, hydrated aluminosilicate of volcanic origin (Ming and Mumpton 1989). The Mg compounds were intended to reduce plant-available K through competitive displacement of K from exchange sites (Haynes 1980; Thompson and Troeh 1978) and zeolite to adsorb exchangeable K (Ming and Mumpton 1989). Each treatment was added in aqueous solution to soil (except for zeolite, which is a solid) and stirred. Clinoptilolite[2] was charged with Na^+ by equilibration with 2-M NaCl for 5.5 d, during which the solution was replaced every 24 h. After drying, the zeolite was mixed in dry form with soil.

TABLE 2. Germination trial treatments. All concentrations except Fe_2O_3 and zeolite are ionically equivalent. The μmol_c value denotes the amount of positive or negative charge added by each compound, and the charge ratio is determined by dividing μmol_c value by 16.7, which is the amount of charge added by NaCl per gram of soil. These values are for the 1× treatment. Quantities were varied up to 5× the concentrations shown (10× in the case of zeolite).

Treatment	Additive	Amount added		Ratio of charge to NaCl charge	Water-solubility[a]
		mg g^{-1} soil	μmol_c g^{-1} soil		
− P	CaO	0.6	44.5	2.7	NWS
− P	$CaCl_2$	0.6	9.9	0.6	WS
− P	Fe_2O_3	28.6	1,074.5	64.5	NWS
+ P	Na_2HPO_4	1.6	22.2	1.3	WS
+ P	Oxalic acid	1.0	22.2	1.3	WS
− K	$MgCl_2$	1.1	22.2	1.3	WS
− K	MgO	0.7	33.3	2.0	NWS
− K	Zeolite	(10% by volume)			NWS
+ K	KCl	1.2	16.7	1.0	WS
+ P and K	K_2HPO_4	1.9	22.2	1.3	WS
+ K + N	KNO_3	1.7	16.7	1.0	WS
+ K + N	$KCl{\cdot}NH_4Cl$	0.6 KCl; 0.5 NH_4Cl	16.6	1.0	WS
+ K + P + N	$K_2HPO_4{\cdot}KNO_3$	1.0 K_2HPO_4; 0.8 KNO_3	19.4	1.2	WS
Osmotic control	NaCl	1.0	16.7		WS
Control	None				

[a] Abbreviations: WS, water-soluble; NWS, non-water-soluble.

We also amended *Stipa* soils, which do not support downy brome populations, to determine if nutrient additions could enhance downy brome germination and emergence. For N, P, and K additions, we first analyzed native soils (Table 1) and then added 1 ×, 2 ×, and 3 × those naturally-occurring levels using NH_4Cl, Na_2HPO_4, and KCl, respectively. Soil pH (1:1 slurry) was manipulated in + N and + P treatments with HCl. Because treatments added salts and thus observed effects could be attributable to osmotic stress, a sodium chloride (NaCl) treatment was used both as an indicator of osmotic stress and as an independent treatment.

Emergence trials were conducted from September 2000 to March 2001 and germination and emergence trials from January 2001 to March 2001. Six grams of the resultant mixture for each treatment was placed in 5 (first set of trials) to 10 (subsequent trials) petri dishes that were 3.7 cm in diameter. Trials were repeated five times; however, amendments that did not suppress downy brome emergence or did suppress *Hilaria* emergence in the first trials were dropped from subsequent trials. Only treatments that suppressed downy brome emergence were applied to *Hilaria* seeds, and *Hilaria* seeds were only tested in downy brome soils (presuming that restoration efforts would occur in invaded soils). Twenty seeds of *Hilaria* or downy brome were placed in each dish, pushed just under the soil surface, and allowed to incubate in a laboratory with fluorescent lighting (approximately 600 photons m^{-2} s^{-1}) and average minimum and maximum temperatures of 19 and 23 C, respectively. Trials ran 10 d; control seeds germinated in 3 to 5 d, and no additional germinations were noted after 7 d for any treatment. Deionized water was added to dishes when the soil was visually dry. Dishes were covered with plastic wrap overnight to prevent drying. Germination was recorded as radicle protrusion from the seed to at least 1 mm and emergence as coleoptile protrusion at least 2 mm above the soil surface. After each trial ended, seeds were exhumed to determine numbers of ungerminated seeds. Each dish was considered a replicate. The value reported for a given treatment is the grand mean of all dishes in all trials of that treatment.

Among untreated (control) soils, one-way analysis of variance (ANOVA) evaluated differences in arcsine-transformed downy brome germination and emergence data. Individual treatments were analyzed for differences from the control and among concentrations with ANOVA and post hoc Student–Newman–Keuls tests. For data presentation in the figures, we divided all data by the corresponding control values to standardize results specific to each trial. We also compared results from the NaCl treatments with other treatments as an indication of whether treatment effects were osmotic or ion-specific. For each concentration of each treatment, mean NaCl values were subtracted from the corresponding values of the treatment (except zeolite and Fe_2O_3, which were not added in ionically equivalent concentrations) and then compared with control values with a *t* test. Unless otherwise noted, statistical significance is reported when $P < 0.05$.

Results and Discussion

Chemical characteristics varied among the downy brome, *Hilaria*, and *Stipa* soils, most notably in NO_3, P, Ca, and Na, before we added amendments (Table 1). *Stipa* and *Hilaria* soils had much lower P, NO_3^-, and Ca than did the downy brome soil, whereas both *Hilaria* and downy brome soils had much higher K, Mg, and K–Mg than did *Stipa* soils. These differences in soil chemistry strongly affected the results of the experiments (see discussion below).

There were no significant differences in downy brome germination ($F = 0.4$, $P = 0.65$) or emergence ($F = 0.0$, $P = 1.00$) among the three unamended control (downy brome, *Stipa*, and *Hilaria*) soils. Downy brome germination in all three soils averaged a very high 99.7%, and emergence of all seeds averaged 92.5% in the downy brome and *Hilaria* soils. In contrast, germination and emergence of *Hilaria*

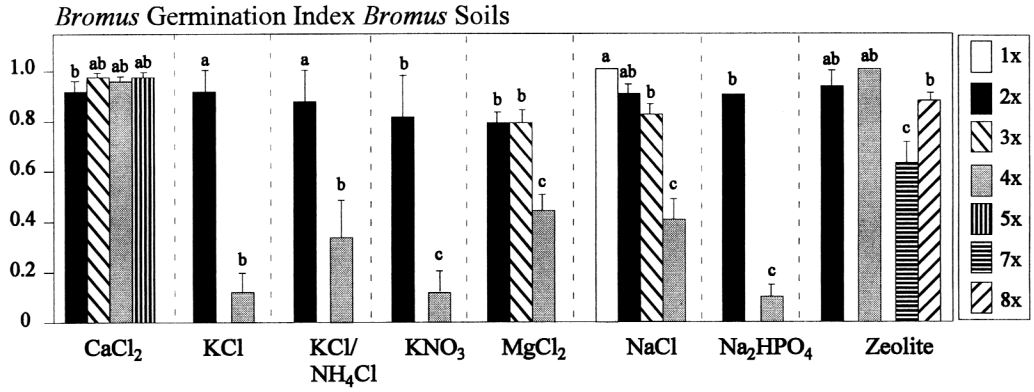

FIGURE 1. Mean ± SE number of downy brome seeds that germinated in downy brome soils. Values are standardized to the control (i.e., presented as a proportion of the control germination levels, with 100% of control = 1). Legend indicates multiples of concentrations of additives listed in Table 2. The letter "a" indicates no significant difference from the control. All other letters indicate significant ($P < 0.05$) differences from the control; different letters within a treatment indicate significant differences among concentrations. If error bars are lacking, germination was 100% for all replicates. Treatments with no significant differences from the control are not shown (CaO, Fe_2O_3, MgO).

seeds in the unamended downy brome soil averaged 68 and 66% respectively. However, 96.8% of the germinated *Hilaria* seeds emerged, indicating that germination and not emergence is a limiting step in *Hilaria* seedling establishment.

Additions to Invaded (Downy Brome–Dominated) or Invadable (*Hilaria*-Dominated) Soils

The first goal of these experiments was to find soil amendments that significantly reduced emergence without reducing germination (otherwise, germinable seeds may be released from inhibition once water-soluble ions flush out of the soil, e.g., with rainfall [Kurth et al. 1986; Manohar 1966]) in downy brome while not substantially affecting either process in *Hilaria*. Both non–water-soluble and water-soluble amendments were applied as treatments. The non–water-soluble treatments were added to reduce plant-available P (using CaO, Fe_2O_3, MgO) or K (using MgO, zeolite). In *Hilaria* soils, all four treatments reduced downy brome emergence without reducing germination (Figure 1; Table 3). In downy brome soils, only zeolite significantly reduced downy brome emergence (Table 3).

Many of the water-soluble treatments suppressed both germination and emergence in downy brome (Figure 1; Table 3). Whereas treatments that suppressed germination were eliminated from further consideration in this study, it is not known if germination was permanently or temporarily suppressed, and some of these treatments are still promising. Three treatments effectively suppressed downy brome emergence with only moderate effects on germination: $CaCl_2$, $MgCl_2$, and NaCl. Unlike the non–water-soluble treatments, they were equally effective on the two soil types.

The four treatments that were effective across the tested soils were then tested on *Hilaria* seeds (Figure 2; Table 3). Zeolite and $CaCl_2$ did not affect either germination or emergence of *Hilaria*. Whereas $MgCl_2$ and NaCl had some negative effect on *Hilaria*, this was substantially less than the effects on downy brome at any given concentration (Figure 2; Table 3). Our results also indicate that (1) soil levels of P and K are less critical for germination than emerging downy brome seedlings; (2) *Hilaria* is better able to tolerate low K and P availability than is downy brome; and (3) the effectiveness of additives will vary with antecedent soil chemistry.

These observed effects could have resulted from either ion-specific effects or osmotic stress, and distinguishing between these two effects is important in guiding future research efforts. Ion-specific effects appear actively involved because (1) ionically-equivalent applications of treatments did not always yield similar effects; (2) many treatments had significantly greater effects than did the NaCl treatment (Table 4); (3) the additives used are known to bind soil K and P. MgO binds P directly, and $MgCl_2$ added to calcareous soils forms $MgCO_3$, which binds P (Carreira and Lajtha 1997). Competitive displacement of K^+ by Mg^{2+} has been shown to reduce K^+ uptake by plants in several studies (Haynes and Goh 1978; Thompson and Troeh 1978); and (4) additions of both MgO and $MgCl_2$ have been previously observed to reduce downy brome germination (Howell 1998; Morrison 1999), emergence (Howell 1998; Miller 2000), and growth (Miller 2000).

Excessive osmotic stress could partially explain the observed effects. All treatments increased soil salt levels. For instance, the NaCl treatment at 1 × added 382 ppm Na^+, whereas natural soil levels at the study site are 40 to 96 ppm. A second indicator that osmotic stress was important was the fact that high levels of N, P, and K, generally expected to benefit the plant, decreased germination and emergence at higher concentrations. Multiple studies of various species have determined an inverse relationship between germination and osmotic stress (e.g., Susko et al. 1999; Wiggans and Gardner 1959). Goodwin et al. (1996) found that osmotic potentials down to − 1.0 MPa had little effect on downy brome germination, whereas Thill et al. (1979) showed downy brome germination and emergence decreasing with soil osmotic potentials at − 0.19 MPa. Our results show significantly diminished germination for most treatments with an osmotic potential of − 1.37 to − 1.83 MPa (i.e., at 3 to 4 × concentrations in Table 2) and emergence for most treatments at an osmotic potential of − 0.91 MPa (i.e., at 2 × the concentrations in Table 2; Figures 1–3).

Our results indicate that plant tissue emergence is more sensitive to salt concentrations than is the process of germination. In addition, *Hilaria* is clearly not as susceptible to the effect of high salt concentrations as is downy brome.

TABLE 3. Percent *Bromus* emergence in *Bromus* and *Hilaria* soils and *Hilaria* emergence in *Bromus* soils. Within a row, significant differences ($P < 0.05$) in *Bromus* emergence between *Bromus* and *Hilaria* soils are marked by an asterisk (*). Within a column (soil type) and within a treatment type, lowercase letters denote significant differences among different concentrations and the controls. The # symbol indicates significant suppression of emergence without significant suppression of germination. The ~ symbol indicates treatments that suppressed both germination and emergence.

		Bromus emergence (%)			*Hilaria* emergence (%)	
			Hilaria soils			
Treatment	Concentration	*Bromus* soils Mean	Mean	Significance	*Bromus* soils Mean	Suppression indicators
Control		100 a	100 a		66 a	
$CaCl_2$	2×	81 bc	65 b			
	4×	66 c	65 b		102 a	
	5×	46 c			88 a	#
CaO	2×	104 a	107 a			
	4×	103 a	20 b	*		
Fe_2O_3	4×	99 a	70 b	*		
KCl	2×	73 b	54 b			
	3×	11 c	35 b			# ~
	4×	2 c	30 b	*		# ~
$KCl{\cdot}NH_4Cl$	2×	78 b	80 b			
	3×	24 c	26 c			# ~
	4×	0 c	23 c			# ~
K_2HPO_4	2×	71 b	107 a	*		
	3×	9 c	76 a	*		
	4×	32 c	40 b			# ~
$K_2HPO_4{\cdot}KNO_3$	3×	13 b	59 b			
	4×	9 b	43 b			# ~
KNO_3	2×	73 b	76 b			
	3×	6 c	52 b			# ~
	4×	4 c	12 c			# ~
$MgCl_2$	2×	34 b	28 b		81 ab	
	3×	8 c	35 b	*	62 b	#
	4×	3 c	10 b	*	16 c	
MgO	4×	96 a	78 b			
NaCl	2×	61 b	52 b		97 a	
	3×	39 c	46 b		79 a	#
	4×	4 d	27 b	*	25 b	
Na_2HPO_4	2×	79 b	96 a			
	3×	11 c	41 b			# ~
	4×	0 c	16 b	*		# ~
Oxalic acid	4×	103 a	89 a			
Zeolite	2×	86 abc	87 b			
	4×	100 ab	52 b	*		
	6×	81 bcd				
	7×	56 c			101 a	#
	8×	65 c			112 a	#
	10×	15 d				#

It is possible that *Hilaria* seedlings can discriminate against Na^+ as an adaptation to growth in salty desert soils. A similar capability is found in tomato plants (*Lycopersicon esculentum* L.) (Kurth et al. 1986). Alternatively, it is perhaps not the discrimination against Na^+ uptake per se as much as preferential retention of other ions such as Ca^{2+} (Kurth et al. 1986) that ensures *Hilaria* success under stressful salt conditions.

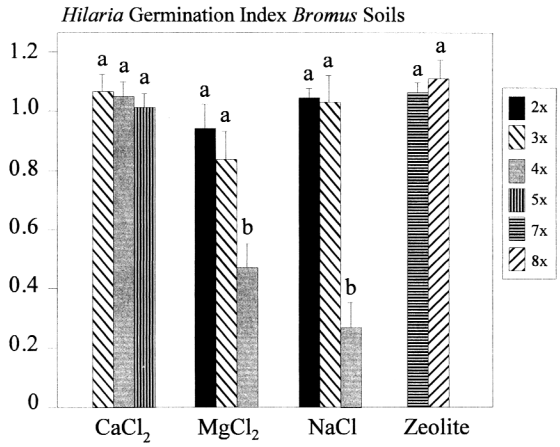

FIGURE 2. Mean ± SE number of *Hilaria* seeds that germinated, standardized to the control. See the caption of Figure 1 for explanation of significant differences. Treatments with no significant differences from the control are not shown (CaO, Fe_2O_3, MgO).

Additions to Noninvadable (*Stipa*) Soils

The second part of this experiment was to see the effects of "fertilizers" (N, P, K) in soils considered noninvadable (Belnap and Phillips 2001). Consequently, we added combinations of N, P, and K at 1 ×, 2 ×, and 3 × field levels to *Stipa* soils. Because germination in control soils was almost 100%, we were not able to assess any enhancement effects. Downy brome germination tended to be depressed at all levels of additional N and N + P + K, but this was only statistically significant at 3 × field levels (Figure 3). Emergence of the germinated seeds (proportional emergence) was generally not affected at 1 × or 2 × field levels but was depressed at 3 × field levels. Emergence was severely diminished at 8 × and 10 × field levels ($P < 0.01$; data not shown). The depression at the higher concentrations was expected as these compounds can be toxic at high concentrations (Haynes and Goh 1978). However, the depression at 3 × field levels was unexpected as N usually increases downy brome establishment and performance (Eckert and Evans 1963; Wilson et al. 1966). *Stipa* soils, which are not invadable by downy brome in the field (Belnap and Phillips 2001), have substantially greater $CaCO_3$ and lower P, Zn^{2+}, Cu^{2+}, Fe^{2+}, K^+, Mg^{2+}, Mn^{2+}, and NH_4^+ than do either *Hilaria* or downy brome soils (Table 1). We used NH_4^+, which, although providing an N supplement, can interfere with absorption of other ions such as K^+ (Haynes and Goh 1978; Thompson and Troeh 1978). However, adding KCl and KCl–NH_4Cl yielded almost identical results and did not prevent depression of either germination or emergence. Addition of NH_4^+ and NO_3^- similarly suppressed both germination and emergence, supporting the idea that high levels of N alone are responsible for the observed depression.

Downy brome emergence was also diminished with increasing soil acidity in *Stipa* soils (Figure 4). Given the apparent susceptibility of downy brome to high salinity (or highly negative osmotic potential), the negative relationship between downy brome emergence and soil acidity may be accounted for by the greater solubilities of nutrients such as Ca^{2+}, Cu^{2+}, Fe^{2+}, K^+, Mn^{2+}, HPO_4^{2-}, and Zn^{2+} at low pH (Gadd 1999; Thompson and Troeh 1978). In contrast to our results, Egley and Duke (1985) state that weed germination should not be affected within the natural range of

TABLE 4. *t* Test values evaluating the differences between treatments and NaCl at corresponding concentrations. The (ND) denotes that a concentration of a treatment or the corresponding concentration of NaCl was not tested. Zeolite was not tested because its ionic additions to or subtractions from soil solution were not quantifiable. ***P < 0.001, **P < 0.01, *P < 0.05.

		Bromus soil				*Hilaria* soil
		Bromus seed		*Hilaria* seed		*Bromus* seed
Treatment	Concentration	Germination	Emergence	Germination	Emergence	Emergence
$CaCl_2$	2×	0.51	2.72	ND		0.71
	3×	9.14***	13.17***	0.58	5.50***	
	4×	29.32***	8.24***	16.45***	15.55***	3.58*
CaO	2×	—[a]	18.48***	ND	ND	26.23***
	4×	—[a]	37.83***	ND	ND	− 0.34
KCl	2×	0.24	0.64	ND	ND	0.63
	3×	ND	− 2.64	ND	ND	− 0.81
	4×	− 3.92*	− 0.57	ND	ND	0.35
$KCl{\cdot}NH_4Cl$	2×	− 0.17	1.54	ND	ND	2.15
	3×	ND	− 0.66	ND	ND	− 2.65
	4×	− 0.47	—[a]	ND	ND	− 0.42
K_2HPO_4	2×	ND	0.66	ND	ND	25.00***
	3×	ND	− 4.59*	ND	ND	1.59
	4×	ND	2.56	ND	ND	1.26
$K_2HPO_4{\cdot}KNO_3$	2×	ND	ND	ND	ND	5.42**
	3×	ND	− 2.51	ND	ND	0.67
	4×	ND	0.61	ND	ND	1.63
KNO_3	2×	− 0.52	0.54	ND	ND	1.19
	3×	ND	− 6.12**	ND	ND	0.42
	4×	− 3.60*	0.28	ND	ND	− 2.44*
$MgCl_2$	2×	− 3.03**	− 4.72***	− 1.21	− 1.79	− 2.14
	3×	− 0.55	− 15.21***	− 2.50*	− 2.02	− 1.51
	4×	0.69	− 0.26	2.31*	− 1.62	− 6.73***
MgO	2×	ND	ND	ND	ND	25.00***
	4×	ND	11.21***	ND	ND	6.19**
Na_2HPO_4	2×	− 0.01	1.47	ND	ND	4.13*
	3×	ND	− 2.05	ND	ND	− 0.22
	4×	− 6.88**	—[a]	ND	ND	− 1.59
Oxalic acid	2×	ND	ND	ND	ND	19.59***
	4×	ND	23.22***	ND	ND	4.51*

[a] SD = 0, and *t* test not performed.

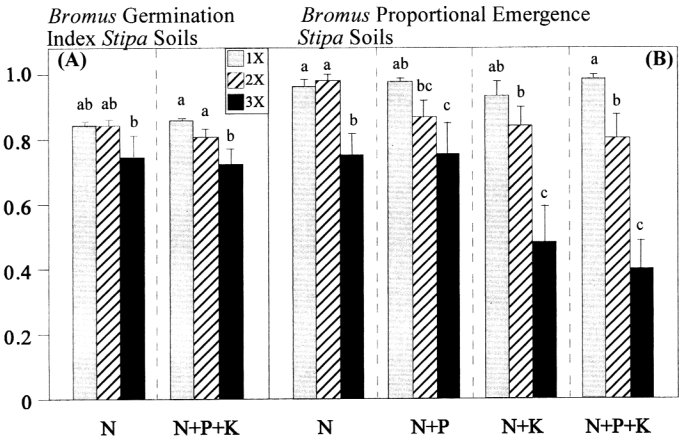

FIGURE 3. Mean ± SE downy brome (*Bromus tectorum* L.) (A) germination and (B) proportional emergence, standardized to control levels in *Stipa* soils. See the caption of Figure 1 caption for explanation of significant differences.

soil pH. We attempted to increase soil pH with NaOH and $CaCO_3$, but equilibration with atmospheric CO_2 or soil buffering prevented appreciable increases, and all buffer solutions investigated contained undesirable nutrients. In separate greenhouse studies we observed that downy brome germination at pH 9.9 was severely reduced, but this may have also been due to very high concentrations of Na^+ (data not shown). Decreased emergence was seen at all pH levels when high N (8.2 × field levels) was added, supporting the argument that high N concentrations reduce downy brome emergence.

Our results offer promising insight into control of downy brome populations in calcareous soils. One option for management of downy brome–invaded sites is to stimulate germination of downy brome seeds while inhibiting emergence. The dynamics of soil P and K appear to strongly affect downy brome performance as reducing the availability of K or P (or both) decreased downy brome emergence. *Hilaria*, on the other hand, appears much less sensitive to reductions in K and P availability in these soils. Of the tested amendments, $CaCl_2$ (at 4 × and 5 × field levels), $MgCl_2$ (at 3 × field levels), NaCl (at 3 × field levels), and zeolite (from 2

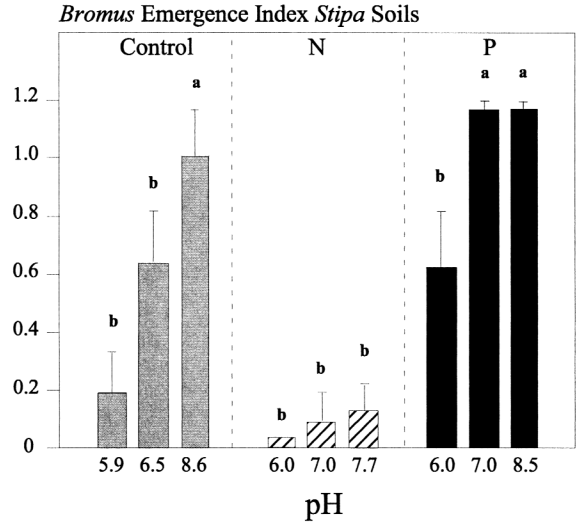

FIGURE 4. Mean ± SE downy brome (*Bromus tectorum* L.) emergence rates standardized to control levels in *Stipa* soils of varying acidity. Different superscripts indicate significant differences within a treatment. N levels were at 8.2 × and P at 2.3 × naturally occurring levels. Treatments with no significant differences from the control are not shown (germination: P, K, N + P, N + K, P + K; proportional emergence: P, K, P + K).

to 10 ×, depending on soil chemistry) have potential as management tools based on their ability to maximize downy brome germination and minimize downy brome emergence without negatively affecting *Hilaria* germination or emergence. In low-P soils, future studies should test CaO, Fe_2O_3, and MgO on downy brome. All these findings need field testing. Future studies should also determine whether *Hilaria* is representative of other native species in its response to these soil amendments.

Sources of Materials

[1] Southwest Seed, Inc., 13260 CR 29, Dolores, CO 81323.

[2] A form of zeolite, GSA Resources, Inc., P.O. Box 509, Tucson, AZ 85652.

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