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Soil Engineering Facilitates Downy Brome (*Bromus tectorum*) Growth — A Case Study

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Soil engineering by downy brome may be a facet of its competitiveness. Using rhizotrons in the greenhouse, we compared the growth and plant–soil relationships of downy brome grown in two field soil types: soil invaded for 12 yr by downy brome and a similar soil not yet invaded. For each soil type, downy brome was grown for two growth cycles. At harvest, root mass and soils were sampled at depths of 10, 40, and 80 cm (4, 16, and 32 in); aboveground biomass was also sampled. After the first growth cycle, downy brome grown in invaded soil had 250% greater aboveground biomass and nearly double the root mass per soil volume at 10 cm relative to downy brome grown in noninvaded soil; root mass per volume was similar at depths of 40 and 80 cm. For the second growth cycle, aboveground biomass declined, but was twice greater for downy brome grown in invaded soil; however, root mass per volume was similar between soil types for each depth. Soil attributes that positively related to aboveground biomass included bicarbonate-extractable P, DTPA (diethylentriamene pentaacetate)-extractable Mn, and solution-phase SO_4^{2-} (80-cm depth). We conclude that the data support our hypothesis that downy brome has engineered the soil to increase its growth potential, but proof will require a more robust experimental design. Plant competition is affected by myriad interactions; however, a plant that can increase the availability of soil nutrients for itself and its growth potential, relative to competing plants, would appear to be at an advantage. The mechanistic underpinnings involved are inconclusive, but may involve increased availability of soil N, P, and Mn.

Nomenclature: Downy brome, *Bromus tectorum* L.

Key words: Cheatgrass, Invasive weeds, plant competition, plant–soil relationships, soil fertility.

No universal mechanism explains why a particular exotic plant may become invasive (Rejmánek et al. 2005). Generalized driving mechanisms are lacking because they likely change as exotic plants adapt to their new host environment; initial invasions often occur in resource-rich disturbed habitats, but subsequent expansion is predicated on plastic responses and genetic adaptation (Dietz and Edwards 2006). Plastic responses and genetic adaptation are a component in the lag phase of plant invasion—the time between introduction and invasion (Sakai et al. 2001). The lag phase can vary greatly, ranging from years to hundreds of years (Aikio 2010; Kowarik 1995; Pyšek and Prach 1993). Our observations in the northern Great Basin suggest that downy brome (*Bromus tectorum* L.) has a relatively short lag phase. Initial invasions of relatively intact shrub communities are characterized by low densities ($<$ 10 plants m^{-2} [1 plant ft^{-2}]) and individual plants that are small-statured and largely reside in shrub subcanopies. It is only after several years of invasion that plant density and stature greatly increases and downy brome begins to occupy shrub interspace locations.

Theories have been proposed to explain this lag period and why some exotic plants perform so well in their new host environment relative to their native environments (Rout and Callaway 2009). Crooks and Soulé (1999) categorized lag periods into two groups: (1) lag related to increases in genetic fitness to the new host environment, and (2) lag related to improvements in ecological conditions over time that favor the alien plant. Persuasive evidence exists suggesting that some exotic plants become invasive via genetic improvement of founder populations (Barrett et al. 2008; Ellstrand and Schierenbeck 2000; Maron et al. 2004). Indeed, the competitive ability and invasiveness of some populations of downy brome may have been facilitated due to outcrossing (Ashley and Longland 2007; Leger et al. 2009). Lag period related to improvement of ecological condition fits into the realm of ecosystem engineering or positive feedback—the ability of invasive plants to modify biotic and abiotic conditions of their new host environment and perhaps become more invasive (Brooker et al. 2008; Crooks 2002; Jones et al. 1994). Although the realm of ecosystem engineering covers

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Management Implications

In the ecosystem studied, our data suggest 12 yr of invasion by downy brome has engineered the soil to facilitate its growth. Mechanistic underpinnings of this positive feedback are possibly due to an increase in soil N, P, and Mn availability. The literature is clear: downy brome benefits and becomes more competitive when provided elevated sources of nutrients, particularly N and P. Given that this is a case study, spatial extrapolation is limited; however, by its ability to increase soil nutrient availability, one can expect downy brome to potentially invade communities thought somewhat resistant to invasion owing to inherently low soil nutrient availability.

a host of processes, alteration of the soil microbial community and increasing the availability of critical soil nutrients, especially N and P, are major factors facilitating the invasiveness of some exotic plants (Blank and Morgan 2011; Ehrenfeld 2003; Hamilton and Frank 2001; Reinhart and Callaway 2006).

There is growing evidence that downy brome can engineer the soil to affect myriad processes, some of which may facilitate its invasiveness (Blank 2008; Blank and Young 2004; Perkins et al. 2011; Sperry et al. 2006). The literature is lacking in direct evidence that soil occupied for a period of time by downy brome becomes a superior growth media for downy brome. We tested the hypothesis that downy brome would grow better in a soil invaded by downy brome for 12 yr than in a similar soil not yet invaded.

Materials and Methods

To test the hypothesis, growth of downy brome was contrasted between two soil substrates: one invaded by downy brome for 12 yr, the other not yet invaded. The substrates were collected in May, 2009 from a 120-ha (296 acres) winterfat (*Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit) community in the Honey Lake Valley, CA (40°08′20″N, 120°04′39″W, elevation 1,242 m (4,074 ft)). The area is mapped as the Ardep series, a coarse-loamy, mixed, superactive, mesic durinodic xeric Haplocalcid. Soil, loamy-sand in texture, was composited from shrub interspace positions, approximately 100 individual subsamples over a 500 m^2 (5380 ft^2) area, 0 to 20 cm (0 to 8 in) deep, which corresponds to the A horizon. The two soil substrates were returned to the greenhouse and individually homogenized; eight 100-g (3.5 oz) subsamples were then randomly collected for initial soil analyses. Continuous monitoring of this winterfat community was begun in 1997, at which time an incipient invasion by downy brome occurred. In 2000, a transect consisting of 13 points, 50 m (164 ft) apart, was established from the invaded area extending into the as-of-yet non-invaded area. Beginning in 2001, soil samples were collected multiple times during the year, from 0 to 20 cm at each point, and analyzed for various attributes (Figure 1 shows invaded and noninvaded sites in 2000 and 2009, when soil for this experiment was collected). From the baseline data collected in 2001, we averaged points 1 to 3 for two sampling times ($n = 6$, corresponds to the area where invaded soil was collected for this study) and points 11 to 13 for the same two sampling times (n = 6, corresponds to area where noninvaded soil was collected for this study). These data provide evidence that the two soils used in this experiment were similar before the invasion had occurred.

Rhizotrons, 30 by 5 by 100 cm deep (11.8 by 1.97 by 39.4 in), were filled with the following actions: six replicates of invaded substrate to be sown to downy brome, two replicates of invaded substrate as unplanted controls, six replicates of noninvaded substrate to be sown to downy brome, and two replicates of noninvaded substrate as unplanted controls. Before planting, all rhizotrons were saturated with deionized water. Rhizotrons were placed as a pair in plastic buckets, which maintained an angle of 25° from the vertical so that roots would grow into the clear plastic viewing window. For the first growth cycle, downy brome was sown on April 16, 2009, and harvested on July 13, 2009. For the second growth cycle, downy brome was sown on August 13, 2009, and harvested October 22, 2009. Downy brome seed was collected in 1998 near Verdi, CA, from a population of robust individual plants. Several seeds were sown in the center of each rhizotron, but after seeds emerged, only one was allowed to grow. Deionized water was added twice weekly as required to keep soils moist—water was not limiting. Rhizotrons were covered with insulation that could be removed to observe, record, and photograph rooting patterns. At the end of each growth cycle, aboveground tissue was cut at the soil surface, dried at 70 C (158 F) for 48 hr, milled, and reserved for analyses. Rhizotrons were placed horizontally and the backs were removed to facilitate soil and root sampling. A coring device (5.4 cm (2.125 in) diam, 5 cm (2 in) depth) attached to a power tool was used to extract soil samples. Sampling was done at depths of 10, 40, and 80 cm at the right side, center, and left side of the rhizotron. For each sample, roots were quantitatively collected and soil was reserved for analyses. Roots were washed, dried at 70 C for 48 hr, and weighed. Prior to the second growth cycle, original soil was used to fill holes and the rhizotron backs were secured. Downy brome was sown as previously outlined, allowed to grow, and harvested. Second-growth roots and soil were taken at the same depths, but the three subsamples were taken adjacent to first-cycle locations.

For plant tissue, total C and N were quantified using a LECO® TruSpec (LECO Corp., St. Joseph, MI) with

Figure 1. Photographs of soil collection sites. In 2000, downy brome had not completely occupied shrub interspace positions in sites where invaded soil for this study was collected (top left). We define invasion as being when downy brome, existing as small plants in winterfat canopies, expands into shrub interspaces. In 2009, when soil for this study was collected, invasion for 12 yr had increased the density of downy brome and considerable mortality of winterfat had occurred (top right). Bottom photos show noninvaded collection area in 2000 (left) and 2009 (right). Notice that in noninvaded areas, winterfat interspaces are largely barren of vegetation. The most noticeable difference in the noninvaded areas between 2000 and 2009 is an increase in the rhizomatous grass, creeping wildrye (*Leymus triticoides* (Buckley) Pilg.).

ethylenediaminetetraacetic acid used to calibrate the instrument. All other nutrients were quantified after dry-ashing followed by solubilization in 1 N HCl and HNO_3 (Kalra 1997). Vanomolybdate chemistry using the Lachat® autoanalyzer (Hach Corp., Loveland CO) was used to quantify P. All other nutrients were quantified using atomic absorption/emission spectroscopy. Soil analyses for this study and for samples collected in 2001 were performed on freshly collected soil and corrected to oven dry weight based on a separate subsample. Total mineral N used KCl extraction with quantification of NH_4^+ and NO_3^- using the Lachat autoanalyzer (Bundy and Meisinger 1994). Net N mineralization potential was determined by subtracting total mineral N from total mineral N following a 30-d aerobic incubation (Hart et al. 1994). The bicarbonate-extractable method was used to quantify plant available P (Olsen et al. 1954). Plant available Mn was indexed using the chelate diethylentriamene pentaacetate (DTPA) extraction (Lindsay and Norvell 1978). Solution-phase SO_4^{2-} and ortho-P was extracted from the soil by immiscible displacement (Mubarak and Olsen 1976) and quantified by ion chromatography. Two attributes were derived. Molar proportion of NH_4^+ was calculated by dividing KCl-extractable NH_4^+ by KCl-extractable NH_4^+ + NO_3^-. Molar proportion NO_2^- was calculated by dividing solution-phase NO_2^- by solution-phase NO_2^- + NO_3^-. As an index of how plant growth affected soil nutrient pools, for each attribute, growth cycle, and soil depth, we subtracted the planted treatment from its corresponding unplanted treatment to determine a percentage loss or gain from the unplanted treatment.

The experimental design is pseudoreplicated and thus represents a case study. All data—including baseline data from 2001, initial subsamples from soil types used in this study, and postharvest data—were analyzed by a *t* test comparing population means between invaded and noninvaded treatments, separated by growth cycle and depth where appropriate.

Results

In 2001, when downy brome had only recently begun to invade the study area, there were no significant differences in several indexes of nutrient availability between invaded and noninvaded soils (Table 1). Moreover, soils from invaded and noninvaded areas in 2001 were statistically similar among all size fractions (data not shown). By 2009,

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Table 1. Selected soil data from 2001 near where soils for the experiment were collected, and initial properties of soils used in greenhouse experiment (collected in 2009).[a]

	Net N								Solution-phase				Mole			
	Mineral N		Mineralization		Bicarb-P		DTPA-Mn		ortho-P		SO_4^{2-}		NH_4^+		NO_2^-	
Date	I	NI	I	NI	I	NI	I	NI	I	NI	I	NI	I	NI	I	NI
	mmol kg^{-1}						μmol kg^{-1}		μmol L^{-1}				%			
2001	0.18	0.12	0.12	0.31	0.29	0.30	nd	nd	6.2	5.5	25	24	22	17	nd	nd
2009	**0.69**[b]	**0.16**	**−0.38**	**−0.07**	**0.46**	**0.39**	**58**	**30**	**12.3**	**9.2**	9	7	**92**	**68**	**40**	**4**

[a] Abbreviations: Bicarb-P, bicarbonate-extractable P; DTPA-Mn, diethylentriamene pentaacetate-extractable-Mn; I, invaded; NI, noninvaded; nd, data not determined.

[b] For each attribute, bolded numbers indicate significant mean differences between I and NI populations as determined by a *t* test.

however, the invaded soil used in this experiment had considerably more mineral N, bicarbonate-extractable P, DTPA-extractable Mn, and solution-phase ortho-P than the noninvaded soil (Table 1). Moreover, both invaded and noninvaded soils had negative net 30-d mineralization potentials, with the invaded soil being far more negative. The molar proportion of NH_4^+ in the mineral N fraction and the molar proportion of NO_2^- in the solution-phase NO_2^- + NO_3^- fraction were both far higher for the invaded soil. Invaded soil collected in 2009 stands out in having greater mineral N, bicarbonate-extractable P, solution-phase P; a greater proportion of NH_4^+ in the mineral N pool; and less solution-phase SO_4^{2-}, relative to invaded soil collected in 2001.

Downy brome showed superior growth potential in soil invaded for 12 yr by downy brome than in a similar noninvaded soil (Figure 2). Aboveground biomass grown in invaded soil was 250 and 158% greater for the first and second growth cycles, respectively, than aboveground biomass grown in noninvaded soil. After the first growth cycle, root mass per unit volume was nearly double in the invaded soil relative to the noninvaded soil, but only at 10 cm (Figure 2). At depths of 40 and 80 cm, root mass per unit volume declined and there were no statistical differences in root mass per unit volume between invaded and noninvaded soil. Root mass per unit volume declined after the second growth cycle and there were no statistical differences between soil types at any depth.

Tissue nutrient concentrations of downy brome differed significantly depending on the soil type grown in (Figure 3). Plants grown in invaded soil had significantly greater tissue concentrations of N (both growth cycles), Ca (second growth cycle), and Cu (second growth cycle) and significantly less P (first growth cycle), Mn (both growth cycles), and Zn (second growth cycle) relative to tissue grown in noninvaded soil. C : N ratios were significantly less for tissue grown in invaded soil (both growth cycles) than that grown in noninvaded soil (Figure 3).

Following harvests of the planted treatment, many soil attributes differed significantly between soil types, often depending on the particular soil depth (Table 2). Averaged over soil depths, the invaded soil generally had greater nutrient availability after both harvests than the non-invaded soil. Nutrients higher in invaded soil included mineral N, bicarbonate-extractable P, DTPA-extractable

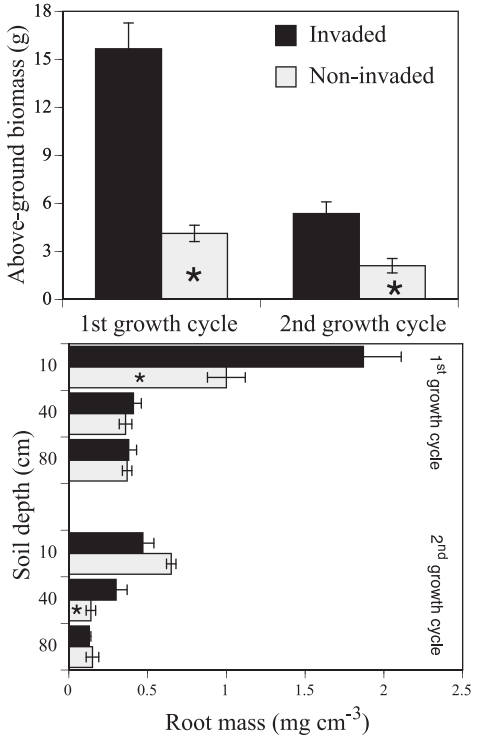

Figure 2. Graphical summarization of mean aboveground biomass and mean rooting mass per unit soil volume. An asterisk denotes significant differences between invaded and noninvaded treatments for each growth cycle (aboveground) and for each growth cycle and soil depth (roots) as judged by a *t* test. Bars are standard errors.

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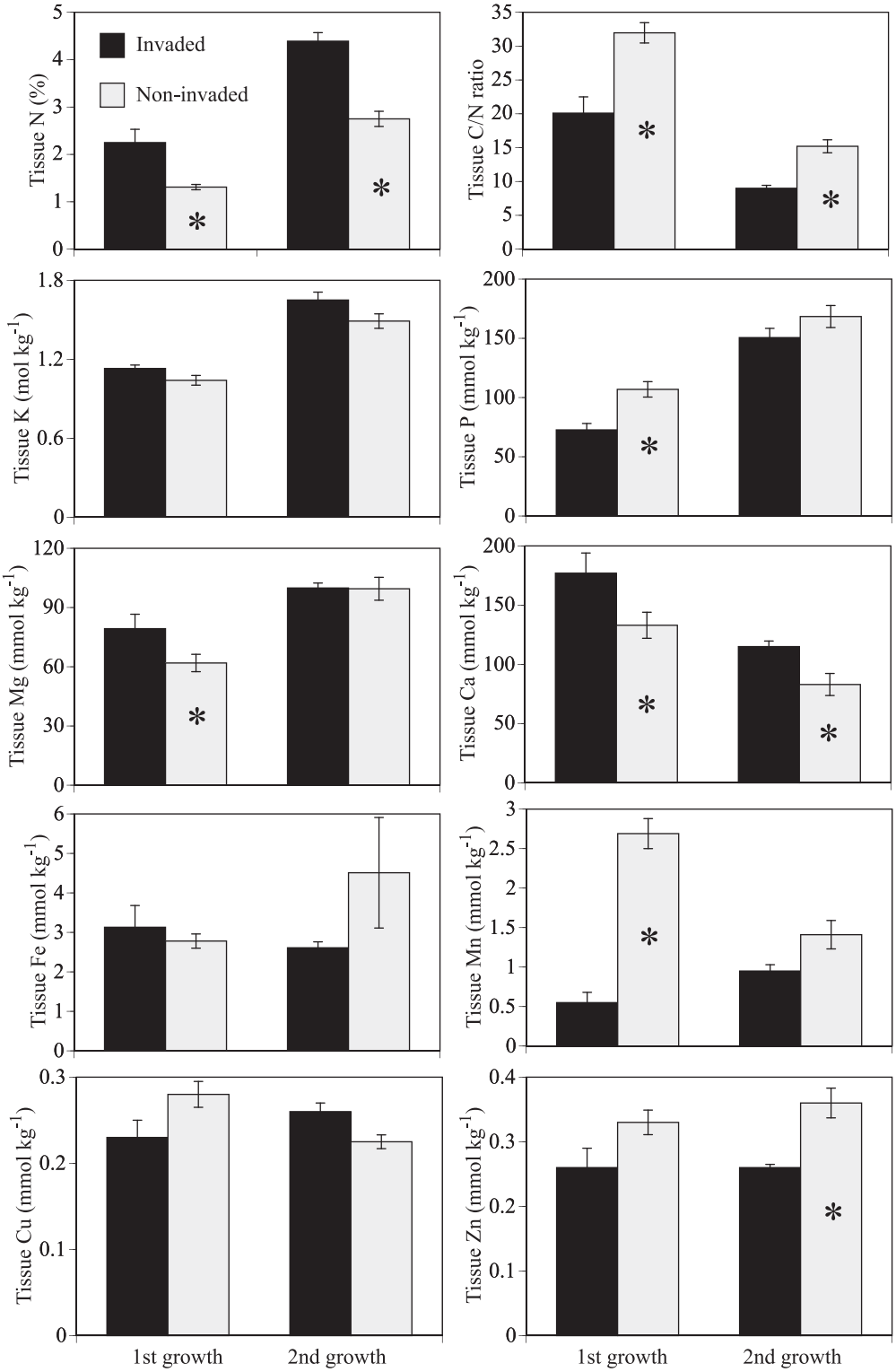

Figure 3. Graphical summarization of mean postharvest aboveground tissue chemistry. For each attribute and growth cycle, an asterisk denotes significant differences between invaded and noninvaded treatments as judged by a *t* test. Bars are standard errors.

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Table 2. Selected soil attributes after plant harvest by soil type (invaded or noninvaded), growth cycle, and depth.[a]

Growth cycle	Depth	Mineral N		Bicarb-P		DTPA-Mn		Solution-phase ortho-P		Solution-phase SO_4^{2-}		Mole NH_4^+		Mole NO_2^-	
		I	NI	I	NI	I	NI	I	NI	I	NI	I	NI	I	NI
	cm	mmol kg^{-1}				µmol kg^{-1}		µmol L^{-1}				%			
First	10	**0.14**[b]	**0.07**	**0.26**	**0.18**	**64**	**50**	**34**	**25**	**26**	**8**	56	91	**15.1**	**0.3**
First	40	0.25	0.11	**0.33**	**0.21**	**62**	**47**	**56**	**31**	**35**	**9**	52	83	**17.6**	**0.0**
First	80	**0.17**	**0.05**	**0.33**	**0.25**	**83**	**47**	**54**	**39**	**67**	**16**	53	90	**21.4**	**2.4**
Second	10	**0.43**	**0.10**	**0.29**	**0.20**	**83**	**51**	**32**	**20**	**61**	**16**	73	93	**14.6**	**5.6**
Second	40	**0.61**	**0.10**	**0.34**	**0.23**	**76**	**44**	**38**	**27**	**97**	**15**	53	89	6.3	2.4
Second	80	**0.87**	**0.19**	**0.33**	**0.26**	**142**	**59**	24	22	**159**	**46**	40	69	6.0	3.8

[a] Abbreviations: Bicarb-P, bicarbonate-extractable P; DTPA-Mn, diethylentriamene pentaacetate-extractable-Mn; I, invaded; NI, noninvaded.

[b] For an attribute, bolded numbers indicate significant mean differences between I and NI populations, as determined by a *t* test, for each growth cycle and depth.

Mn, and solution-phase ortho-P and SO_4^{2-}. Additionally, the invaded soil had a smaller molar proportion of NH_4^+ in the mineral N fraction and elevated molar fraction of NO_2^- in the solution-phase $NO_2^- + NO_3^-$ pool compared to the noninvaded soil. Nutrient availability often increased with depth as exemplified by mineral N (invaded soil, second growth cycle), bicarbonate-extractable P (invaded soil, first growth cycle), DTPA-extractable Mn (invaded soil, second growth cycle), solution-phase ortho-P (invaded soil, first growth cycle), and solution-phase SO_4^{2-} (invaded soil, first growth cycle and both soils, second growth cycle). It is apparent that the increase in nutrient availability with depth occurred largely in the invaded soil. For both invaded and noninvaded soils, the molar proportion of NH_4^+ declined with depth, but only for the second growth cycle.

To more clearly express how plant growth affected soil nutrient pools, a table was constructed summarizing the relative loss or gain of nutrients in unplanted controls relative to the planted treatments (Table 3). Plant growth used up a considerable portion of the mineral soil N pool at all soil depths and in both soil types, but notable is the relatively low utilization in the invaded soil for the second growth cycle at 10 cm. Plant growth generally reduced the bicarbonate-extractable P pool with greatest use in the invaded soil after the first growth cycle. The only gain in the bicarbonate-extractable pool due to plant growth occurred after both growth cycles at 80 cm in the

Table 3. Average percent decrease (−) or increase (+) in soil nutrient pools after plant growth relative to unplanted controls by soil type (invaded or noninvaded), growth cycle, and soil depth.[a]

Growth cycle	Depth	Mineral N		Bicarb-P		DTPA-Mn		Solution-phase Ortho-P		Solution-phase SO_4^{2-}	
		I	NI	I	NI	I	NI	I	NI	I	NI
	cm	mmol kg^{-1}				µmol kg^{-1}		µmol L^{-1}			
First	10	**−96**[b]	**−77**	**−33**	**−3**	+1	+8	**−37**	**−3**	**−90**	**−74**
First	40	−92	**−87**	**−15**	**−7**	+9	+6	+22	+18	**−81**	**−80**
First	80	−92	**−94**	**−21**	**+16**	+63	+6	**−31**	**+37**	**−56**	**−68**
Second	10	−12	**−15**	**−18**	**+3**	+28	+36	**−48**	**−67**	**−50**	**−58**
Second	40	−78	**−72**	**−6**	**−3**	+35	+15	**+17**	**+120**	**−65**	**−46**
Second	80	**−80**	**−65**	**−17**	**+17**	+27	+3	**+8**	**+209**	**−83**	**−81**

[a] Abbreviations: Bicarb-P, bicarbonate-extractable P; DTPA-Mn, diethylentriamene pentaacetate-extractable-Mn; I, invaded; NI, noninvaded;

[b] For an attribute, bolded numbers indicate significant mean differences between I and NI populations, as determined by a *t* test, for each growth cycle and depth.

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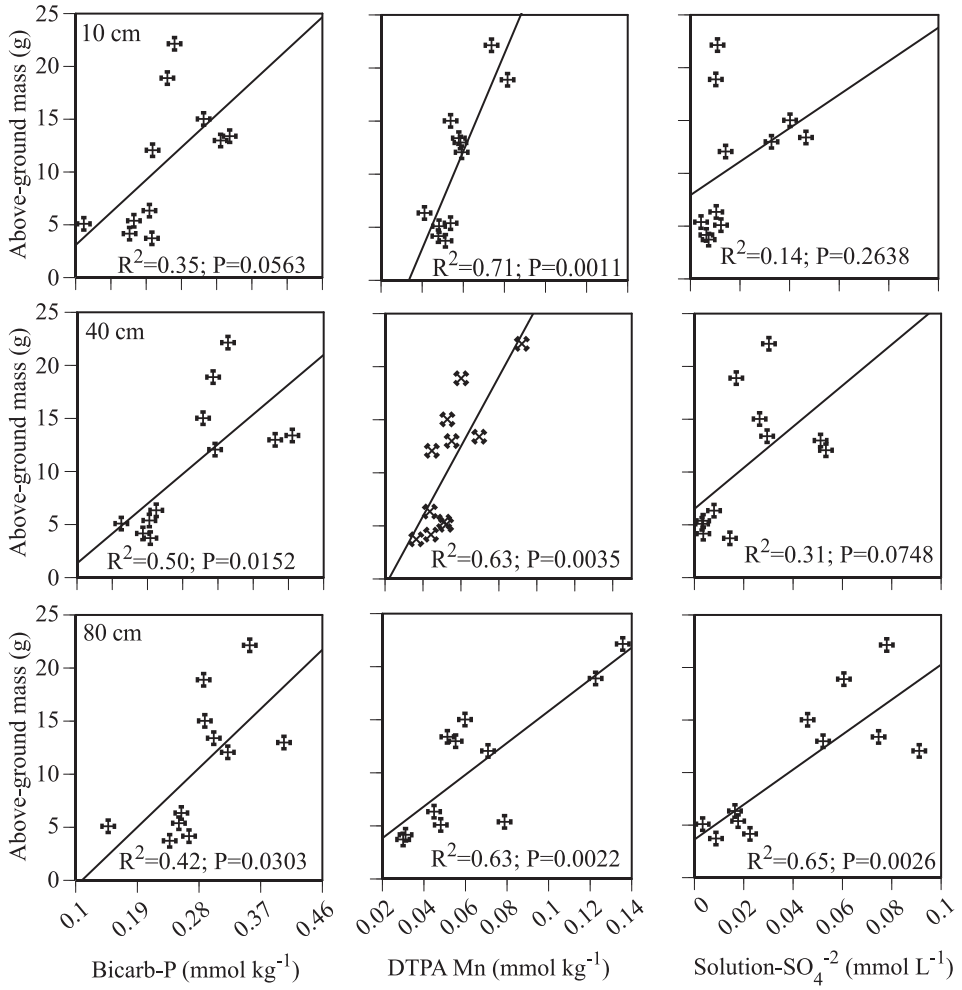

Figure 4. Graphical summarization of soil variables (means), by depth, that significantly correlated with aboveground biomass. Data pooled over growth cycle and invasion class.

noninvaded soil. Except for the noninvaded soil at 10 cm following the second growth cycle, plant growth facilitated an increase in DTPA-extractable Mn pools. The effect of plant growth on solution-phase ortho-P was variable, showing both increases and decreases relative to unplanted controls. Prominent is a large increase in solution-phase ortho-P after the second growth cycle for the invaded soil at 80 cm and the noninvaded soil at 40 and 80 cm. After both growth cycles, overall plant growth dramatically increased solution-phase SO_4^{2-} for the invaded soil, but decreased SO_4^{2-} for the noninvaded soil.

Correlation was used to identify soil variables that relate to aboveground tissue biomass (Figure 4). Aboveground biomass did not significantly correlate with soil mineral N. Aboveground biomass significantly and positively correlated with bicarbonate-extractable P and DTPA-extractable Mn for most soil depths tested. Solution-phase ortho-P and SO_4^{2-} significantly correlated, but only at 40 cm for P and 80 cm for SO_4^{2-}.

Discussion

The data suggest that the working hypothesis be accepted: a soil conditioned or engineered upon long-term occupation by downy brome is a better growth medium for downy brome than a similar soil not yet invaded by downy brome. A key assumption in testing this hypothesis is that, prior to invasion by downy brome, the two soils collected for this experiment were similar in soil characteristics. Our long-term monitoring of this site indicates that in 2001 there were no significant differences in several indexes of nutrient availability (Table 1) and particle size distribution in the same invaded and noninvaded areas where soil for this study was collected. Moreover, winterfat communities, from which both invaded and noninvaded soils were collected, are limited to a narrow range of soil characteristics (Gates et al. 1956).

Invasive plants often alter soil characteristics of ecosystems relative to native vegetation (Ehrenfeld 2003).

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Moreover, these soil changes often facilitate (positive feedback) the growth and invasibility of the exotic plant species (Jordan et al. 2008). What soil changes engineered by downy brome are responsible for increasing its growth potential. Our data suggest that engineering caused by long-term occupation of downy brome involves changes in the N, P, and Mn cycles.

Evidence that long-term occupation by downy brome affected the soil N cycle is myriad. Firstly, the original invaded soil used in this experiment had far greater mineral N than the noninvaded soil (Table 1). This finding alone is remarkable given the N sequestered in downy brome litter (noninvaded interspaces were largely barren of vegetation). Secondly, downy brome aboveground tissue grown in the invaded soil had greater N concentration than tissue from noninvaded soil (Figure 3). Thirdly, the original invaded and noninvaded soils differed considerably in the molar proportion of NH_4^+ in the mineral N pool and the molar proportion of NO_2^- in the solution-phase NO_2^- + NO_3^- pool (Table 1). That the invaded soil had greater than 90% molar proportion of NH_4^+ suggests, at least initially, inhibition of nitrification relative to the noninvaded soil (see Hawkes et al. 2005). That the molar proportion of NO_2^- was far higher in the invaded soil initially suggests that the rate-limiting step involves nitrobacter (Robertson and Groffman 2007). Finally, following plant harvest, the invaded soil had far greater mineral N than did the noninvaded soil. Given that the calculated uptake of N (average N tissue concentration × average aboveground mass) was 514 and 304% greater for the first and second growth cycles, respectively, for the invaded soil than the noninvaded soil, it is remarkable that the invaded soil still had more mineral N. All these data suggest invasion by downy brome has affected, in some way, the N cycle to facilitate greater N availability. It is widely reported that invasive plants affect the soil N cycle. The first author of this manuscript measured natural abundance ^{15}N at the present study sites (Blank and Morgan 2011). The same plant species in different downy brome invasion classes (noninvaded, invaded for 3 yr, invaded for 10 yr) had significantly different natural abundance of ^{15}N, which suggests downy brome changed the pool of N available to the plants. In a meta-analysis, Liao et al. (2008) reported that plant invasion, in general, increases soil N pools, N fluxes, and soil N availability. Plant species differentially affect N mineralization rates (Wedin and Tilman 1990). In northwestern Europe, Dassonville et al. (2008) reported that soil beneath invasive plants often has higher availability of N than that under indigenous species, but mostly on sites with initially low nutrient availability. The coarse-textured soil types used in our study would be considered to have low fertility. Alteration of the soil N cycle due to plant invasion is often attributed to changes in microbial community structure (Kourtev et al. 2002). Niu et al. (2007) reported that sites in China heavily invaded by an exotic aster had significantly greater soil availability of nitrate-N, ammonium-N, and P than sites only recently invaded. Indeed, downy brome invasion has been shown to affect soil biota and N dynamics relative to native communities (Belnap and Phillips 2001; Evans et al. 2001). Moreover, in greenhouse and field studies, supplementation with N fertilizers has almost universally been shown to increase the growth potential of downy brome (Brooks 2003; Kay and Evans 1965; Monaco et al. 2003). Booth et al. (2003) reported that downy brome was a strong sink of NO_3^- and had greater nitrification rates, greater total N, and greater mineralization than soil beneath sagebrush and the native bunchgrass *Elymus elymoides* (Raf.) Swezey.

Three lines of evidence suggest that downy brome invasion has engineered the soil P cycle to increase its availability. Firstly, soil invaded by downy brome for 12 yr had a far greater pool of bicarbonate-extractable P than the noninvaded soil (Table 1); yet in 2001, much earlier in the invasion process, levels of bicarbonate-extractable P were more similar between invaded and noninvaded sites (Table 1). Secondly, original invaded soil used in this experiment contained more solution-phase ortho-P than the noninvaded soil (Table 1). Thirdly, levels of solution-phase ortho-P after each growth cycle were overall statistically higher for the invaded soil than for the noninvaded soil (Table 2), even after far greater uptake due to plant growth in the invaded soil (Figure 2). At the site where soil for this study was collected, downy brome–invaded areas utilize about 7% of the bicarbonate-extractable P pool per year based on a rooting depth of 1 m (39.375 in) (Blank 2008). That the bicarbonate-extractable P pool of surface soil could so increase upon invasion suggests two potential mechanisms. Downy brome may increase the rate of P cycling from deeper horizons, thereby increasing the availability in the surface soil layer via mineralization of plant litter and roots (Jobbágy and Jackson 2001). In addition, downy brome may affect P availability via an interaction with its rhizosphere, including such processes as increased weathering of P-bearing primary minerals and release of P sequestered on mineral surfaces (Hinsinger 1998). Indeed, invasive plants have been shown to increase soil P availability relative to native communities (Chapuis-Lardy et al. 2006; Dassonville et al. 2008). Next to water and N, the availability of P is the most limiting factor for plant growth (Schachtman et al. 1998). Moreover, the competitive ability of some invasive weeds, including downy brome, have been shown to increase with elevated soil P availability (Dakeel et al. 1993; Huenneke et al. 1990; Suding et al. 2004).

Our data also suggest that downy brome influences the soil Mn cycle as documented by the far higher levels of DTPA-extractable Mn in the original invaded soil relative to the noninvaded soil (Table 1). Moreover, even after robust plant growth by downy brome and considerable

uptake of soil Mn, the DTPA-extractable Mn pool was far higher in the invaded soil compared to the noninvaded soil (Table 2). Very meager literature exists on the role of micronutrients for invasive plant growth and competitiveness. The necessary role of Mn in photosynthesis (Marschner 1995) suggests that obtaining optimal levels from the soil would be potentially important in competitive interactions. We could only find one reference of a study where an invasive plant increased soil Mn availability relative to the native species (Dassonville et al. 2008). Miller et al. (2006) determined that, in calcareous soils of Utah, downy brome growth correlated with soil DTPA-Mn availability and that the soils were likely deficient in Mn for optimal downy brome growth. For the present study, based on greater availability of Mn in the invaded soil, one might predict that downy brome tissue grown in that soil would have greater Mn concentration than that grown in the noninvaded soil; however, the opposite occurred (Figure 3). A potential explanation is that the greater biomass for the invaded soil may have simply diluted the Mn. Alternatively, the DTPA extraction may not truly measure plant-available Mn; there is a pool of Mn more available in the noninvaded soil not quantified by DTPA extraction. The DTPA test was developed for agronomic crops to relate soil micronutrient availability to what is plant available (Lindsay and Norvell 1978) and the test may not be valid for native plants.

We do not claim that engineering by downy brome is the sole, or indeed the most important, facet of its competitiveness. Using plant invasion models, Levine et al. (2006) concluded that strong positive feedbacks can increase density of invasion and potential impacts, but does not likely affect spreading velocity. What are the potential long-term effects of soil engineering by downy brome? Thorpe and Callaway (2005) speculated that invasive plants may create a positive feedback and so alter microbial communities and nutrient cycling that invasional meltdown (Simberloff and Von Holle 1999) may occur. It remains speculative, but the first author has hypothesized that some invasive plants may engineer soil properties so as to create a deficiency in a critical nutrient, a nutrient Achilles heel (Blank et al. 2002). Does long-term soil engineering by downy brome have the potential to limit its growth and competitive ability? We simply have no definitive answer at this time. Speculating on one potential scenario, increasing soil N availability by the annual grass downy brome may allow greater leakiness to N, especially during the winter, resulting in loss of N capital—only time will tell if this is the case.

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