

Performance of *Bromus tectorum* L. in relation to soil properties, water additions, and chemical amendments in calcareous soils of southeastern Utah, USA

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Received: 15 December 2005 / Accepted: 21 February 2006 / Published online: 21 August 2006
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Abstract In drylands of southeastern Utah, USA, the invasive exotic grass *Bromus tectorum* L. occurs in distinct spatial patterns suggesting soil control of ecosystem susceptibility to invasion. To improve our understanding of these patterns, we examined performance of *B. tectorum* in relation to additions of water, KCl, MgO, and CaO at seventeen 1600 m² sites distributed across a calcareous soil gradient in

Canyonlands National Park. Water additions resulted in a 57% increase in *B. tectorum* establishment. Fall establishment was significantly correlated with silt and clay content in wet plots but not in dry plots, suggesting that texture effects on *B. tectorum* establishment patterns may be greater in wet years than in dry years. Applications of MgO resulted in a 49% decrease in *B. tectorum* establishment, although MgO had no effect on whole-plot biomass at the end of the growing season. *B. tectorum*–soil relations were strongest during winter (December–March) when relative growth rates were negatively related to soil acid-neutralizing potential, sand and CaCO₃ content, and a measure of bioavailable Mg; and positively related to silt and clay content, total N, measures of bioavailable Mn, P, and K, and a measure of magnetite indicating distributional patterns of eolian dust. As soils were persistently moist during this period, we attribute strong *B. tectorum*–soil patterns in winter to effects of low temperature on diffusion, microbial activity, and/or production of root exudates important for nutrient mobilization and uptake. In spring, there was a reversal in *B. tectorum*–soil relations such that loamy soils with higher *B. tectorum* densities were unfavorable for growth relative to sandy soils with higher warm-season water potentials. We conclude that resource limitations for *B. tectorum* in this study area shift seasonally, from water limitation of fall establishment, to nutrient limitation of winter growth, and back to water limitation of spring growth. Because study sites generally were arrayed along a

Section Editor: T. Kalapos.

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Electronic Supplementary Material Supplementary material is available for this article at <http://dx.doi.org/10.1007/s11104-006-0058-4> and is accessible for authorized users.

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hillslope gradient with downslope trends in soil vtexture and nutrient content, close *B. tectorum*–soil relations documented in this study indicate that a geomorphic framework is useful for understanding and predicting *B. tectorum* invasion patterns in dryland ecosystems of this region.

Keywords Invasive species · Magnesium · Manganese · Phosphorus · Potassium · Spatial patterns

Introduction

A mechanistic understanding of plant–soil relations is particularly important with respect to the conservation problem of invasive exotic species. The prediction of potential invasion patterns as well as the restoration of ecosystems degraded by invasive exotic plants both depend for their success on an understanding of processes responsible for observed invader–environment relations (Crawley 1987; Lodge 1993; Williamson and Fitter 1996). Several authors have hypothesized that dynamic processes controlling the availability and acquisition of limiting soil resources are key factors responsible for variations in invasion success among ecosystems and species (Blumenthal 2005; Davis et al. 2000; With 2002). Consistent with this resource-based hypothesis, there is increasing empirical evidence that spatiotemporal patterns in the availability of soil resources shape patterns in ecosystem susceptibility to exotic species' invasion across a wide range of environments (Búrquez-Montijo et al. 2002; Huenneke et al. 1990; Planty-Tabbachi et al. 1996).

The invasive exotic grass *Bromus tectorum* L. is one of the most significant plant invaders in western North America because of its broad geographic distribution and its ecological effects on the structure and functioning of wildland ecosystems (Mack 1981). Within this region where it was accidentally introduced from Eurasia in the late 19th century, *B. tectorum* has been reported to be the most common species (and frequently the dominant) on >410,000 km² (Mack 1981). Because of the rapidity, spatial extent, and ecological consequences of *B. tectorum* invasion, the species has been the focus of numerous studies (e.g., Mack and Pyke 1983,

1984; Norton et al. 2004; Young and Evans 1985) and reviews (e.g., Knapp 1996; Mack 1981). Some broad-scale studies have found positive relations between spatial patterns of *B. tectorum* abundance and levels of soil phosphorus (Bashkin et al. 2003). But despite the large volume of work that has been conducted on various aspects of *B. tectorum* invasion, plant–soil relations underlying spatial patterns of invasion in particular landscapes remain poorly understood, and few studies have investigated such patterns experimentally (but see Beckstead and Augspurger 2004; Meyer et al. 2001).

In this study, we conducted a field experiment to examine variations in *B. tectorum* performance across a range of soils and in relation to experimental manipulations involving additions of water and KCl, CaO, and MgO. This work was motivated by observations of *B. tectorum* invasion patterns that were correlated with soil content of silt and exchangeable K at a relatively pristine site in southeastern Utah, USA, where land-use disturbances did not confound the investigation of spatial plant–soil relations (Belnap and Phillips 2001). Pilot studies conducted in preparation for this work further suggested that carbonates in calcareous soils of the study area might play a role in generating observed *B. tectorum* patterns by constraining the bioavailability of P or micronutrients (Marschner 1995). In this research, we sought to understand soil and resource relations of *B. tectorum* over the full fall–winter–spring growth cycle of this annual plant. We measured rates of *B. tectorum* establishment, seasonal growth rates, foliar nutrient concentrations, total shoot length, and whole-plot aboveground biomass at the end of the growing season in relation to soil properties and additions of water and KCl, CaO, and MgO.

Methods

Study area

Field studies were conducted in the southern portion of Canyonlands National Park (CNP) in southeastern Utah, USA. CNP (38°09' N, 109°45' W) lies in the Canyon Lands Section of the Colorado Plateau Physiographic Province (Hunt 1974) and is characterized by an arid climatic regime. Between 1965 and 2001, mean annual temperature was 11.8°C and mean

annual precipitation was 215 mm, with 45% of total annual precipitation occurring during the four months July through October.

In a 2600-ha area of CNP, 17 study sites each measuring approximately 1600 m² were selected to represent a range of soil characteristics and *B. tectorum* abundances. Grassland communities dominated the vegetation at all sites, with total live plant cover ranging from 12.3% to 29.2% at the time of site selection in January 1997 (Miller 2000). Live *B. tectorum* cover ranged from 2.7% to 20.3% (mean 8.8). Other common grass taxa were *Stipa hymenoides* R. & S (mean cover 4.7%), *Hilaria jamesii* (Torr.) Benth. (mean cover 1.6%) and *Sporobolus* R. Br. spp. (mean cover 1.1%). All sites were located at approximately 1550 m in elevation, aspects varied, and slopes ranged from 0% to 8%. Study area landscapes are dominated geologically by outcrops of sedimentary rock formations consisting primarily of Permian-aged eolian sandstones cemented by CaCO₃ (Stanenco and Campbell 1989), and a fundamental characteristic of area soils is the presence of inherited carbonate compounds. Soils were classified as coarse-loamy, mixed, mesic Ustollic Camborthids (fine sandy loams of the Begay series) and mixed, mesic Typic Torripsamments (loamy fine sands of the Sheppard series) (U.S.D.A. Soil Conservation Service 1991).

Experimental treatments

At each of the 17 study sites, six circular plots (102 plots total) measuring 1.2 m in diameter were established by removing all plants (including most roots) and above-ground litter. In September 1997, interiors of each plot (0.8 m diameter) were seeded with 1150 *B. tectorum* seeds (~2300 seeds/m²) collected at CNP in late-summer 1997. Seeds were mixed by hand in the top 1–2 cm of soil, and plots were caged with fencing to exclude vertebrate herbivores and granivores.

Plots were assigned randomly to one of six treatment combinations involving manipulations of water (two levels) and soil chemistry (four levels). “Wet” plots were watered by hand biweekly from 1 October through 15 November, and again from 1 March through 15 May at rates that approximated 1.5–2.0 times the average amount of precipitation when combined with ambient precipitation levels. “Dry”

plots also were watered biweekly or monthly in an effort to attain the average amount of precipitation. From October through the following June, precipitation received (91 mm) was 61% of the long-term average (148 mm). Over the same period, total amounts of water received by wet plots and dry plots were 245 mm (165% of average) and 125 mm (85% of average), respectively. Chemical manipulations involved applications of KCl (30 g, in solution), MgO (25 g, powder form), and CaO (34.6 g, powder form) in fall 1997 and again in spring 1998. The KCl treatment was crossed with both levels of water manipulations because we hypothesized that KCl and water could have interactive effects on *B. tectorum* performance due to positive effects of soil moisture on rates of K⁺ diffusion and uptake (Barber 1995) or due to the physiological significance of K⁺ for stomatal functioning and plant water relations (Marschner 1995). Amendments of MgO and CaO were included (though not crossed with water treatments) because observations made during a spring 1997 pilot study suggested that spatial variations in soil carbonate characteristics might influence *B. tectorum* performance (Miller 2000). Calcium oxide and MgO were used rather than CaCO₃ and MgCO₃ because the former two compounds are more reactive than the latter two, although both the oxide and the carbonate forms first react in the soil to produce bicarbonate compounds (e.g., Ca(HCO₃)₂) (Brady and Weil 1996). Both CaO and MgO were used because we hypothesized that MgO would be more reactive in soils than CaO due to higher concentrations of Ca²⁺ than Mg²⁺ in CNP soils. Water and chemical treatments were applied to the entire 1.2-m plot area, whereas *B. tectorum* was seeded and caged only within the interior 0.8-m diameter area.

Soil measures

Among-site soil variation was characterized by analyses conducted on composite soil samples collected systematically from 0 to 10 cm at each study site with a 2.4-cm soil probe or an 8-cm bucket auger. Soils were air dried and analyzed for pH (saturated paste extract); cation exchange capacity (CEC; Na displacement by 1 M NH₄OAC at pH 7.0); organic matter (OM) content (Walkley and Black method); NaHCO₃ extractable P (P-Bicarb); total Kjeldahl N (TKN); amounts of micronutrients

Mn, Fe, Cu, and Zn extractable with diethylenetriaminepentaacetic acid (Mn-Dtpa, Fe-Dtpa, Cu-Dtpa, and Zn-Dtpa); and amounts of exchangeable cations Ca^{2+} , Mg^{2+} , K^+ , and Na^+ extractable with NH_4OAc buffered to pH 8.5 (Ca-Ex, Mg-Ex, K-Ex, and Na-Ex). Soil acid-neutralizing potential (ANP) was determined following the acid-neutralizing method of carbonate analysis (Allison and Moodie 1965), and carbonate content was determined with a Chittick apparatus (Dreimanis 1962). Gypsum content was determined by the crystal water-loss method (Nelson 1982). The particle-size distribution of each composite sample was measured with a Malvern laser particle sizer following removal of carbonates and organic material by acid digestion.

In the CNP study area, the content of far-travelled eolian dust in sandy soils can be estimated by soil magnetic properties which reflect the presence of magnetite grains that are absent from surrounding sandstones (Neff et al. 2005; Reynolds et al. 2006). Reynolds et al. (2006) found that eolian dust is an important source of rock-derived nutrients for these sandy soils. In this study, we measured isothermal remnant magnetization (IRM; Thompson and Oldfield 1986) as a proxy for the relative abundance of eolian dust in composite soil samples. IRM was imparted in an induction of 0.3 T and then measured using an Agico JR-5A 90-Hz spinner magnetometer.

Soil nutrient bioavailability also was characterized on the basis of extractions performed with ion-exchange resins. All macronutrient ions K^+ , HPO_4^{2-} , NH_4^+ , NO_3^- , Ca^{2+} , Mg^{2+} , SO_4^{2-} , and micronutrient ions Mn^{2+} , Zn^{2+} , Fe^{2+} , Cu^{2+} , and Na^+ were extracted simultaneously from soils with mixed-bed (cation+anion) ion-exchange resin capsules manufactured by Unibest, Inc., Bozeman, Montana, USA. Each resin capsule consists of a 2-cm-diameter spherical ball with 4 ml of mixed-bed resin beads (H^+ – OH^- saturated) contained within a plastic screen mesh. Capsule surface area is approximately 11.4 cm^2 . For each sample, water and 50 g of dry soil were mixed to form a saturated paste, and a resin capsule was inserted into the center of the paste. After a 7-day incubation period, capsules were removed and washed free of all soil particles with a directed stream of deionized water. Adsorbed ions were stripped by placing the capsule in a small container with 20 ml of 2 M HCl and shaking on a reciprocal shaker for 20 min.

The solution was collected, and the process repeated two additional times, yielding 60 ml of solution for analyses. Solution concentrations of all ions, with the exception of NH_4^+ and NO_3^- , were measured simultaneously by inductively coupled plasma (ICP) atomic emission spectroscopy. NH_4^+ and NO_3^- were recovered separately in a H_3BO_3 indicator solution by steam distillation with MgO and Devarda alloy, and were determined by titration with H_2SO_4 (Keeney and Nelson 1982). To estimate background ion concentrations found on resin capsules, 10 unused capsules were extracted with HCl and ion concentrations determined following the same methods used for incubated capsules. Mean background concentrations were not subtracted from values determined for incubated capsules but are reported below for reference.

Soil water content was measured on a biweekly basis at two sites with contrasting soil properties from October 1997 through May 1998. During each sampling event, two 60-cm-long continuous soil cores of 2.4-cm diameter were extracted from a plot where plants had been removed at the beginning of the experiment. Cores were split into 10-cm increments, composited by sample depth, and analyzed for gravimetric water content. Gravimetric data were converted to volumetric data on the basis of bulk density measurements made in January 1998. In addition, soil samples were directly analyzed for water potential prior to oven drying using a sample chamber thermocouple psychrometer (model HR-33T-R dew point microvoltmeter with C-52 sample chamber, Wescor Inc., Logan, Utah, USA).

To assess treatment, soil, and plant effects on in situ nutrient dynamics, at five sites four nylon-mesh bags containing 10 g of moist, mixed-bed ion-exchange resins (H^+ and Cl^- saturated) were buried in all experimental plots (including plots with no plants) at depths of 5–10 cm. Bags were first placed at the beginning of the pilot study in January 1997 and were replaced seasonally thereafter. After replacement, macro- and micro-nutrient ions were desorbed from exposed resin bags with HCl and nutrient determinations were made following methods described above for resin capsules. Results of the resin-bag studies are the focus of a companion paper (Miller et al. submitted), but a subset of these data are presented herein.

B. tectorum measures

Several measurements were made to assess treatment and soil effects on *B. tectorum* performance from fall 1997 through spring 1998. After seeding in late September, *B. tectorum* measurements were made once following germination in October, at the onset of winter in early December, and monthly in spring from mid-March to mid-May. *B. tectorum* densities were estimated by counting the number of live plants occurring in a rectangular 250-cm² quadrat frame aligned with the four cardinal directions in each circular plot (1000 cm² sampled per plot). Densities estimated during the December measurement period are reported here as “fall establishment.” Ten individual plants per plot (1020 total) were marked in mid-October, and total shoot lengths (sheaths plus blades) of marked plants were measured to the nearest mm during each measurement period. Data for marked plants were used to calculate relative growth rates (RGR, in mm mm⁻¹ day⁻¹) for intervals between 3- and 5-day measurement periods, and data for marked plants within a given plot were averaged to derive plot-level values. Seasonal RGR data are reported for fall (12 October–11 December), winter (11 December–14 March), early spring (14 March–13 April), and mid-spring (13 April–12 May). Leaf tissues were collected in spring 1998 (22–23 April) from *B. tectorum* plants in plots at the same subset of five sites that were used for resin-bag studies. Tissues were air dried, ground through a 0.37-mm screen mesh with rotating mill, and foliar concentrations (% dry weight) of Zn, Fe, Mn, Cu, Ca, Mg, K, Na, S, and P were determined by ICP following digestion with nitric and perchloric acids (Association of Official Analytical Chemists 1980). Foliar N was determined colorimetrically on an autoanalyzer following digestion by a modified Kjeldahl procedure (Association of Official Analytical Chemists 1980). In late June after final shoot-length measurements, *B. tectorum* plants were harvested (above-ground tissues only). Harvested materials were air dried in an uncooled garage during summer and weighed to obtain total end-of-season biomass per plot.

Data analyses

Principal components analysis (PCA) with varimax factor rotation was used to reduce the multivariate

soil dataset and describe among-site soil variation in relation to two principal axes (Kent and Coker 1992). On the basis of site scores associated with the first PCA axis, the 17 study sites were categorized into three discrete site groupings using the *k*-means clustering method. This clustering technique uses an algorithm which assigns sites to a user-defined number of clusters (3 in this case) to minimize within-cluster variation and maximize among-cluster variation (analogous to ANOVA, in reverse) (StatSoft 1999). All statistical analyses were conducted using the software package STATISTICA™ v5.5 on a PC platform (StatSoft 1999).

Treatment effects on *B. tectorum* performance measures were analyzed in an incomplete 3-way, fixed effects multivariate analysis of variance (MANOVA) design (Underwood 1997). Factors were (1) soil categories defined on basis of PCA and cluster analysis, (2) water addition, (3) and chemical amendment (KCl, none, CaO, and MgO). Response measures were fall establishment, seasonal relative growth rates, total per-plant shoot length in June, and total whole-plot above-ground biomass in June (hereafter referred to as “end biomass”). Because CaO and MgO treatments were not crossed with water, the design was not completely factorial. Thus analyses were by tests of specific effects in the MANOVA module of STATISTICA. All *B. tectorum* measures except fall establishment and end biomass were log-transformed [$x'=\ln(x+1)$] prior to analysis (Zar 1999). Results are presented graphically as untransformed means for ease of interpretation. Following MANOVA, Tukey’s honestly significant difference (HSD) *post hoc* procedure was used to test for differences among levels of factors with significant main effects (Zar 1999). Simple linear correlation analysis (Zar 1999) also was used to evaluate relations between *B. tectorum* performance measures (log transformed or not, as in MANOVA analyses) and selected soil measures from the 17 study sites. Correlation analyses also were used to evaluate relations between *in situ* nutrient dynamics (measured by resin bags) and site characteristics described by PCA site scores, as well as relations between foliar nutrient concentrations with PCA site scores and selected *B. tectorum* performance measures. MANOVA and Tukey’s HSD *post hoc* test were used to evaluate effects of the water treatment

on selected arcsin-transformed measures of foliar nutrient concentrations.

Results

Soil variation

Shallow study area soils (0–10 cm depth) were calcareous loamy fine sands and fine sandy loams, with carbonate contents ranging from 4.4% to 11.0% by mass, sand contents ranging from 77% to 90% by volume, and pH ranging from 8.02 to 8.26 (see electronic supplemental material). Due to high sand and low OM content, soils possessed low CEC (mean 4.5 cmol_c/kg soil). Resin-capsule data indicated that Ca²⁺ was the most abundant cation in the soil environment, with values 7–8 times higher than Mg²⁺ on a charge basis. Together, these two accounted for approximately 94% of measured cation charges. Measured anions provided less than 5% of the charges required to balance measured soil cations. Based on soil pH and carbonate content, it is probable that HCO₃⁻ was the major charge-balancing anion in the soil. Relative to mean ion concentrations on capsules

incubated in soils, mean background concentrations on unused capsules were high for several ions including NH₄⁺ (29.3%), Zn²⁺ (36.2%), SO₄²⁻ (45.9%), Fe²⁺ (52.4%), Na⁺ (57.4%), and Cu²⁺ (150.0%).

The first two axes derived from the PCA of soil variables explained 50.1% of the variation in the analyzed dataset (Fig. 1). We interpret axis 1 as representing a complex soil-resource gradient, with high ($r > 0.70$) positive loadings for CEC, exchangeable cations (Mg-Ex, Ca-Ex, and K-Ex), micronutrient measures Cu-Dtpa and Mn-Dtpa, silt and clay content, TKN, resin HPO₄²⁻, and IRM. The high loading for IRM ($r = 0.94$) confirms the relation of soil magnetics and dust content with soil texture and rock-derived nutrient content in these soils. Variables with high ($r < -0.70$) negative loadings on axis 1 were sand content and ANP. Resin Ca²⁺ and SO₄²⁻ were positively loaded on axis 2. On the basis of axis 1 site scores, cluster analysis grouped sites into three soil categories hereafter referred to as loamy (four sites), intermediate (eight sites), and sandy (five sites).

Volumetric soil–water content at a representative loamy site was consistently higher than that at a representative sandy site from late October until late April (Fig. 2a). Soil water potentials at the contrast-

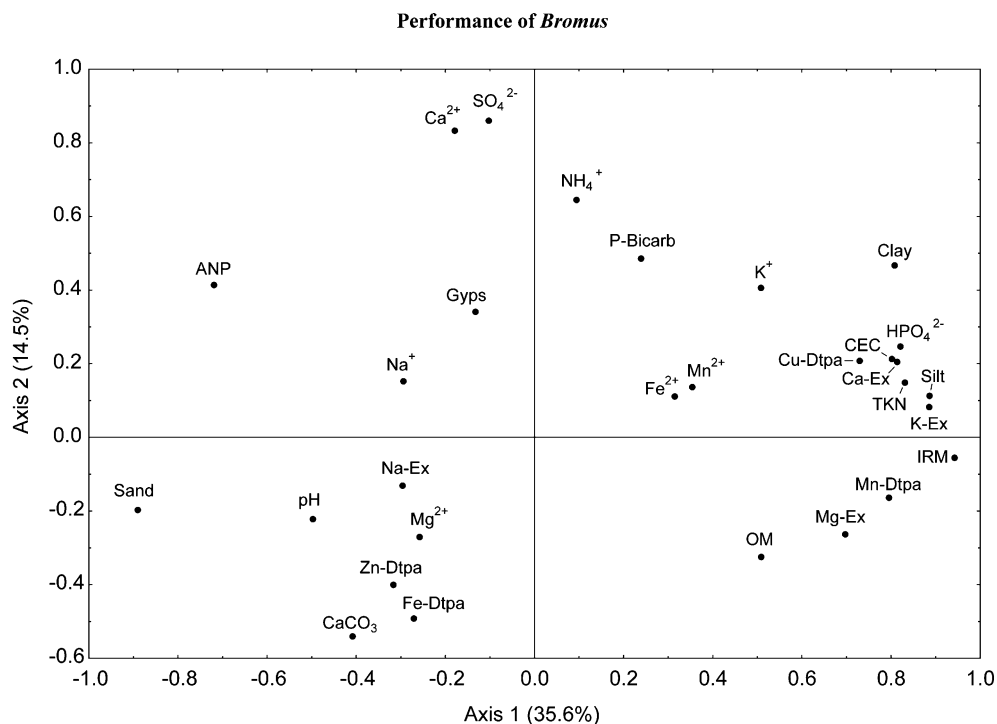
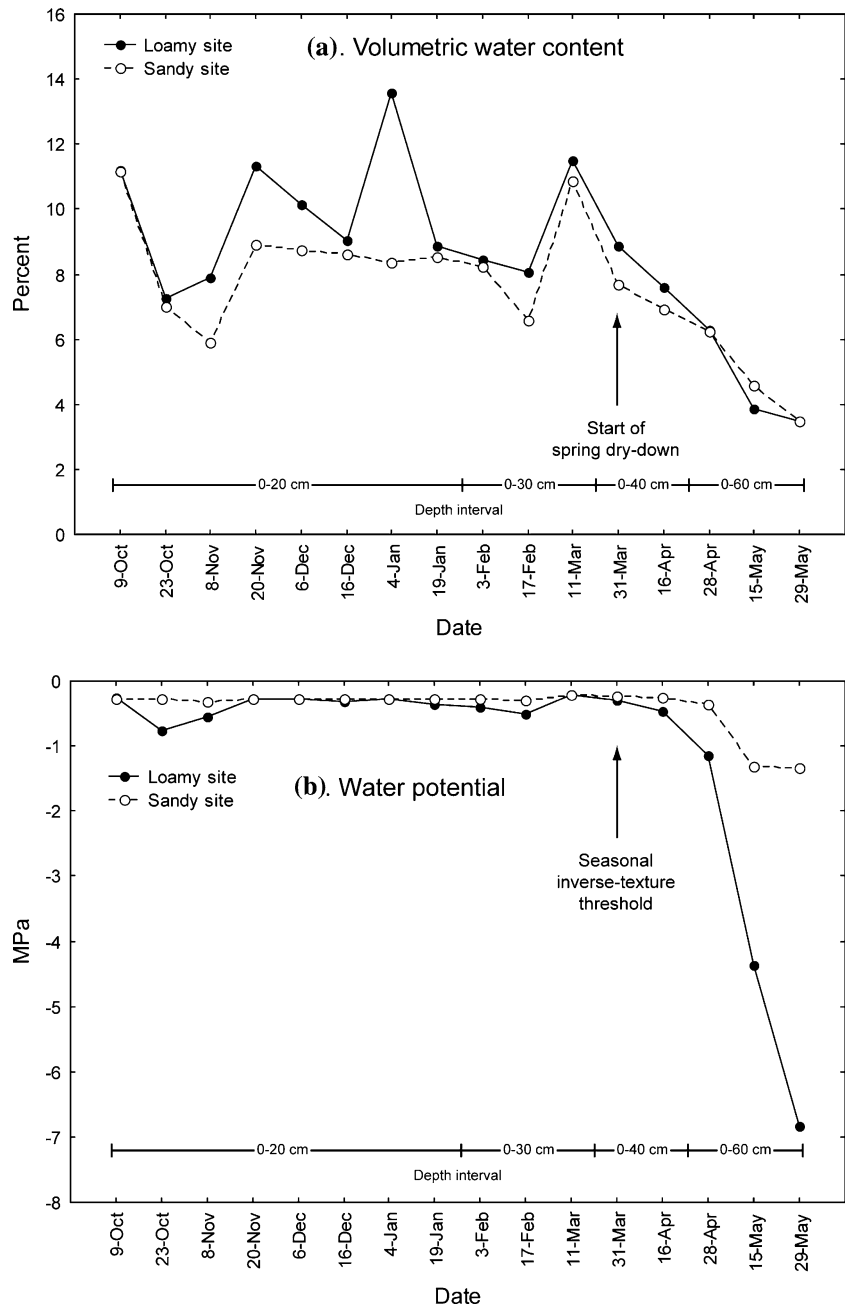


Fig. 1 Plot of soil-variable loadings in relation to PCA axes 1 and 2

Fig. 2 Seasonal variations in volumetric water content **a** and soil water potential **b** at representative loamy and sandy sites (one site per category) in plots without plants. Depth intervals indicate 10-cm increments that were included in the site averages for particular dates. The depth interval was increased through the growing season to approximate maximum depth of water extraction by *B. tectorum*



ing sites were similar from October until late March, but in early April the comparatively fine-textured soils at the loamy site experienced a more rapid decline in soil water potential than soils at the sandy site (Fig. 2b). Thus, whereas soils at both sites had similar volumetric water contents in late spring, soil moisture was more available to plants in sandy soils

due to greater water potentials relative to the loamy site.

B. tectorum performance

Soil category ($P < 0.0001$), water addition ($P < 0.0001$), and chemical amendments (dry plots only;

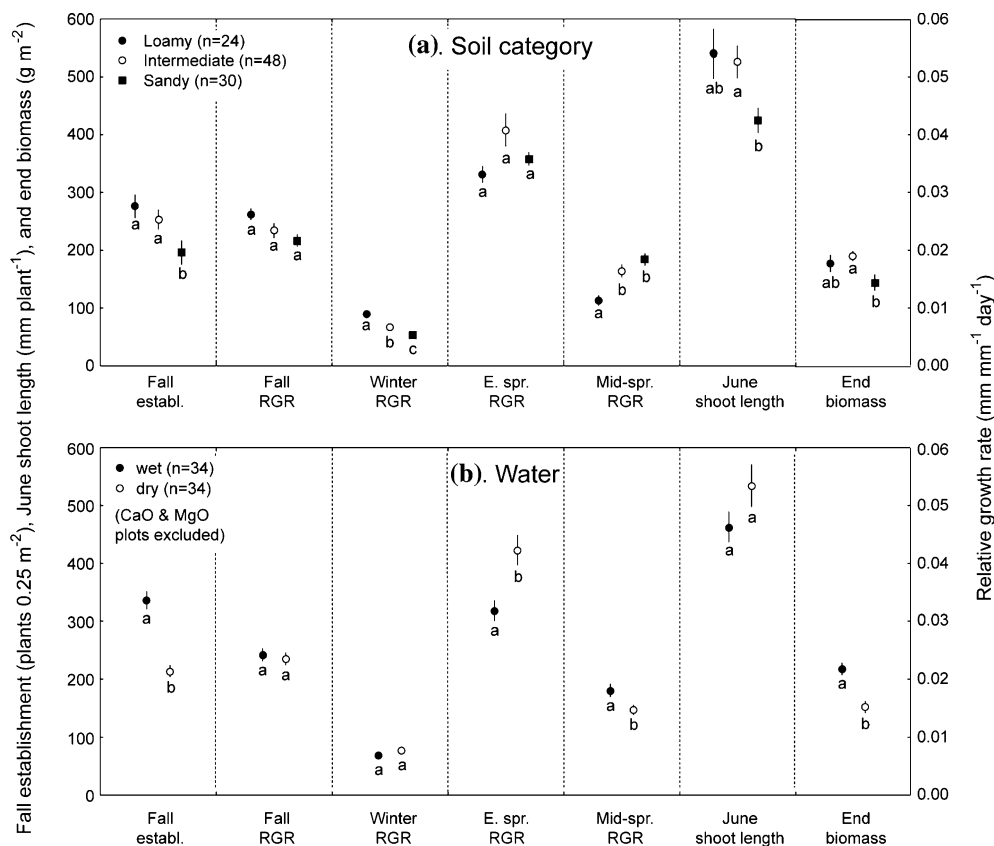


Fig. 3 Main effects of soil category, water, and chemical amendments (KCl, CaO, and MgO in dry plots; KCl only in wet plots) on fall establishment, seasonal relative growth rates (RGR), June shoot length, and end-of-season whole-plot above-ground biomass (means \pm 1 SE) during the fall 1997–spring 1998

$P < 0.0001$) had significant effects on *B. tectorum* performance measures (Fig. 3). All interaction effects were statistically insignificant (see electronic supplemental material).

Across all water and chemical-amendment treatments, fall establishment was lower in sandy sites relative to sites in other soil categories (Fig. 3a). Fall RGR tended to vary positively in relation to the soil-resource gradient represented by axis 1, but the trend was not significant. During the winter period (mid-December through mid-March), among-soil differences in *B. tectorum* RGR were statistically significant, with the highest growth rates at loamy sites and the lowest growth rates at sandy sites. During the early-spring period (mid-March through mid-April) when RGR was highest, there was no difference in RGR among site categories, although mean RGR values at sites in the intermediate soil

growing season. For significant main effects (soil category, water, and chemical amendments in dry plots), treatment means with different letters were significantly different by Tukey's HSD multiple-comparison test. Effects of chemical amendments in wet plots **d** were not statistically significant

category tended to be greater than those at loamy and sandy sites. During the mid-spring period (mid-April through mid-May), loamy sites were characterized by lower *B. tectorum* RGR values than sites in other soil categories. At the end of the experiment in June, mean total shoot length per plant and end biomass were lower at sites in the sandy soil category than at sites in the intermediate soil category. Plants at loamy sites tended to have the greatest total shoot length at the end of the season, but this result was not statistically significant. Measurements of a subset of 120 plants in mid-June confirmed that above-ground biomass of individual plants was positively correlated with total shoot length ($R^2=0.87$, $P < 0.0001$).

Across all sites and KCl fertilization plots (excluding unwatered CaO and MgO plots), water had a significant effect on fall establishment, early and mid-spring RGR, and end biomass (Fig. 3b). In

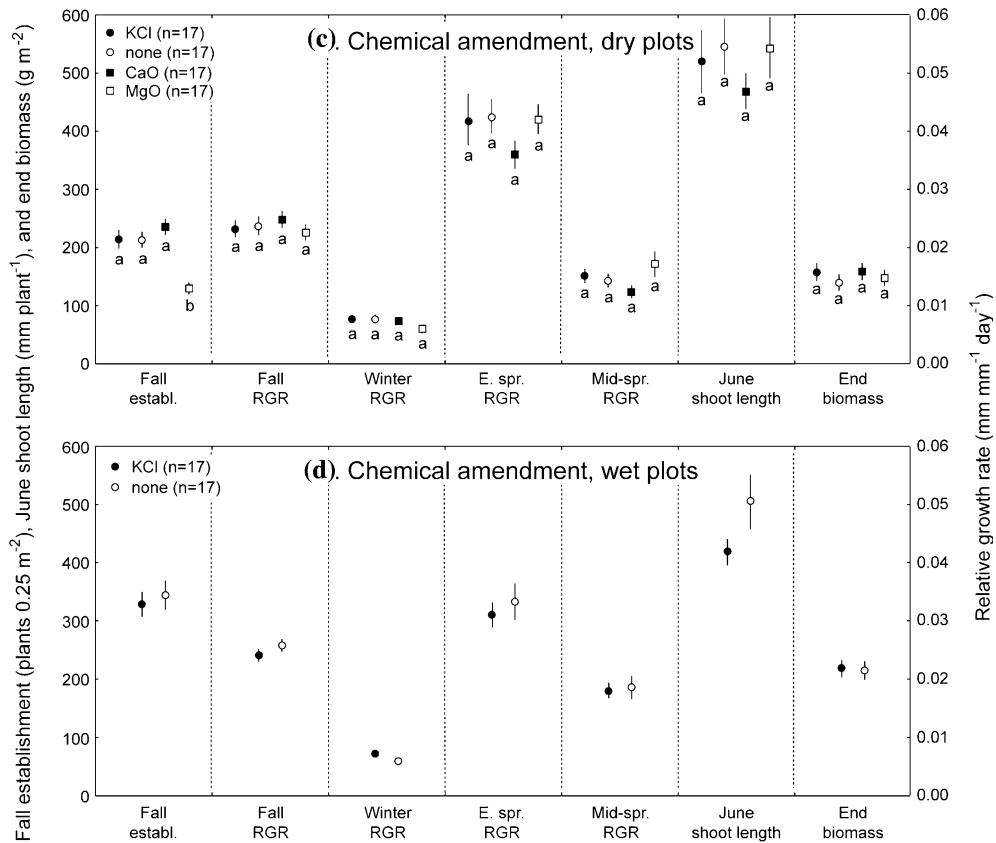


Fig. 3 continued

fall, *B. tectorum* establishment was 57% greater in wet plots relative to dry plots (1343 vs. 856 plants m^{-2}). There was no difference between wet and dry plots with respect to fall and winter *B. tectorum* growth. During early spring, *B. tectorum* growth in dry plots was greater than in wet plots, whereas the opposite was true during the mid-spring period. In June, there was a tendency for plants in dry plots to have greater total shoot length than plants in wet plots, although this trend was statistically insignificant. End biomass was significantly greater in wet plots than in dry plots.

Across all sites, effects of chemical amendments in dry plots were significant only for fall establishment (Fig. 3c). *B. tectorum* establishment was 49% lower in plots amended with MgO than in other dry plots (498 vs. 984 plants m^{-2}). Although the main effect of KCl amendments in wet plots was statistically insignificant ($P=0.10$), there was a tendency in winter for greater *B. tectorum* growth in KCl plots than in wet plots receiving no chemical amendments.

Correlative relations of *B. tectorum* performance measures with soil characteristics of the 17 study sites varied among seasons and between wet and dry plots, although patterns were directionally consistent between wet and dry plots in most cases (Fig. 4). Fall establishment was positively related to axis 1 site scores, clay, and silt content (significant in wet plots only); IRM (wet plots), Mn-Dtpa (wet and dry plots), Cu-Dtpa (wet plots), and resin-capsule K^+ (dry plots; Fig. 4a). Establishment was negatively related to sand content (wet plots) and Mg^{2+} (wet and dry plots). With the exception of K^+ , establishment-soil relations generally were stronger in wet plots relative to dry plots. Relations of fall growth with soil measures were less significant overall than for establishment, with significant negative correlations in dry plots for ANP and significant positive correlations in dry plots for axis 1 site scores, IRM, Mn-Dtpa, HPO_4^{2-} , and Mn^{2+} (Fig. 4b). The relation between fall RGR and soil texture was directionally similar to establishment patterns but not statistically significant.

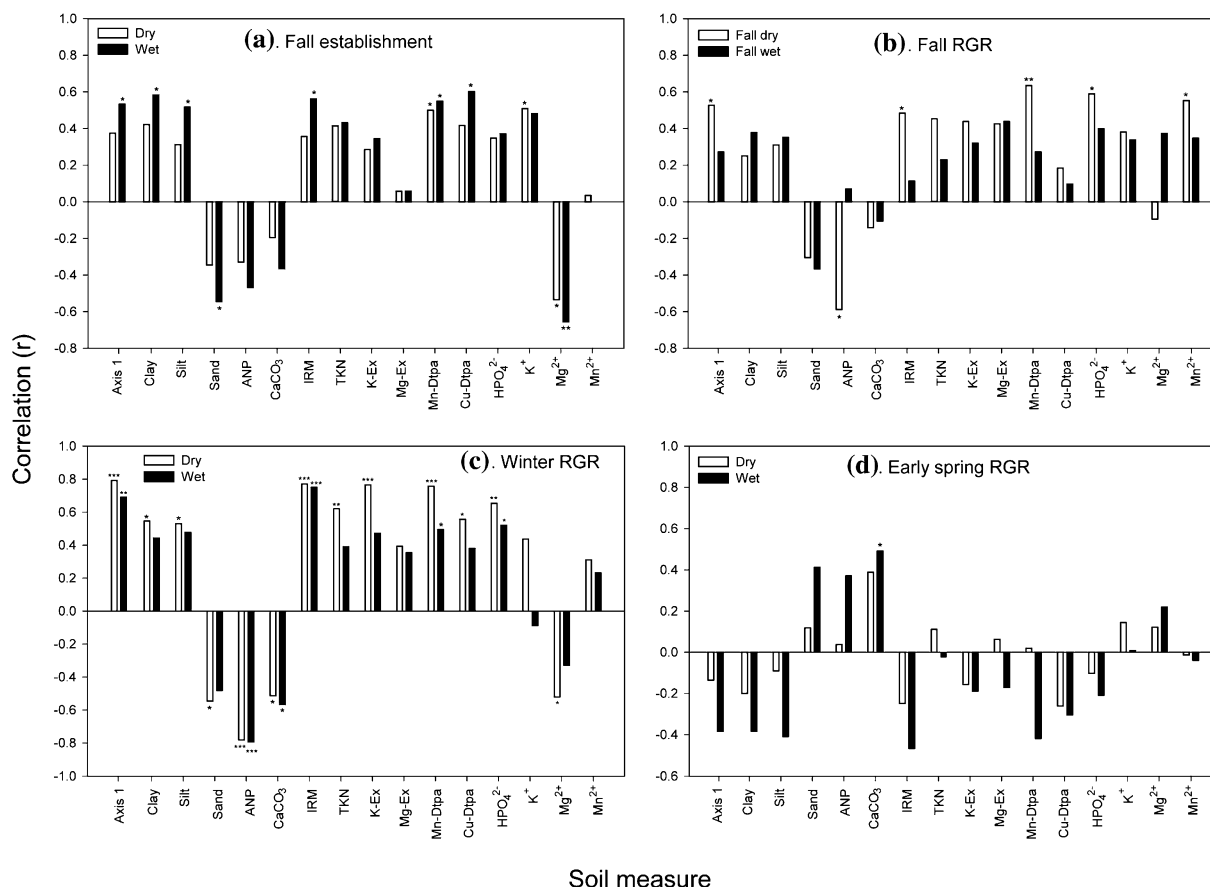


Fig. 4 Correlations (Pearson's r) of *B. tectorum* performance measures in wet and dry plots (site averages) with soil measures from 17 study sites. Asterisks indicate statistically

significant correlations (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; $n = 17$). Plots treated with MgO were excluded from the site average for dry plots in a

Of all performance measures, winter RGR was most strongly related to measured soil characteristics (Fig. 4c). Highly significant positive correlations ($P < 0.01$ or $P < 0.001$) occurred for axis 1 site scores (wet and dry plots), IRM (wet and dry plots), TKN (dry plots), K-Ex (dry plots), Mn-Dtpa (dry plots), and resin HPO₄²⁻. The correlation between winter RGR and ANP also was highly significant, but the relation was negative. Winter growth also was positively, but less strongly, related to clay (dry plots) and silt content (dry plots) and negatively related to sand (dry plots), Mg²⁺ (dry plots) and soil carbonate content (wet and dry plots).

Correlative relations of early and mid-spring RGR with soil characteristics were weaker than patterns observed for winter growth. Early spring growth was positively correlated with CaCO₃ in wet plots, but

other growth-soil correlations were insignificant (Fig. 4d). Mid-spring growth was negatively correlated with axis 1 site scores (dry plots), clay content (wet and dry plots), IRM (dry plots), K-Ex (dry plots), and HPO₄²⁻ (dry plots). Positive growth-soil correlations in mid-spring occurred for sand (dry plots), ANP (dry plots), and Mg²⁺ (wet and dry plots). Growth-soil correlations during spring tended to be directionally opposite (negative versus positive) of those observed during fall and winter.

Soil relations of June shoot length (Fig. 4f) and end-of-season whole-plot biomass (Fig. 4g) were weak but directionally similar to *B. tectorum*-soil patterns that occurred during fall and winter. June shoot length was positively correlated with Mg-Ex and Mn-Dtpa in dry plots, and end-of-season whole-plot biomass was positively correlated with Mn-Dtpa in wet plots.

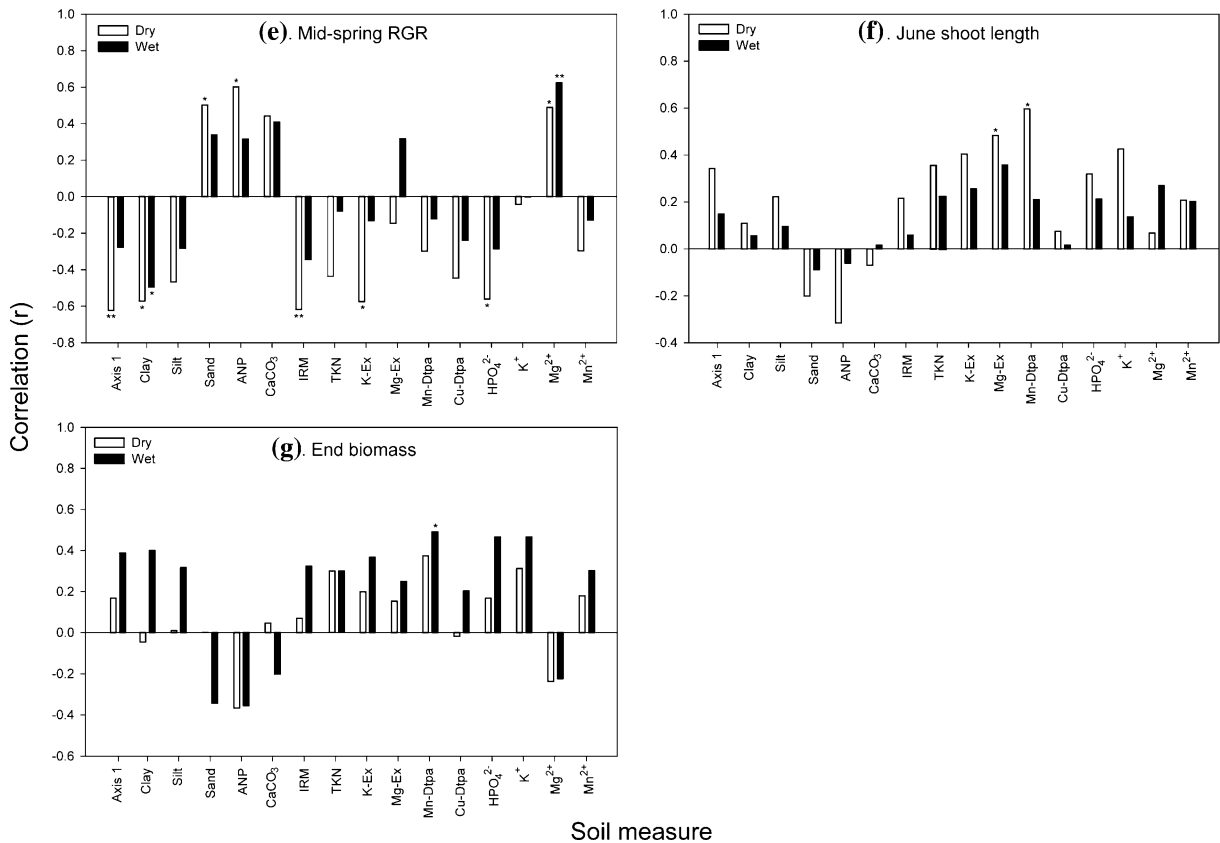


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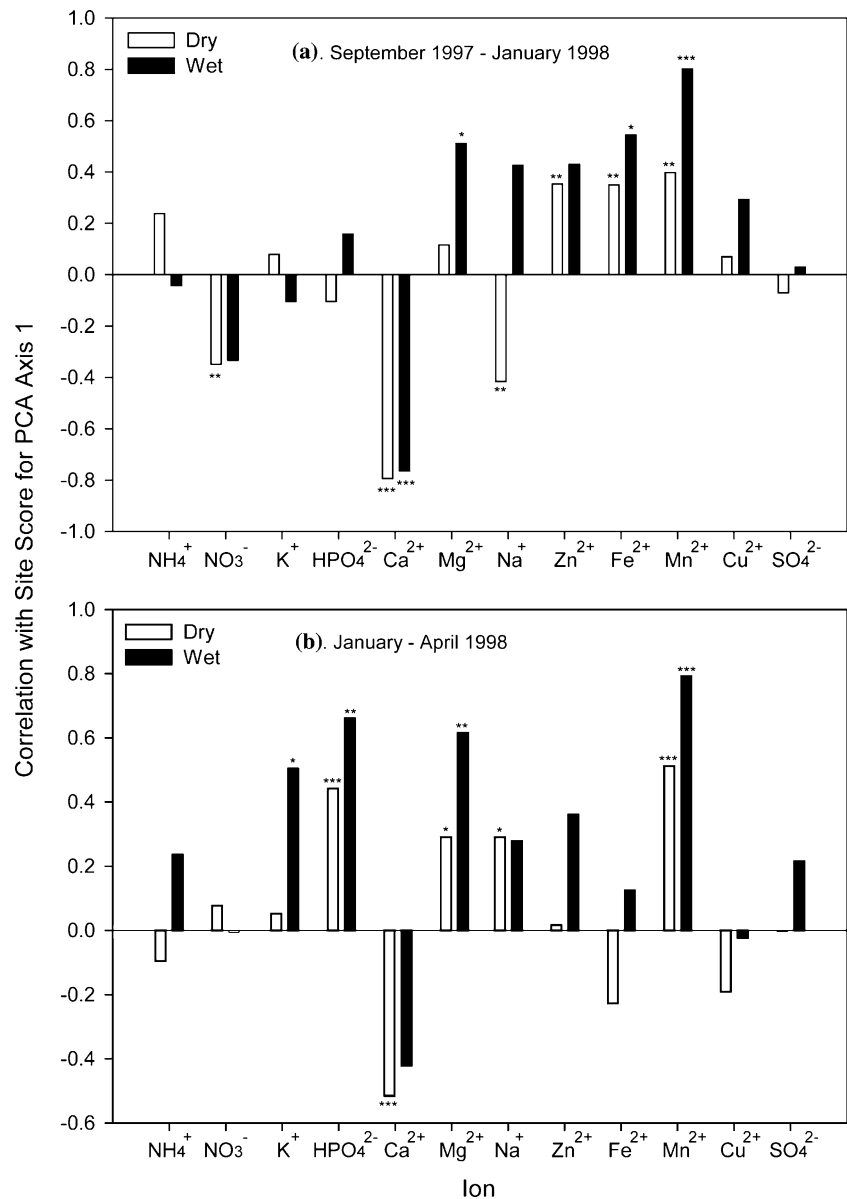
In situ resin bags

Data from resin bags in plots at five sites provide information concerning in situ nutrient dynamics in relation to site scores for PCA axis 1 (as integrated measures of site characteristics) during the fall-winter-spring *B. tectorum* growing season. During the period from mid-September 1997 through mid-January 1998, adsorption rates ($\mu\text{mol}/\text{bag}/100$ days) for Ca^{2+} (wet and dry plots), NO_3^- (dry plots) and Na^+ (dry plots) were negatively correlated with axis 1 site scores, whereas Mn^{2+} (wet and dry plots), Zn^{2+} (dry plots), Fe^{2+} (wet and dry plots), and Mg^{2+} (wet plots) were positively correlated with axis 1 site scores (Fig. 5a). During the January–April 1998 period, Ca^{2+} adsorption alone (dry plots) was negatively correlated with axis 1 site scores, whereas adsorption rates for Mn^{2+} (wet and dry plots), HPO_4^{2-} (wet and dry plots), Mg^{2+} (wet and dry plots), K^+ (wet plots), and Na^+ (dry plots) were positively correlated with axis 1 site scores (Fig. 5b).

Foliar nutrient concentrations

Figure 6 summarizes correlative relations between nutrient concentrations in *B. tectorum* leaf tissues and PCA axis 1 site scores (integrated measures of soil characteristics), winter RGR (the *B. tectorum* measure most strongly related to soil characteristics), and mid-spring RGR (*B. tectorum* growth during the period when tissues were collected). Tissue Mn was highly positively correlated ($P < 0.001$) with axis 1 site scores in wet and dry plots (Fig. 6a), consistent with the high loading of soil Mn-Dtpa on axis 1 (Fig. 1) and patterns of Mn^{2+} adsorption on in situ resin bags (Fig. 5). Tissue Mg (wet plots) and tissue N:K (dry plots) also were positively correlated with axis 1 site scores, whereas tissue K (wet and dry plots), tissue P (dry plots), tissue N (wet plots), and tissue S (wet plots) were inversely correlated with axis 1 site scores. Positive correlations between winter RGR and tissue Ca, Mg, and Mn in wet plots were highly significant ($P < 0.001$; Fig. 6b). Tissue

Fig. 5 Correlations (Pearson's r) of resin-bag ion-adsorption rates (umol/bag/100 days) with PCA axis 1 site scores during September 1997–January 1998 **a** and January–April 1998 **b**. Asterisks indicate statistically significant correlations ($*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$; $n=40$ dry plots and 20 wet plots). Plots fertilized with KCl were excluded



N:K and N:P in dry plots also were positively correlated with winter RGR, whereas tissue N (wet plots), tissue P (dry plots), and tissue Cu (dry plots) were negatively correlated with winter RGR. During the period when tissues were collected in April, *B. tectorum* RGR was positively correlated with tissue N (wet and dry plots), tissue K (dry plots), tissue N:P (wet and dry plots), and tissue K:P (wet and dry plots; Fig. 6c). Tissue Mn was inversely correlated with mid-spring RGR in dry plots. As with growth-soil correlations reported in Fig. 4, correlations of foliar nutrient concentrations with mid-spring *B. tectorum*

growth tended to be directionally opposite (negative vs. positive) of those observed for winter growth.

In Table 1, April shoot length, density, and leaf nutrient concentrations are compared between wet and dry plots at three loamy sites and at two sandy and intermediate sites. Relative to sandy and intermediate soils, loamy soils tended to have larger plants and greater plant densities in April when tissues were collected. Water application had a significant effect on mean leaf nutrient concentrations in loamy soils (MANOVA, Wilks' lambda=0.19, $F=3.8$, effect df=9, error df=8, $P < 0.05$) but not in sandy and

Fig. 6 Correlations (Pearson's r) of foliar nutrient concentrations with PCA axis 1 site scores and *B. tectorum* performance measures. Asterisks indicate statistically significant correlations (* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; $n=20$ dry plots and 10 wet plots)

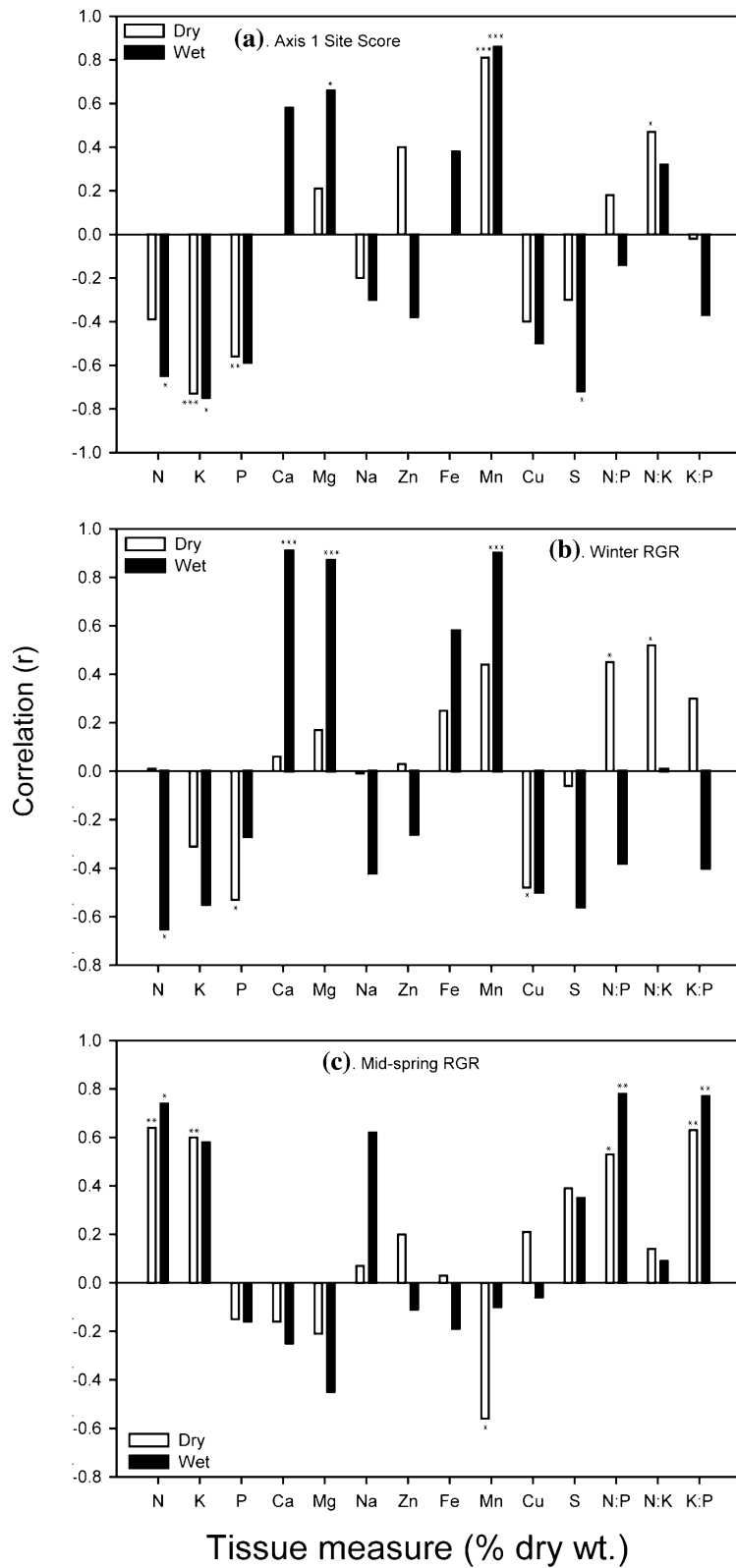


Table 1 April shoot length, density, and foliar nutrient concentrations in dry and wet plots at three loamy sites and at two sandy and intermediate sites

Measure	Loamy soils (three sites)					Sandy and intermediate soils (two sites)				
	Dry plots (n=12)		Wet plots (n=6)			Dry plots (n=8)		Wet plots (n=4)		
	Mean	CV	Mean	CV	Wet:dry	Mean	CV	Mean	CV	Wet:dry
Apr shoot length (mm plant ⁻¹)	401.5	34.6	359.9	24.8	0.90	335.5	28.1	290.0	18.6	0.86
Apr density (plants m ⁻²)	770.7	35.2	1724.8	14.4	2.24	682.4	37.8	1207.3	40.7	1.77
<u>Leaf N (% dry wt)</u>	1.929	12.9	1.839	8.8	0.95	2.232	14.1	2.126	6.2	0.95
<u>Leaf K</u>	1.157	7.3	1.186	5.9	1.02	1.449	8.8	1.464	6.9	1.01
<u>Leaf P</u>	0.066***	17.6	0.089***	9.0	1.35	0.077	9.7	0.096	5.3	1.25
<u>Leaf Ca</u>	0.369	28.5	0.328	6.7	0.89	0.357	17.0	0.294	9.3	0.82
<u>Leaf Mg</u>	0.085*	13.2	0.097*	6.4	1.14	0.082	13.1	0.084	10.0	1.02
Leaf Na	0.007	32.8	0.008	34.6	1.06	0.010	24.9	0.010	12.6	1.06
Leaf Zn	0.002	25.8	0.002	14.7	0.91	0.002	12.2	0.002	23.6	1.14
Leaf Fe	0.037	42.3	0.036	22.3	0.97	0.037	34.3	0.030	22.2	0.81
Leaf Mn	0.004	16.3	0.004	14.7	0.97	0.003	21.4	0.003	16.2	0.94
Leaf Cu	0.001	26.6	0.001	12.1	0.98	0.001	13.8	0.001	20.1	0.97
Leaf S	0.096	9.9	0.096	3.1	1.00	0.108	13.3	0.115	13.8	1.07
<u>Total measured leaf nutrients</u>	3.753	8.9	3.686	5.9	0.98	4.358	9.1	4.227	5.5	0.97
<u>Leaf N:P</u>	30.3*	25.4	20.7*	12.8	0.68	29.2	17.3	22.2	10.2	0.76
<u>Leaf N:K</u>	1.7	8.6	1.6	6.8	0.93	1.5	8.2	1.5	6.8	0.95
<u>Leaf K:P</u>	18.0**	19.3	13.4**	10.7	0.74	19.0	13.1	15.2	7.4	0.80

Effects of water on underlined leaf measures were evaluated with a one-way MANOVA; asterisks indicate significant differences between wet and dry plots by MANOVA and Tukey's HSD *post hoc* test (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). The full set of measures was not included in statistical analyses due to sample-size constraints (small number of replicates in relation to large number of measures included in MANOVA)

intermediate soils (MANOVA, Wilks' lambda=0.06, $F=3.3$, effect df=9, error df=2, $P=0.25$). Tukey's HSD test indicated that mean leaf concentrations of N, K, Ca, and total measured leaf nutrients were not different between dry and wet plots in loamy soils, but mean leaf P and Mg concentrations were significantly lower and mean leaf N:P ratios and K:P ratios were significantly higher in dry plots than in wet plots ($P=0.0008$, 0.025, 0.01, and 0.007 respectively). Wet-versus-dry trends in leaf nutrient concentrations in sandy and intermediate soils were statistically insignificant but directionally similar to those in loamy soils. Except for Ca, Mg, and Mn, mean leaf-nutrient concentrations tended to be lower in loamy soils than in sandy and intermediate soils (also see Fig. 6b).

Discussion

Results of this study suggest that resource constraints on *B. tectorum* performance in the Canyonlands area shift seasonally, from water limitation of fall establishment, to nutrient limitation of winter growth, and

back to water limitation of spring growth. Seasonal shifts in resource constraints drive spatial patterns in *B. tectorum* performance that are predictable due to effects of geomorphic processes on the distribution of key soil properties including texture and the availability of rock-derived nutrients such as Mn, P, and K.

Responses to water additions in wet plots indicate that *B. tectorum* establishment in this environment is water-limited. Thus soil and microsite factors affecting water availability to seeds and emerging seedlings can be expected to play a strong role in the generation of spatial patterns. Fall establishment was correlated with silt, clay, and several nutrient measures; but soil texture alone may explain among-soil variations in *B. tectorum* establishment through positive effects of silt and clay content on soil water-holding capacity (e.g., Fig. 2; Hillel 1998). Fall establishment was significantly correlated with silt and clay content in wet plots but not in dry plots (Fig. 4a), suggesting that texture effects are greater in wet years than in dry years because the greater water-holding capacity of loamy soils makes them more responsive to precipitation differences in terms of the amount of water they can retain

and supply to plants. Uncontrolled variables such as depth of seed burial (e.g., Evans and Young 1972) also may have masked effects of soil texture on moisture conditions experienced by *B. tectorum* seeds and seedlings in dry plots. Potassium fertilization had no effect on *B. tectorum* establishment in this study, but in a short-term laboratory experiment conducted with the same accession of *B. tectorum* seeds from CNP, K addition had positive effects on lengths of *B. tectorum* root radicles and hypocotyls over a 3-day period immediately following germination in Petri dishes (R. Morrison, pers. commun.).

Effects of MgO applications also indicate a potential role for soil chemistry in generating *B. tectorum* patterns. The only significant effect observed for any chemical amendment in this study was the large reduction in *B. tectorum* establishment in plots treated with MgO (Fig. 3). The reaction products of MgO in soil are bicarbonate and carbonate compounds (Brady and Weil 1996), and this result supports one of our initial hypotheses that soil carbonate characteristics play a role in the absence of *B. tectorum* from shallow, residual soils in the study area. Such soils possess high levels of bicarbonate and carbonate evaporites produced by weathering of underlying calcareous sandstones in winter. Additions of MgO in this study increased soil pH by 0.7–1.1 units in the top 3 cm, but effects lasted less than two months (Miller 2000). In comparison, CaO additions increased pH by 0.4–0.5 units. Because average Ca levels in soils greatly exceeded those of Mg, added MgO probably was more reactive in soils than CaO. Through increases in soil pH and ANP, MgO may have reduced establishment by inhibiting the capacity of emerging seedlings to acquire Ca-bound P or micronutrients (Tyler 1992, 1994). The significant negative correlation of resin-capsule Mg^{2+} with *B. tectorum* establishment (Fig. 4a) suggests that Mg^{2+} itself could have an adverse, ion-specific effect on establishment, but the potential mechanism is unclear. Competing cations (e.g., K^+ , NH_4^+ , Ca^{2+} , Mn^{2+} , and H^+) have been reported to decrease Mg^{2+} uptake by plants, but the opposite case has not been reported (Barber 1995; Marschner 1995). Despite large effects of MgO on establishment, this treatment had no significant effects on other measures of *B. tectorum* performance—most notably on whole-plot biomass at the end of the growing season (Fig. 3c). We interpret this latter finding as an indi-

cator of the importance of density and intraspecific competition as a factors regulating *B. tectorum* production in the study area.

This is the first study to demonstrate strong *B. tectorum*–soil relations during winter (Fig. 4c), and we attribute these patterns to nutrient limitations. Soils were persistently moist during the December–March period, with average water potentials of -0.28 and -0.47 MPa at representative sandy and loamy sites (0–10 cm depth), respectively. Moist soils and low evapotranspirational demands during this period suggest that strong spatial patterns in winter *B. tectorum* growth likely were related to among-site patterns in nutrient bioavailability rather than to direct effects of water limitations. Low-temperature conditions during winter may have induced nutritional constraints in winter-active *B. tectorum* through adverse effects on nutrient diffusion, microbial activity, and/or production of root exudates important for nutrient mobilization. Seasonal patterns of nutrient uptake are not necessarily coincident with seasonal patterns of biomass accumulation (Veresoglou and Fitter 1984), suggesting that nutritional conditions during winter may be important for subsequent stages of growth and reproduction. In annual plants, for example, a majority of the total nutrient accumulation already may have occurred by the time plant biomass reaches only 25% of its total dry-weight value (Bouma 1983). In this study, winter increases in *B. tectorum* shoot length ranged from 21% to 126%, and *B. tectorum* shoot lengths at the end of winter in March ranged from 13% to 65% of their final June values.

Winter *B. tectorum* growth was positively correlated with K-Ex, TKN, Cu-Dtpa, Mn-Dtpa, and HPO_4^{2-} , with stronger correlative relations in dry plots than in wet plots (Fig. 4c). Wet plots had higher *B. tectorum* densities than dry plots, and intraspecific competition (or facilitation, see below) associated with higher densities may have masked *B. tectorum*–soil relations evident in dry plots. Potassium is important for frost tolerance in plants (Marschner 1995), and in wet plots there was a tendency for greater winter growth in plots fertilized with KCl than in unfertilized plots. But average foliar K in April (1.28%, $n=30$) was higher than the concentration (1%) reported to be adequate for unconstrained growth in plants (Epstein and Bloom 2005). Likewise, average foliar N (2.02%, $n=30$) and Cu (11.2 ppm, $n=30$) were greater than concentrations (1.5%

and 6 ppm, respectively) reported to be adequate for unconstrained growth (Epstein and Bloom 2005). Given the design of this study, it is not possible to unambiguously determine the exact nature of winter resource constraints, but most evidence suggests limitation by Mn and/or P.

In calcareous soils, bioavailability of Mn and P are constrained due to sorption reactions with carbonates, the formation of weakly soluble carbonate or phosphate compounds, and the presence of high Ca^{2+} and HCO_3^- levels which inhibit nutrient dissolution due to common-ion effects and acid-neutralization reactions (Barber 1995; Marschner 1995). Average foliar Mn for *B. tectorum* in this study was somewhat lower (38.2 ppm, $n=30$) than the concentration reported to be adequate (50 ppm) for unconstrained growth in plants (Epstein and Bloom 2005), but 3–4 times greater than the concentration (10–14 ppm) reported to be critical for unconstrained growth of agronomic monocots (Hannam and Ohki 1988). Other studies in the region have reported Mn concentrations in *B. tectorum* tissues ranging from about 50 ppm (Ganskopp and Bohnert 2003) to 93 ppm (Blank et al. 1994).

Unlike foliar Mn which was positively related to winter growth, foliar P was inversely related to winter growth (Fig. 6b). Under conditions of extreme nutrient deficiency, increased growth caused by addition of a deficient nutrient may be accompanied by a decrease rather than an increase in the tissue concentration of that element because growth exceeds uptake (Daoust and Childers 2004; Marschner 1995). Average foliar P for *B. tectorum* in this study was 0.078% ($n=30$), less than one-half of the concentration reported to be adequate (0.2%) for unconstrained growth in plants (Epstein and Bloom 2005) and well below the value (0.16%) reported for *B. tectorum* at a comparable developmental stage at a site with soil P-Bicarb levels four times greater than those in this study (Rickard and Vaughan 1988).

In loamy soils, *B. tectorum* foliar P was significantly greater in wet plots than in dry plots, and the same trend was apparent (but statistically insignificant) in sandy soils (Table 1). Water additions may have resulted in greater P uptake by facilitating diffusion in wet plots, but an alternative hypothesis is that this difference in foliar P was caused by positive effects of plant density on the production of root exudates (e.g., organic acids) and the dissolution and bioavailability of Ca-bound P. If rhizosphere acidification (Hinsinger et al. 2003) is an

important nutrient-acquisition mechanism for *B. tectorum*, it may explain the strong inverse relation between soil ANP (an index of pH buffer capacity) and winter *B. tectorum* growth (Fig. 4c). The hypothesis that *B. tectorum* activity enhanced levels of soil-solution P is supported by data indicating an apparent tendency for greater HPO_4^{2-} adsorption on *in situ* resin bags in plots with *B. tectorum* than in plots without *B. tectorum* during winter (Miller et al. submitted). This trend was evident in wet plots but not dry plots, and was consistent for HPO_4^{2-} , Ca^{2+} , Mn^{2+} , and Mg^{2+} -ions with dynamics controlled by carbonate dissolution processes in calcareous soils. Greater plant densities in wet plots ($1724.8 \text{ plants m}^{-2}$) relative to dry plots ($770.7 \text{ plants m}^{-2}$) presumably would have been mirrored by differences between wet and dry plots in root density, exudate production, and rates of nutrient dissolution. In associated studies conducted in the Canyonlands study area, *B. tectorum*-invaded soils have been found to have greater levels of labile P than uninvaded soils in wet years but not in dry years (Belnap and Sanford unpubl.), potentially due to higher *B. tectorum* density or biomass in wet years.

Although high plant densities may have enhanced resource conditions for *B. tectorum* during winter, it appears that the opposite was true during spring. Early-spring growth was significantly lower in wet plots than in dry plots (Fig. 3b), and the most likely explanation is greater intraspecific competition in wet plots due to greater densities relative to dry plots. Water addition during the period of rapid soil–water decline increased mid-spring growth in wet plots relative to dry plots, but density effects during the period of maximum growth in early spring remained evident at the end of the season when total shoot length tended to be greater in dry plots than in wet plots. Intraspecific competition also may have contributed to the mid-spring reversal in *B. tectorum* performance when RGR patterns were opposite previous among-soil trends evident in establishment and in fall and winter growth (Fig. 3a). This mid-spring reversal also coincided with the rapid decline in soil water potential which was greater in loamy soils than in sandy soils (Fig. 2b). The inverse-texture hypothesis (Noy-Meir 1973) is regularly invoked to explain vegetation patterns in dryland environments (McAuliffe 2003), but seasonal aspects of the hypothesis have rarely been considered. In this study, *B. tectorum* performance was greatest in loamy soils during fall and winter but greatest in sandy soils during

spring, consistent with a seasonal shift in the applicability of the inverse-texture hypothesis.

Sites for this study were not selected specifically to represent a range of geomorphic settings but rather a range in pre-experiment abundances of *B. tectorum*. Geomorphic studies in this area have demonstrated the consistent occurrence of downslope trends in soil content of silt and clay, rock-derived nutrients, and measures of soil magnetic properties (e.g., IRM) along hillslope transects extending from sandstone outcrops to the bottoms of topographic basins (Neff et al. 2005; Reynolds et al. 2006). Such patterns indicate geomorphic control of ecologically significant soil properties, consistent with catena studies conducted elsewhere (e.g., Norton et al. 2003; Rosenbloom et al. 2001). Interpreting study-area soil variability within this geomorphic context, it is apparent that study sites generally were arrayed along a hillslope gradient (Fig. 2). The close relation of *B. tectorum* performance in this study (particularly establishment and winter growth) with the hillslope soil gradient described by PCA axis 1 suggests that a geomorphic framework is useful for understanding and predicting *B. tectorum* invasion patterns in dryland ecosystems of this region. The tight spatial association of IRM with laboratory soil measures linked with *B. tectorum* performance further suggests that field measures of soil magnetic properties, when calibrated to establish landscape-specific relations with measures of soil texture and nutrient content, may provide a useful means for conducting rapid assessments of site susceptibility to *B. tectorum* invasion.

Acknowledgements We thank Ann Welshko and Lean Henri for field and lab assistance, Sue Phillips for logistical support, Tina Kister and Jessica Walsh for editorial assistance, and the staff of Canyonlands National Park for their cooperation and encouragement. Comments from Jason Neff, Bob Blank, Tibor Kalapos, and two anonymous reviewers improved the quality of the manuscript. This research was funded by the United States Environmental Protection Agency (Science to Achieve Results graduate fellowship program) and the United States Geological Survey (Southwest Biological Science Center and Earth Surface Dynamics Program).

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