Components of Spatial and Temporal Soil Variation at Canyonlands National Park: Implications for P Dynamics and Cheatgrass (*Bromus tectorum*) Performance

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Abstract—From January 1997 through October 1998, research was conducted at Canyonlands National Park to investigate soil traits responsible for distinct spatial patterns of cheatgrass (*Bromus tectorum)* occurrence. Field experiments were conducted at sites representing a broad range of soil conditions and cheatgrass abundances. Standard physicochemical soil measures in combination with innovative ion-exchange resin capsules and bags were used to describe spatial and seasonal soil variations. Cheatgrass performance varied along a complex, multivariate soil gradient, with the strongest cheatgrass-soil relationship occurring during winter. Biogeochemical principles, soil measures, growth rates, and leaf-tissue analyses support the hypothesis that this complex soil gradient represents a gradient in P dynamics for cheatgrass. A seasonal increase in the solubility of carbonate and calcium-phosphate (Ca-P) compounds should theoretically occur in winter, when cold-moist soil conditions favor the reaction of CO_2 and soil H_2O to generate carbonic acid, H_2CO_3. The magnitude of this seasonal acidification phenomenon should vary spatially in relation to pH buffer capacity (acid-neutralizing potential)—an important component of soil variation that affects Ca-P dynamics. Insights concerning the significance of pH buffer capacity for P dynamics and cheatgrass nutrition have several implications for research and management.

Introduction

Distinct soil-vegetation patterns are particularly evident in arid and semiarid landscapes. In low-precipitation environments, the scarcity of water results in slow rates of weathering, leaching, and soil formation (Cooke and others 1993). As a consequence, the relative importance of parent material as a factor determining physicochemical soil properties generally increases with aridity (Birkeland 1999), and many arid-land vegetation patterns are attributable to parent-material contrasts (Whittaker and Niering 1968). In addition, geomorphic processes such as erosion and deposition can produce mosaic landscapes composed of soil patches differentiated on the basis of pedogenic age and degree of profile development. Resultant among-soil variations in profile characteristics can strongly influence vegetation patterns through effects of pedogenic horizons on spatiotemporal soil-resource dynamics (McAuliffe 1994). Distinct vegetation patterns also may result from topographic variations (for example, aspect, slope gradient, and slope position) that affect microclimate, pedogenic processes, and the redistribution of water and mineral elements among landscape units positioned along a soil catena (Birkeland and Gerson 1991).

Although vegetation patterns often are correlated with parent materials, profile development, and topography, identification of the ultimate mechanisms underlying these plant-soil relationships is more problematic and illusive. Soil variation is complex and multivariate in time and three-dimensional physical space, but most plant-soil studies focus on a very limited set of soil measures (see Hammer 1998 for critique). Because of the significance of water in arid environments, soil effects on plant water relations often are emphasized (Comstock and Ehleringer 1992). Nutritional aspects of plant-soil patterns in arid environments have received comparatively little attention, despite increasing evidence for the importance of nutrient relations on population and community dynamics in arid systems (Bilbrough and Caldwell 1997). Water and nutrient uptake by plants are not independent (Barber 1995), and Chapin (1991) has argued that the effects of low soil moisture on nutrient availability to plants may be almost as significant as the direct effects of water stress on plant performance. Additional complexity can arise from strong seasonal variations in soil conditions, such that the availability of limiting soil resources may vary asynchronously with other limiting resources or conditions as well as with plant phenology and resource demand (Bilbrough and Caldwell 1997). Complex, multi-factor variations in space and time render the elucidation of mechanistic plant-soil relationships a major challenge for ecologists.

A mechanistic understanding of plant-soil patterns is particularly important with respect to the applied problem of invasive exotic species. The prediction of potential invasion patterns as well as the ecological restoration of ecosystems degraded by invasive exotics both depend for

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their success on a solid understanding of the mechanisms underlying observed invader-environment relationships (Crawley 1987). In this paper, we examine the plant-soil mechanisms responsible for distinct spatial patterns in the distribution and abundance of the invasive exotic grass cheatgrass (*Bromus tectorum* L.) in arid landscapes of Canyonlands National Park, Utah. This research was designed to address two questions. First, what are the major components of soil variation in the study area? Second, how does cheatgrass performance vary in relation to identified components of soil variation? We approached these questions through extensive soil characterization and by conducting field experiments to assess the effects of altered soil-resource conditions on seasonal aspects of cheatgrass performance along a calcareous soil gradient.

Methods

Study Species

Cheatgrass is an autogamous winter annual grass native to Eurasia (Mack 1981). Following its introduction to North America in the late nineteenth century, cheatgrass spread to most of North America north of Mexico, with the exception of the southeastern region of the United States (Stubbendieck and others 1992). It is most abundant in the Intermountain West, where it reached its present distribution within 50 years of introduction; currently it is the most common species on >410,000 km^2 of the region (Mack 1981). Cheatgrass seeds typically germinate in response to autumn precipitation, but recruitment can occur at any time from autumn through late spring (Mack and Pyke 1983). Germination has been recorded at temperatures just above freezing (Evans and Young 1972). Seedlings have high rates of root elongation, and root growth occurs at soil temperatures as low as 2 to 3 °C (Harris 1967). Comparatively rapid winter root growth has been cited as a major factor responsible for cheatgrass' competitive advantage over native grass seedlings (Harris 1967).

Study Sites

In September 1997, 17 study sites measuring approximately 40 m x 40 m were selected at Canyonlands National Park (fig. 1). Sites were selected to represent a range in abundances of cheatgrass and the native C_3 bunchgrass Indian ricegrass (*Stipa hymenoides* R. & S). Grassland communities dominated the vegetation at all sites. In addition to cheatgrass and Indian ricegrass, other common taxa were galleta (*Hilaria jamesii* [Torr.] Benth.) and dropseeds (*Sporobolus* R. Br. spp.). All sites were located at approximately 1550 m in elevation, aspects varied, and slopes ranged from 0 to 8 percent (Miller 2000). Soils were classified as mesic Ustollic Camborthids (Begay series) and mesic Typic Torripsamments (Sheppard series) (USDA Soil Conservation Service 1991).

At each of the 17 sites, six circular ricegrass-centered plots measuring 1.2 m in diameter were established (102 plots total). Plots were centered on ricegrass clones to control for micro-scale soil conditions among the four sets of companion studies. All litter and plants including the center ricegrass were removed by hand, and plot interiors (0.8 m diameter) were seeded with 1150 cheatgrass seeds (~2300 seeds/m^2) collected at Canyonlands. Seeds were mixed by hand in the top 1 to 2 cm of soil, and plots were caged with fencing to exclude vertebrate herbivores and granivores.

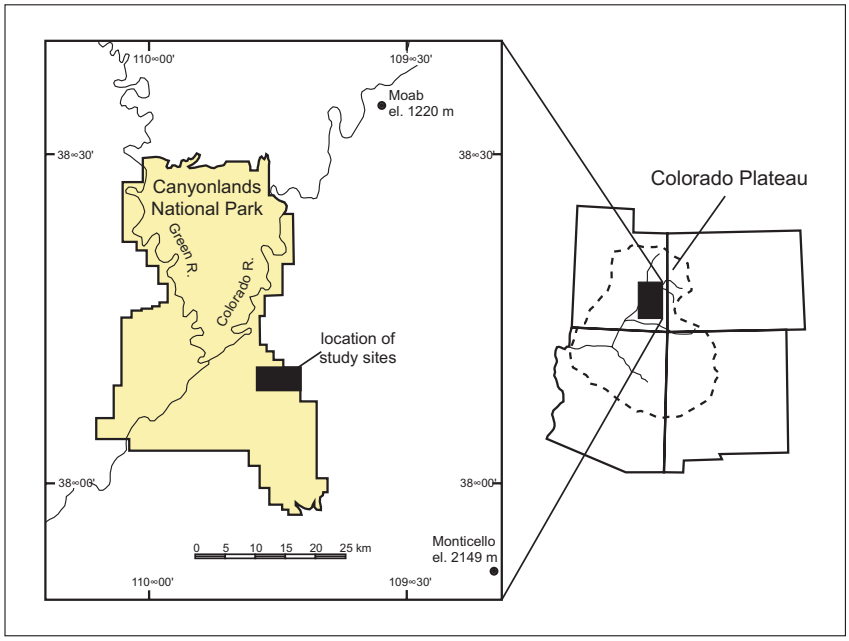

Figure 1—Map showing location of study sites in Canyonlands National Park, Utah.

Soil Measures

At each site, 10 soil samples were collected systematically with an 8-cm-diameter bucket auger from each of three depths 0 to 10, 20 to 30, and 50 to 60 cm. Samples were composited by depth, air dried, and analyzed by the Plant and Soil Analysis Laboratory at Brigham Young University (BYU) for electrical conductivity (EC), pH, cation exchange capacity (CEC), organic matter content, $NaHCO_3$-extractable P, NH_4OAc-extractable K^+ ("K-EX"), and acid-neutralizing potential (ANP) following the acid-neutralizing method of carbonate analysis described by Allison and Moodie (1965). Measurement of ANP involves reaction of a sample with dilute HCl, followed by titration to pH 7.0 with NaOH to determine the quantity of neutralized acid. In soils where the only acid-neutralizing compounds are carbonates and bicarbonates (for example, $CaCO_3$ and $Ca(HCO_3)_2$), ANP estimates soil carbonate levels. However, to the degree that soil constituents other than carbonates (for example, oxides, hydroxides, and $CaSO_4$) also react with the HCl, this measure is best viewed as a general index of the sample's total acid-neutralizing potential (Allison and Moodie 1965). ANP is the most reactive component of the soil's total acid-neutralizing capacity (ANC) as discussed by van Breemen (1983), and is conceptually analogous to pH buffer capacity (Nye 1986).

All macronutrients K^+, HPO_4^{2-}, NH_4^+, NO_3^-, Ca^{2+}, Mg^{2+}, SO_4^{2-}, and micronutrients Mn^{2+}, Zn^{2+}, Fe^{2+}, Cu^{2+}, and Na^+ were extracted simultaneously with mixed-bed (cation + anion) ion-exchange resin "capsules" (acquired from UNIBEST, Inc., P.O. Box 5095, Bozeman, MT 59717, http://www.wecsa.com/) at BYU following methods described by Miller (2000). Each manufactured resin capsule consisted of a 2-cm-diameter spherical ball with 4 ml of mixed-bed resin beads (H^+ - OH^- saturated) contained within a plastic screen mesh. Ion-exchange resin beads and membranes have been used for laboratory and in-situ nutrient measurements for over 40 years (see Skogley and Dobermann 1996 for review). The approach used here, with a simultaneous resin extraction of multiple elements from a saturated paste, has been referred to as the "phytoavailability soil test" (PST) (Skogley and Dobermann 1996). The PST provides an integrated index of nutrient bioavailability because it is sensitive to ion activities in the soil solution, as well as to ion diffusion and other soil properties that are important components of soil nutrient buffering capacity (Skogley and others 1990).

Soils were analyzed by the U.S. Geological Survey (USGS) Central Region Geology Laboratory, Denver, for particle size, carbonate content, and magnetic susceptibility. Particle size was measured with a Malvern laser particle sizer following the removal of carbonates and organic material by acid digestion. Carbonate content was determined gasometrically by measuring the volume of evolved CO_2 produced by reacting a sample with acid (Dreimanis 1962). Magnetic susceptibility (MS) measurements were conducted with a susceptometer. MS is a rapid, non-destructive measure that provides an index of the concentration of magnetic grains in a sample (Mullins 1977). Among-soil variations in MS have been interpreted to result from pedogenic processes (Singer and Fine 1989) or aeolian deposition of silt-sized particles bearing magnetic minerals (Reynolds and King 1995; Hanson 1999).

To assess in-situ nutrient dynamics, at five sites four nylon-mesh bags containing 10 g of moist, mixed-bed ion-exchange resins (H^+ - Cl^- saturated) were buried in all experimental plots at depths of 5 to 10 cm (Lajtha 1988). Ion-exchange resin bags were first placed at the beginning of experimentation in January 1997 and were replaced seasonally thereafter (approximately 3-month intervals). After replacement, exposed resin bags were extracted with HCl and analyzed for macro- and micronutrients at BYU.

Cheatgrass Measures

Cheatgrass 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. Fall establishment was estimated in December by counting the number of live plants occurring in a rectangular 250-cm^2 quadrat frame aligned with each of the four cardinal directions in each plot (1000 cm^2 sampled per plot). Ten individual plants per plot (1020 total) were marked with numbered sticks in late October. Total leaf lengths (sheaths plus blades) of all marked plants were measured to the nearest mm, averaged to obtain a single measure per plot per growth period, and used to calculate relative growth rates (mm/mm/day). In spring, foliar tissues were collected from plants in a subset of plots. Tissues were air dried, ground, and analyzed at BYU for tissue concentrations (percent dry weight) of mineral elements following wet digestion. At the end of the growing season, above-ground tissues were harvested, air dried, and weighed to obtain total biomass per plot.

Statistical Analyses

To describe among-site soil variation, 40 soil variables were analyzed by principal components analysis (PCA) with varimax factor rotation (Kent and Coker 1992). Included in the analysis were soil measures from 0 to 10 cm, total profile values for macro- and micronutrients (sum of resin-capsule values for 0 to 10, 20 to 30, and 50 to 60 cm samples within a single core), and the surface:depth ratio for ANP (0 to 10 cm:50 to 60 cm ratio), the latter measure providing an index of profile development. Simple linear correlation (Zar 1999) was used to assess relationships between seasonal measures of cheatgrass performance and spatial components of soil variation identified through PCA. All statistical analyses were conducted using the software package STATISTICA™ v5.5 on a PC platform (StatSoft 1999).

Results

Soil Variation

Table 1 summarizes selected soil characteristics of the 17 study sites considered together as a group. In general, study area soils were sandy and calcareous. Soil ANP tended to be slightly higher and more variable than carbonate content, suggesting the presence of acid-neutralizing compounds in addition to carbonates. Soils had low organic-matter (OM) content, low CEC, and low levels of $NaHCO_3$-extractable P. Resin-capsule data indicated that Ca^{2+} was the most active cation in the soil environment, with values 8-9 times higher

Table 1—Descriptive statistics for selected soil characteristics of 17 study sites at Canyonlands National Park, Utah.

Variable (units)	Mean	Min.	Max.	s.d.	CV[a]
0 to 10 cm					
Acid-neutralizing potential (% $CaCO_3$ equiv.)	7.35	4.41	11.03	2.08	28.27
Carbonate content (% $CaCO_3$ equiv.)	6.45	5.02	8.20	1.02	15.80
Magnetic susceptibility (m^3/kg x 10^{-8})	7.26	2.59	14.83	3.94	54.27
Coarse sand (%)	15.26	7.70	24.23	4.48	29.33
Fine sand (%)	70.74	61.93	77.60	4.06	5.74
Total sand (%)	86.01	77.30	90.38	3.86	4.49
Silt (%)	9.97	6.03	17.00	3.07	30.80
Clay (%)	4.02	2.83	5.74	0.89	22.10
pH	7.50	7.17	7.99	0.22	2.96
EC (dS/m)	0.38	0.28	0.46	0.05	13.10
CEC ($cmol_c$/kg soil)	4.52	1.74	8.74	1.82	40.21
Organic matter (%)	0.26	0.04	0.42	0.10	40.73
K-EX (ppm)	168.46	86.92	323.60	61.49	36.50
$NaHCO_3$-P (ppm)	7.98	4.02	14.34	2.43	30.45
K (μmol_c/capsule)	39.64	23.42	61.80	10.15	25.60
HPO_4 (μmol_c/capsule)	10.87	4.91	18.02	4.46	41.01
NH_4 (μmol_c/capsule)	14.40	6.51	21.49	5.22	36.25
NO_3 (μmol_c/capsule)	2.79	0.33	6.18	1.82	65.23
Ca (μmol_c/capsule)	990.55	491.03	1973.42	423.64	42.77
Mg (μmol_c/capsule)	111.48	40.92	252.39	63.54	57.00
SO_4 (μmol_c/capsule)	27.66	15.98	48.88	10.14	36.65
Mn (μmol_c/capsule)	2.00	0.84	3.63	0.95	47.75
Zn (μmol_c/capsule)	0.25	0.10	0.64	0.15	59.26
Fe (μmol_c/capsule)	4.90	3.41	6.73	1.06	21.61
Cu (μmol_c/capsule)	0.12	0.06	0.20	0.04	35.27
Na (μmol_c/capsule)	9.25	1.79	16.08	5.30	57.36
Surface:depth (0 to 10 : 50 to 60 cm)					
Acid-neutralizing potential	0.76	0.32	1.07	0.21	27.59
K	1.20	0.47	2.50	0.61	50.67
HPO_4	2.73	1.21	8.14	1.55	57.00
NH_4	1.33	0.54	3.00	0.68	50.89
NO_3	1.72	0.14	10.01	2.33	135.47
Ca	0.94	0.41	2.28	0.40	42.52
Mg	1.05	0.54	2.31	0.38	36.37
SO_4	0.89	0.18	2.08	0.37	41.77
Mn	2.28	0.86	5.28	1.13	49.66
Zn	1.37	0.45	3.05	0.64	47.16
Fe	1.08	0.75	1.37	0.18	17.04
Cu	1.19	0.70	1.91	0.31	25.97
Na	1.20	0.02	7.21	1.62	134.94
HPO_4:Ca	3.06	1.52	6.99	1.50	49.07
Mn:Ca	2.69	1.01	7.23	1.68	62.31

[a]CV = coefficient of variation (100*s.d./mean).

(on a charge basis) than Mg^{2+}, the second most active cation. Together, these two accounted for approximately 94 percent of measured cation charges. Of the measured anions, SO_4^{2-} was the most active. Measured anions reported in table 1 provided less than 5 percent of the charges required to balance measured soil cations. Based on water analysis (Miller 2000), it is probable that HCO_3^- was the major charge-balancing anion in the soil.

Surface:depth ratios in table 1 indicate several soil-profile trends. On average, ANP, Ca^{2+}, and SO_4^{2-} tended to increase with depth whereas K^+, HPO_4^{2-}, N, and micronutrients tended to have higher values at the surface than at depth. HPO_4^{2-}:Ca^{2+} and Mn^{2+}:Ca^{2+} ratios also tended to be much higher at the surface than at the 50 to 60 cm depth. NO_3^- levels were extremely variable in the sampled profiles. Of the single-ion measures, average, minimum, and maximum surface:depth ratios were greatest for HPO_4^{2-} and Mn^{2+} (with the exception of the maximum value for NO_3^-), indicating a strong tendency for resin-extractable P and Mn both to be concentrated at the soil surface.

The first four axes derived from the PCA of soil variables explained 62 percent of the variation in the analyzed data set (table 2). Variables with highly significant ($p<0.01$) positive loadings for the first axis included 0 to 10 cm carbonate content, HPO_4^{2-}, Ca^{2+}, Mg^{2+}, SO_4^{2-}, Mn^{2+}, and Na^+; and total-profile HPO_4^{2-}, Ca^{2+}, Mg^{2+}, and Mn^{2+}. The second PCA axis was characterized by high positive loadings for 0 to 10 cm ANP and sand content, as well as for the ANP surface:depth ratio. Variables with high negative loadings for axis II included 0 to 10 cm MS, percent silt and clay, CEC,

Table 2—Summary of the first four axes derived from principal-components analyses (PCA) of soil data describing 17 study sites at Canyonlands National Park, Utah. For surface:depth variables, only significant correlations are reported.

	PCA Axes			
	I	II	III	IV
Proportion of variation explained	**0.23**	**0.17**	**0.13**	**0.09**
Variable correlations (loadings for included variables)				
0 to 10 cm				
Acid-neutralizing potential	0.18	0.78***	–0.22	–0.14
Carbonate content	0.86***	0.22	0.15	0.11
Magnetic susceptibility	–0.24	–0.91***	0.07	–0.07
Coarse sand	0.17	0.48	–0.10	–0.08
Fine sand	0.02	0.25	0.06	0.37
Total sand	0.21	0.82***	–0.05	0.30
Silt	–0.13	–0.82***	0.09	–0.28
Clay	–0.44	–0.71***	–0.08	–0.31
pH	–0.16	–0.12	0.17	0.81***
EC	–0.25	–0.30	–0.06	–0.21
CEC	–0.34	–0.74***	–0.13	–0.17
Organic matter	0.09	–0.56*	0.50*	0.11
K-EX	–0.10	–0.88***	–0.12	0.11
K	0.39	–0.35	0.33	0.66**
HPO_4	0.63**	–0.14	0.45	0.05
HPO_4:Ca[1]	–0.33	–0.78***	0.12	0.06
NH_4	0.22	–0.04	0.91***	0.19
NO_3	–0.40	0.20	0.40	–0.03
NH_4+NO_3	0.07	0.03	0.93***	0.16
Ca	0.65**	0.18	0.37	0.03
Mg	0.91***	0.27	–0.01	0.15
SO_4	0.70**	0.17	0.35	0.05
Mn	0.85***	0.17	0.14	0.03
Mn:Ca[1]	0.58*	–0.01	–0.19	0.01
Zn	0.40	0.19	0.12	0.81***
Fe	0.30	0.21	0.14	0.02
Cu	0.44	0.13	0.48	0.15
Na	0.75***	0.02	0.46	–0.07
Total profile sum (sum 0 to 10, 20 to 30, and 50 to 60 cm)				
K	0.37	0.19	0.25	0.68**
HPO_4	0.71***	0.06	0.33	0.13
NH_4	0.44	–0.07	0.66	0.14
NO_3	–0.07	0.01	0.58	0.06
NH_4+NO_3	0.33	–0.06	0.70***	0.13
Ca	0.70**	0.16	0.23	0.18
Mg	0.86***	0.30	–0.05	0.20
SO_4	0.42	0.10	0.28	0.05
Mn	0.88***	0.32	0.06	0.07
Zn	0.08	0.32	0.06	0.79***
Fe	0.46	0.26	0.33	0.14
Cu	0.36	0.15	0.44	0.27
Na	0.14	0.04	0.25	–0.05
Surface:depth ratio (0 to 10 : 50 to 60 cm ratio)				
Acid-neutralizing potential	0.31	0.76***	0.25	–0.17
K[1]	–0.38	–0.68**	0.03	0.13
HPO_4:Ca[1]	–0.33	–0.80***	–0.23	0.07
NH_4[1]	–0.26	0.09	0.52*	0.27
Ca[1]	0.03	0.13	0.53*	–0.26
Mn[1]	–0.36	–0.51*	0.10	–0.06
Mn:Ca[1]	–0.40	–0.69**	–0.33	0.14
Zn1	0.37	0.08	0.30	0.74***

[1]Not included in PCA; * p <0.05; ** p <0.01; *** p <0.001

K-Ex. Other soil measures that were significantly inversely correlated with axis II (though not included in the PCA) were the 0 to 10 cm HPO_4^{2-}:Ca^{2+} ratio, as well as surface:depth ratios for K^+, HPO_4^{2-}:Ca^{2+}, and Mn:Ca^{2+}. Correlations of surface:depth HPO_4^{2-} with PCA axes were highly influenced by a single outlier. Removal of the outlier also resulted in a significant inverse correlation of surface:depth HPO_4^{2-} with axis II ($r = -0.71$, $p < 0.05$). Variables with highly significant loadings for axis III were 0- to –10-cm and total-profile NH_4^+ and NH_4^++NO_3^-. The fourth axis was characterized by high loadings for 0- to –10-cm pH, K^+, and Zn^{2+}, as well as total-profile K^+ and Zn^{2+}. The surface:depth ratio for Zn^{2+} also was correlated with axis III, although not included in the PCA.

Cheatgrass performance measures were most highly and consistently correlated with axis II (table 3). Performance also was correlated with axis IV, though to a lesser degree. A plot of significant soil variables in relation to these two PCA axes shows that axis II can be conceptualized as a complex soil gradient (fig. 2). At one end of the conceptual soil gradient (high axis-II scores) were sandy sites characterized by high ANP and high surface:depth ANP. Maximum surface:depth ANP in the data set was 1.07 (table 1), indicating a lack of profile differentiation at that end of the gradient. At the other end of the conceptual gradient (low axis-II scores) were sites with higher silt and clay content, as well as greater CEC, K-EX, OM, and HPO_4^{2-}:Ca^{2+} values at 0 to 10 cm. At this extreme of the gradient, low surface:depth ANP was associated with high surface:depth HPO_4^{2-}:Ca^{2+}, K^+, Mn^{2+}, and Mn^{2+}:Ca^{2+}. These measures, all indicative of profile differentiation, tended to covary with MS in 0 to 10 cm soils. Variations in profile differentiation along the conceptual gradient were consistent with taxonomic identity. Soils with differentiated profiles generally were classified as Camborthids, whereas soils without profile differentiation generally were classified as Torripsamments (USDA Soil Conservation Service 1991).

Cheatgrass Performance

Figure 3 summarizes seasonal variations in cheatgrass performance in relation to selected soil variables and PCA axes II and IV. Net cheatgrass establishment in fall was greatest at relatively fine-textured sites with low ANP and high HPO_4^{2-}:Ca^{2+} values. Among-soil patterns in fall growth rates tended to parallel establishment patterns. Winter (early December to mid-March) growth rates varied linearly along the conceptual soil gradient described by PCA axis II (Pearson's $r = -0.78$, $p < 0.001$, table 3). It was during this 3-month winter period that the greatest relationship of cheatgrass performance to measured soil variation was found, with the highest growth rates found in low-ANP, fine-textured soils. Relative growth rates increased markedly in early spring, but sites with the highest winter growth rates consistently had the lowest growth rates during both the early and mid-spring periods (Miller 2000). Spring growth was greatest at sites that were intermediately positioned along PCA axis II and high on PCA axis IV (fig. 3). By the end of the growing season, whole-plot biomass tended to be greater at these intermediate sites, but the biomass difference between sites where cheatgrass performed best during fall and winter and sites where cheatgrass performed best during spring was statistically insignificant (Miller 2000).

Data from resin bags in plots at selected study sites provide information concerning in-situ nutrient dynamics during the fall-winter-spring cheatgrass growing season. During the January to April winter period when cheatgrass performance varied inversely with soil ANP and PCA axis II, resin-bag Mn^{2+}, HPO_4^{2-}, K^+, and Mg^{2+} also varied inversely with soil ANP (fig. 4). Ca^{2+} and Fe varied positively with ANP during this period, and correlations of NH_4^+ and NO_3^- with ANP were insignificant (fig. 4).

In figure 5, leaf-tissue nutrient concentrations for cheatgrass in this study are compared with concentrations reported for cheatgrass in shrubsteppe environments of south-central Washington (Rickard and Vaughan 1988), values for the native winter-annual grass sixweeks fescue (*Festuca octoflora* Walter) in sandy, calcareous soils of southeastern Utah (Belnap and Harper 1995), and average mineral contents reported to be adequate for unrestrained plant growth (Epstein 1965, cited in Marschner 1995). Average tissue N (2.02 percent) and K (1.28 percent) for cheatgrass in this study were higher than or similar to values reported for cheatgrass in Washington, sixweeks fescue in Utah, and average values for unrestrained plant growth. In contrast, concentrations of the carbonate-related minerals P (0.08 percent), Ca (0.35 percent), Mg (0.09 percent), and Mn (0.004 percent) all were lower in this study than in the comparative data sets. Of these, P content was the lowest in comparison with concentrations reported elsewhere. Tissue Fe (0.04 percent), N:P, and K:P documented in this study all tended to be much higher than comparative values.

Table 3—Correlation coefficients (Pearson's r) describing relationships among cheatgrass performance measures and axes I to IV derived from principal components analyses of soil characteristics, Canyonlands National Park, Utah. Performance measures used in the analyses were site averages with all manipulative treatments combined (n = 17). (RGR = relative growth rate.)

	PCA Axes			
Performance measure	**I**	**II**	**III**	**IV**
Net fall establishment	–0.38	–0.51*	0.31	0.02
RGR, Oct. to Dec.	0.15	–0.53*	–0.12	–0.07
RGR, Dec. to Mar.	–0.40	–0.78***	0.14	0.17
RGR, Mar. to Apr.	0.38	0.10	0.03	0.55*
RGR, Apr. to May	0.44	0.49*	0.11	0.34
End-of-season biomass	0.06	–0.35	0.10	0.44

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

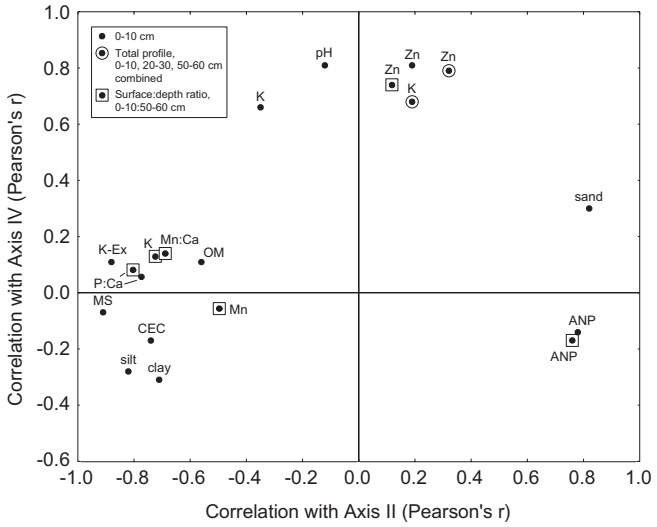

Figure 2—Plot of soil variables significantly correlated with PCA axes II and IV, Canyonlands National Park.

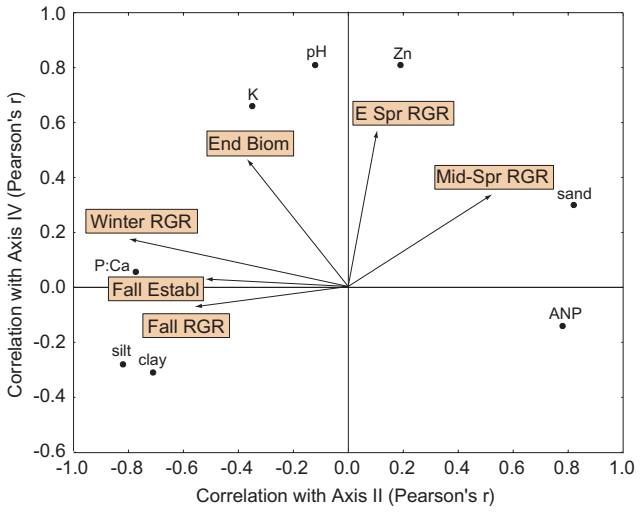

Figure 3—Vector plot illustrating correlations of seasonal cheatgrass measures with soil PCA axes II and IV, Canyonlands National Park.

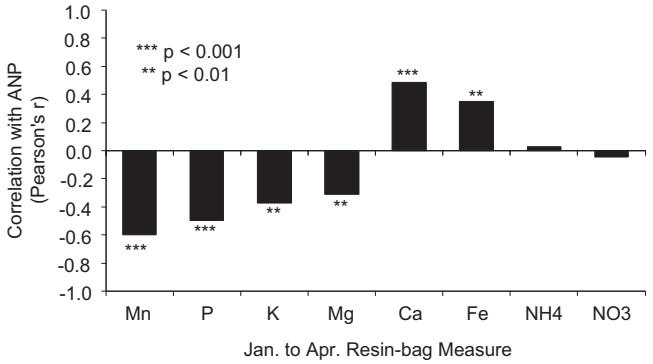

Figure 4—Correlations of in-situ resin-bag measures with soil acid-neutralizing potential, January to April 1998, Canyonlands National Park.

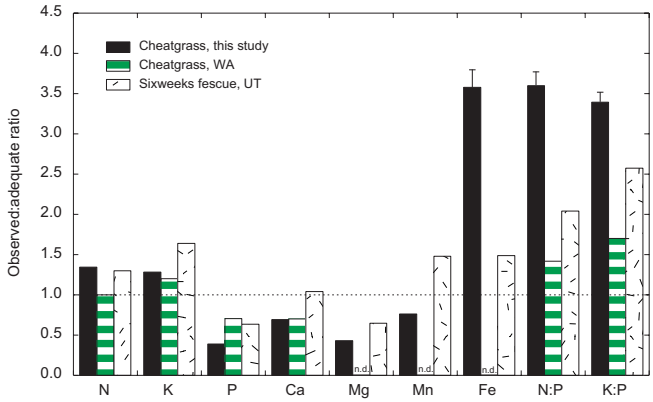

Figure 5—Comparison of average mineral contents of cheatgrass at Canyonlands National Park (this study) with those of cheatgrass in shrubsteppe environments of south-central Washington (Rickard and Vaughan 1988) and those of the native annual grass sixweeks fescue (*Festuca octoflora*) in southeastern Utah near Canyonlands (Belnap and Harper 1995). Values on the y-axis were derived by dividing observed mineral contents by average mineral contents reported to be adequate for unrestrained plant growth (Epstein 1965, cited in Marschner 1995). For cheatgrass in this study, error bars extend 1 SE above means (n = 30).

Discussion

Results presented here demonstrate the complex, multivariate nature of soil variation and plant-soil relationships. Cheatgrass-soil relationships varied by season and performance measure, but the most significant pattern occurred during the 3-month December to March period when cheatgrass growth varied strongly in relation to PCA axis II. Winter growth varied positively with 0 to 10 cm silt and clay content, CEC, K-Ex, MS, and resin-capsule HPO_4^{2-}:Ca^{2+}, whereas growth varied inversely with both 0 to 10 cm and surface:depth ANP. Which of these variables, either alone or in combination, best explains winter variations in cheatgrass growth along the conceptual soil gradient described by PCA axis II?

CEC is considered an important component of soil fertility (Brady and Weil 1996). In this study, CEC and K-EX both covaried with silt and clay content, consistent with the pattern observed for most soils (Brady and Weil 1996). However, with the important exceptions of NH_4^+ and K^+, the availabilities of most nutrient cations (Ca^{2+}, Mg^{2+}, Mn^{2+}, Cu^{2+}, Zn^{2+}, Fe^{2+}) to plants in calcareous soils are likely to be more strongly influenced by carbonate reactions (including sorption, desorption, precipitation, dissolution, and pH buffering) than by ion-exchange properties of soil colloids (Knight 1991). On the basis of resin-capsule data, it can be inferred that Ca^{2+} and Mg^{2+} together occupied approximately 94 percent of the exchange sites on soil colloids. Resin bags buried at five study sites indicated that in-situ NH_4^+

adsorption did not vary in relation to CEC or axis II during winter. In-situ K^+ was weakly correlated with CEC and axis II during the winter period, but KCl additions did not enhance cheatgrass performance during any period (Miller 2000). These observations suggest that variations in CEC and K-Ex cannot alone explain winter variations in cheatgrass performance along axis II. MS, because it simply serves as a proxy indicator of variations in aeolian silt content (Reynolds and King 1995; Hanson 1999) and/or pedogenic profile development (Singer and Fine 1989), by itself cannot provide a mechanistic explanation for spatial variations in cheatgrass performance.

In contrast with CEC, K-Ex, and MS, ANP can provide a mechanistic explanation for winter variations in cheatgrass performance due to the importance of rhizosphere acids for plant nutrition in calcareous soils. Chemical conditions in the rhizosphere are known to be drastically different than bulk-soil measures as a consequence of biotic processes (Hinsinger 1998). In calcareous soils, solubilities of nutrients P, Mn, Zn, and Fe typically are low due to one or more of the following interrelated geochemical factors: (1) sorption reactions with carbonate minerals, (2) the formation of insoluble Ca and/or carbonate compounds, and (3) the presence of high Ca^{2+} and HCO_3^- levels which further inhibit nutrient dissolution due to common-ion effects and/or acid-neutralization reactions (Barber 1995). Rhizosphere acidification due to the combined activities of roots, mycorrhizal symbionts, and associated rhizosphere microbes is a common means by which nutrient dissolution and acquisition can be enhanced in calcareous soils (Hinsinger 1998). Rhizosphere acidification most often is caused by protons excreted to balance uptake of cations such as NH_4^+ and Ca^{2+} (Haynes 1990), but respiratory CO_2 also can be an important acidification mechanism through its reaction with H_2O to form carbonic acid, H_2CO_3 (Hinsinger 1998).

The generation of H_2CO_3 in the soil environment depends on (1) the partial pressure of CO_2, (2) soil water content, and (3) CO_2 solubility in H_2O (Krauskopf and Bird 1995). CO_2 solubility in H_2O, like that of other gases, is greater at cold temperatures than at warm temperatures (Krauskopf and Bird 1995). Thus, all else being equal, H_2CO_3 formation in the soil environment should exhibit a seasonal increase during winter when soils are moist and cold. Cheatgrass also exhibits considerable below-ground growth during winter (Harris 1967), presumably producing respiratory CO_2, enhancing rhizosphere H_2CO_3 generation, and facilitating the dissolution and acquisition of carbonate-bound nutrients.

The enhancement of nutrient dissolution and acquisition due to rhizosphere H_2CO_3 generation is a temporal phenomenon, and the magnitude of this temporal phenomenon should vary spatially in relation to soil characteristics. The major soil properties influencing soil susceptibility to plant-induced rhizosphere acidification are initial soil pH and soil pH buffer capacity (Marschner and Römheld 1996), the latter measured here as ANP. Rhizosphere pH, which cannot be measured from bulk soil samples, is strongly dependent on pH buffer capacity (Marschner and Römheld 1996). Accordingly, ANP or other indices of pH buffer capacity should be more widely applied in studies of plant-soil relationships because they describe a dynamic, plant-relevant soil property that cannot be inferred from static pH measurements alone. Measured pH can vary due to differences in soil texture (as it effects soil water capacity), salt concentrations, and technique; pH buffer capacity can vary widely among soils in which pH varies only slightly (van Breemen and others 1983; Bache 1984).

Data from in-situ resin bags and leaf tissues suggest that the conceptual soil gradient associated with ANP and PCA axis II was a gradient in P and Mn bioavailability for cheatgrass. Resin-bag HPO_4^{2-} and Mn^{2+} covaried in relation to PCA axis II and ANP similar to the among-site pattern observed for winter cheatgrass growth. Although average tissue P and Mn concentrations for cheatgrass in this study both were lower than "adequate" levels reported by Epstein (1965, cited in Marschner 1995), Mn concentrations were 3 to 4 times greater than those "critical" for growth of agronomic monocots (Hannam and Ohki 1988). DeLucia and others (1989) found experimentally that cheatgrass was P-limited in hydrothermally altered soils possessing $NaHCO_3$-extractable-P levels similar to those found in Canyonlands soils. Thus the evidence suggests that PCA axis II, in association with ANP, primarily was a gradient in P limitation for cheatgrass.

Conclusions

Findings of this study emphasize the complex nature of plant-soil interactions and the importance of temporal plant-soil dynamics for understanding spatial plant-soil patterns. Cheatgrass performance varied along a complex, conceptual soil gradient characterized by variations in particle size, acid-neutralizing potential (pH buffer capacity), exchangeable K, and several profile indices indicative both of pedogenesis and of plant-soil feedbacks. Cheatgrass-soil relationships were strongest during winter when relative growth rates were inversely correlated with acid-neutralizing potential and positively correlated with silt and clay content and exchangeable K. Biogeochemical principles, as well as evidence from in-situ resin bags, tissue chemistry, and experimental manipulations of K availability suggest that this conceptual soil gradient primarily was a gradient of P limitation for *Bromus*. We hypothesize that spatial variations in soil acid-neutralizing potential affected the degree to which P dissolution and acquisition were enhanced in winter by the formation of carbonic acid in cold, moist soils. The complex space-time dynamics described here indicate the need for ecological plant-soil studies to expand and investigate a broader range of resources and relationships.

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