2013

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Published April 30, 2013

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We tested the performance of Plant Root Simulator (PRS) probes as a tool to determine plant nutrient availability across the semiarid environments of the central Rocky Mountains. We used PRS probes in a lab-field comparison representing the climatic and physiographic complexity in a high-elevation watershed in the Wasatch Range, northern Utah. We determined soil nutrient supply rates for 10 selected soils in the lab at two soil temperatures (5 and 25°C) and three moisture levels (10, 30, and 50% volumetric soil moisture content), and compared them to nutrient pools and field nutrient supply rates. Using two independent techniques, simple regressions and principal component analysis (PCA) ordination, we concluded that soil moisture content was the most important driver of nutrient supply, while incubation temperature had no influence, and nutrient pool sizes were generally poor predictors of nutrient supply rates. Lab supply rates correlated well with field PRS results. Therefore, lab PRS assays can serve as a reasonable substitute for the field use and can be beneficial for large-scale comparison of nutrient supply rates among semiarid wildland ecosystems of the western United States.

Abbreviations: CRF, coarse rock fraction; PCA, principal component analysis; PRS probes, Plant Root Simulator; SMC, soil moisture content.

Together with climate, land physiography, and geomorphology, soil properties play an important role in plant species distributions by creating soil fertility gradients, and in habitat (site) quality by affecting plant productivity (Schoenholtz et al., 2000). There are multiple ways to assess plant nutrient availability via (i) relatively static soil nutrient pools (classic lab assays, extractions, and soil analyses), (ii) measurement of nutrient fluxes (bio assays, incubations, and lysimetry), and (iii) measurement methods that simulate or approximate nutrient diffusion to and uptake by plant roots (exchange resins) (see Johnson et al., 2005). Among the latter techniques, Plant Root Simulator probes (Western Ag Innovations Inc., Saskatoon, Canada), a combination of anion and cation exchange membranes encapsulated in a plastic device, simulating a plant root surface, is frequently used in situ or under lab conditions (Qian and Schoenau, 1997; Schoenau et al., 1993; Qian and Schoenau, 2002).

The use of PRS probes has become a standard tool in forest ecology to assesses anion and cation supply rates, especially in production forestry, for example, for the prediction of fertilization response of trees and to determine soil fertility of mesic environments (Hangs et al., 2003, 2005; Huang and Schoenau, 1996, 1997; Jerabkova and Prescott, 2007; Switzer et al., 2012). They have also been used in the study of nonforest wildland systems (Drohan et al., 2005; Lantz et al., 2009; Andrew et al., 2012). Their use, however, has remained limited in arid and semiarid conditions (e.g., Qian and Schoenau, 2002).

Soil Sci. Soc. Am. J. 77:1057–1062
doi:10.2136/sssaj2012.0432n
Received 21 Dec. 2012.
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Interpreting field PRS results in seasonally dry systems such as semiarid mountainous environments of the central Rocky Mountains may not be straightforward as nutrient supply rates may differ considerably in space and time, that is, among environmentally different sites (ecosystems) and as a result of temporally fluctuating climatic conditions (e.g., snowy winters vs. dry summers), expressed in terms of soil temperature and moisture (Kusbach, 2010; Kusbach et al., 2012). Plants derive their nutrients largely from the solution phase, and soil nutrient supply capacity is controlled by the combined effect of (i) available nutrient pools in terms of total reserves and their relative mobilization (e.g., weathering, desorption, microbial turnover, and solubilization); (ii) the ability of plants to access nutrients (i.e., their conversion to soluble forms, movement through the soil from the source to a plant root, or fine root distribution); and (iii) potential competing sinks such as microorganisms or other plant roots which might decrease supply rates (Johnson et al., 2005; Binkley and Fisher, 2012). Seasonally dry conditions may thus preclude nutrient diffusion at some sites or particular times, while other sites may stay moist longer (north-facing slopes in higher elevations) and even wet (riparian strips and wetlands) (Kusbach, 2010). This makes intersite comparisons of nutrient availability in semiarid areas challenging, especially when the sampling area is spatially extensive and complex in physiography. Use of PRS probes in the field thus becomes logistically difficult as it is nearly impossible to synchronize their burial periods. Such slight offset in the timing of the burial period and concomitant climatic conditions may introduce unknown differences in nutrient supply rate estimates among seasonally dry sites.

We performed combined field and lab assays using PRS probes to compare nutrient supply rates among montane wildland ecosystems in northern Utah. The overarching goal in this study was to gain better insight into plant nutrient availability across the complex semiarid environment of the central Rocky Mountains. Specifically, we (i) determined important drivers of nutrient supply rates and (ii) assessed whether lab assays using PRS probes under controlled conditions are a reasonable, reliable, and more practical alternative to field deployment of PRS probes.

MATERIALS AND METHODS

Study Area

As our study area we chose the Franklin Basin, an ecologically heterogeneous montane-subalpine watershed (20,000 ha) situated between the Bear River Range and the Wasatch Range in the central Rocky Mountains on the Utah and Idaho border (Kusbach, 2010). The mean annual air temperature ranges from 2.4 to 5.7°C, and mean annual precipitation ranges from 720 to 1250 mm for the Temple Fork, Tony Grove Lake, Franklin Basin, and Utah State University Doc Daniel SNOwpack TELemetry (SNOTEL) weather stations (http://www.wcc.nrcs.usda.gov/snow/). Most of the annual precipitation (78%) falls in the form of snow from October through April.

The terrain is mountainous, rocky, and steep with occasional flat to gently sloping high ridge plateaus and benches. The elevation ranges from 1590 to 3060 m. The highest area of the Bear River Range was glaciated during the Pleistocene as manifested by glacial geomorphologic features (Degraff, 1976). The area is mostly built from calcareous sedimentary rocks (limestone and dolomite) with interlayered quartzite and from Tertiary sediments consisting of grit, conglomerate, and siltstone of the Wasatch Formation. The soils are formed in residuum, colluvium, alluvium, glacial till, and outwash and occur on diverse landforms such as cliffs, talus slope, moraines, karst valleys, mountain slopes, landslides, plains, valleys, depressions, ravines, and wetlands (Schoeneberger et al., 2002).

Over half of the study area is occupied by forest ecosystems including Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.], Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], aspen (*Populus tremuloides* Michx.); woodland ecosystems including mountain mahogany (*Cercocarpus ledifolius* Nutt.) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.); and riparian, mostly willow (*Salix* spp.) ecosystems. Nonforested ecosystems include willow-riparian communities, shrublands (*Artemisia* spp.), meadows, and grasslands, which may represent stable or temporary communities. Despite human impacts in last 120 yr, the study area is considered as relatively natural in terms of plant species composition (Bird, 1964).

Data Collection

The original field experiment encompassed a total of 163 sites distributed across the study area, expected to represent major vegetation cover types and also complex and contrasting environmental and soil conditions. We focused on mature, late-successional, and relatively stable plant communities and tried to avoid ecotones as well as degraded or atypical stands. One soil pit was dug in each sample plot to the unweathered parent material or permanent water table and described following practices and terminology of the National Cooperative Soil Survey (Schoeneberger et al., 2002; Soil Survey Staff, 1999, 2006). One composite soil sample (0–30 cm) was collected from a pedon face in each plot, air-dried, and sieved (<2 mm), and the fine fraction analyzed for texture using the feel-method (Thien, 1979) and for pH (1:1 soil in water) using a Corning pH analyzer. Nutrient pool "snapshots" (exchangeable K, Ca, Mg, and extractable Fe, S) were determined by soil extraction with 1 M NH_4Cl at pH 7.0 using a mechanical vacuum extractor (Holmgren et al., 1977) and analysis of the extractant using an inductively coupled plasma spectrophotometer (Iris Advantage, Thermo Electron, Madison, WI). Extractable P (PO_4) was determined by the Olsen P method (Olsen et al., 1954) using a spectrophotometer (Spectronic 20 Genesys, Thermo Electron, Madison, WI). Total mineralizable (inorganic) N was determined from 7-d anaerobic incubation and extraction with 2 M KCl (Keeney and Bremmer, 1966) followed by NH_4 analysis (Lachat Quickchem 8000, Loveland, CO). Extractable NH_4–N was determined by extraction

with 2 M KCl and NH_4 analysis (Lachat Quickchem 8000, Loveland, CO). Total C and N concentrations were determined with a LECO CN analyzer (LECO Corp., St. Joseph, MI). We did not measure NO_3 pools in the field.

Four PRS probe pairs were buried vertically into the mineral soil surface at each field site for 6 wk in fall (mid-September through mid-November). We opted for this burial period as a compromise between logistical constraints (i.e., snow pack accumulation from mid-October through mid to late June severely restricts site access) and a likelihood of capturing nutrient movement during fall (i.e., drier periods with low nutrient diffusion, typically until mid-October, transitioning into moist fall conditions before snowpack when diffusion is more likely). Six weeks of burial was chosen as a reasonable limit to avoid exceeding the membranes' adsorption capacity. Upon retrieval, PRS probes were thoroughly cleaned by deionized water, placed into labeled plastic bags, and sent to Western Ag Innovations for extraction and analysis of NH_4–N, NO_3–N, PO_4–P, K, Ca, Mg, Fe, and S. Four blank PRS probe sets (i.e., four anion and four cation membranes not in contact with soil) were included in the design to track potential procedural contamination. Blanks values were subtracted from measured rates to obtain nutrient supply rates for each plot.

For the field-lab PRS comparison, 10 soil samples were selected among these 163 sites to represent contrasting vegetation, environmental, and soil conditions (Table 1). Forty milliliters of air-dried soils were placed in 50-mL plastic tubes incubated at two temperatures (5 and 25°C) and three soil moisture levels: air-dry, 10% volumetric soil moisture content (SMC); field capacity, 30% SMC; and saturated, 50% SMC, after adding the appropriate amount of water (i.e., 4 mL, 12 mL, and 20 mL, respectively) with a pipette to each tube. Two pairs of PRS probes (2 anion probes + 2 cation probes) were used for each of 6 temperature and moisture levels per soil, that is, for a total of 240 incubation tubes for 10 selected soils. All tubes were sealed by a transparent tape to prevent water evaporation and incubated for 1 wk, after which the PRS probes were carefully removed from tubes, thoroughly cleaned by deionized water, placed into labeled plastic bags, and analyzed by Western Ag Innovations as described above. Four blank PRS probe sets were included in the design to track potential procedural contamination, and nutrient supply rates were obtained as described above.

Data Analysis

Several steps were taken in the analysis: (i) PCA of the field PRS nutrient supply rates for the entire data set (163 sites) and for the subset of 10 sites to determine between-site variability and ascertain representativeness of the 10 sites selected; (ii) analysis of the role of soil temperature, SMC, and nutrient pools on nutrient supply rates using simple regression and PCA of lab supply rates for ($N = 60$); and (iii) comparison of lab with field supply rates to evaluate to what extent the lab measurements can be used as an alternative to field measurements ($N = 20$).

In the PCA, orthogonal rotations and correlation type of a cross-products matrix were used to get independent, mutually uncorrelated principal components PCs (Lattin et al., 2003). We transformed the factors and variables with |skewness| > 1 to be close to multivariate normality, standardized the data by adjustment to standard deviate (z-scores), and checked the data set for outliers (either factors or plots) using a cutoff of 2.0 standard deviations from the grand mean (McCune et al., 2002). Significance of PCs was tested by a Monte Carlo randomization test based on proportion-based *p* values and the broken-stick eigenvalue for each PC (McCune and Mefford, 2011). To document the relationship of the variables with the PCs and interpret PCs, we calculated correlation coefficients (loadings) with each ordination axis, and the linear (parametric Pearson's *r*) and rank (nonparametric Kendall's *tau*) relationships between the ordination scores and the observed variables. Our use of *r* and *tau* is suggested to be, even in relatively small data sets,

Table 1. Site characteristics associated with the 10 soils selected for the lab experiment.

Site	Community†	Elevation	Aspect	Slope	O hor depth	A hor depth	Soil depth	Parent material‡	Texture§	CRF¶	pH	Major horizons	Soil classification#
		m	azimuth °	%	——— cm ———					%			
1	ABLA	2390	350	45	8	4	150	t	l	30	6.1	A,E,Bt	Typic Haplocryalf
2	ABLA	2155	45	19	6	19	100	t	l	35	6.1	A, AE, E Bt	Xeric Haplocryalf
3	PSME	2400	320	58	7	20	50	l	c	30	6.5	A, Bt, Cr	Lithic Haploxeroll
4	NF	2820	155	9	0	5	10	q	s	90	5.7	A, R	Lithic Cryorthent
5	POTR	2390	250	7	0.1	50	120	c	c	10	6.3	A, AE, Btg	Pachic Palecryoll
6	CELE	2340	135	75	1	20	10	l	l	80	7.5	A, R	Lithic Cryorthent
7	CELE	2375	225	53	1	20	25	l	l	70	7.9	A, R	Lithic Cryorthent
8	NF	2380	210	50	0	10	<10	q	s	80	5.8	A, R	Lithic Cryorthent
9	PSME	1830	280	17	6	10	150	c × t	l	15	6.4	A, AE, Bt	Pachic Palecryoll
10	POTR	2600	250	42	0.1	38	100	l	c	15	6.6	A, AE, E, Bt	Pachic Palecryoll

† ABLA, subalpine fir (*Abies lasiocarpa*); PSME, Douglas-fir (*Pseudotsuga menziesii*); POTR, Aspen (*Populus tremuloides*); CELE, curlleaf mahogany (*Cercocarpus ledifolius*); NF, nonforested, rocky-quartzite.

‡ Parent material: t, till; l, limestone; q, quartzite; c, colluvium.

§ Texture: l, loamy; c, clayey; s, sandy.

¶ Coarse rock fragment content (>2 mm).

Soil Survey Staff (2006).

more conservative than p values for the null hypothesis of no relationship between ordination scores and variables (McCune et al., 2002). We set the threshold for r and *tau* >0.4.

In the regression analysis, we regressed soil temperature, SMC and nutrient pools (total N; extractable NH_4–N; inorganic N, extractable P; extractable cations K, Ca, Mg, Fe; and S), that is, predictors, against nutrient supply rates, that is, responses. Data were power- and/or log-transformed when necessary to achieve close-to-normal distributions of nutrient frequencies. In the last step, we compared lab vs. field PRS results by regressing lab supply rates on field supply rates for all macronutrients. We used R software v. 2.15.0. (http://www.r-project.org/) for regressions and PC-ORD 6 (McCune and Mefford, 2011) for PCA.

RESULTS

The PCA of the entire field data set (163 sites) reduced dimensionality to three significant PCs ($p < 0.001$), explaining respectively, 27, 15, and 13% of total variance: PC1 was associated with metals (e.g., Zn) and inorganic N (Nmin); PC2 with cations (e.g., Mg, Ca:, Mn, K:); and PC3 with inorganic N (NO_3) and K. The 10 soils selected for the lab experiment (Table 1) were evenly distributed across the ordination space and thus reflected heterogeneity of the environmental and soil conditions (data not shown).

The PCA of the field data from the 10-site subset reduced dimensionality to two significant PCs ($p = 0.02$, $p < 0.001$), with PC1, associated with metals (e.g., Al), inorganic N (NH_4) and P, explaining 33% of total variance; and PC2, associated with cations (e.g., Mg, Ca, K) and inorganic N (NO3), explaining 28% of variance. Interpretation of the gradients and numerical outputs of PCA for the entire data set and subset were very close, providing further evidence that the 10 selected soils were good representatives of the environmental complexity of the study area.

In the lab experiment, incubation temperature (5 vs. 25°C) did not influence soil nutrient supply rates (Table 2), with one exception, Fe at 50% volumetric SMC. For most nutrients, nutrient supply rates were significantly and positively correlated with SMC, irrespective of incubation temperature. Correlations were not significant for K, inorganic N, and NO_3–N at 25°C (Table 2). For most nutrients, total extractable nutrient pools as determined in this study were not good predictors of nutrient supply rates (Table 2). Only for PO_4–P did lab supply rates

Table 2. Response of lab supply rates of various nutrients to temperature at three moisture levels, soil moisture content at two temperature levels, and nutrient pool at three soil moisture levels across the different soil types.

Supply rate	Soil temperature				Soil moisture				Extractable nutrient and inorganic N pool				Total N pool			
	SMC†	N	Adj. R^2	p	Temp†	N	Adj. R^2	p	SMC	N	Adj. R^2	p	SMC	N	Adj. R^2	p
	%				°C				%				%			
NH_4–N	10	20	−0.03	0.300	5	30	0.51	**<0.001**‡	10	20	0.00	0.319	10	20	0.01	0.296
	30	20	−0.01	0.400	25	30	0.22	**<0.001**	30	20	−0.06	0.938	30	20	0.05	0.163
	50	20	0.01	0.300					50	20	0.01	0.308	50	20	0.16	**0.047**
NO_3–N	10	20	0.05	0.200	5	30	0.12	**0.030**	10	20	NA	NA	10	20	0.04	0.209
	30	20	−0.07	0.300	25	30	−0.01	0.400	30	20	NA	NA	30	20	−0.01	0.352
	50	20	0.10	0.090					50	20	NA	NA	50	20	0.17	**0.039**
Inorganic N,	10	20	0.06	0.200	5	30	0.18	**0.010**	10	20	0.10	0.100	10	20	0.01	0.308
NH_4+NO_3	30	20	0.00	0.300	25	30	0.02	0.500	30	20	−0.04	0.600	30	20	−0.03	0.488
	50	20	−0.05	0.700					50	20	0.05	0.200	50	20	0.02	0.262
PO_4–P	10	20	−0.05	0.800	5	30	0.44	**<0.001**	10	20	0.23	**0.020**				
	30	20	0.00	0.300	25	30	0.34	**<0.001**	30	20	0.42	**0.001**				
	50	20	−0.03	0.500					50	20	0.51	**<0.001**				
K	10	20	−0.04	0.600	5	30	0.11	**0.040**	10	20	0.01	0.300				
	30	20	−0.05	0.700	25	30	0.00	0.300	30	20	0.03	0.200				
	50	20	−0.04	0.600					50	20	−0.01	0.400				
Ca	10	20	−0.03	0.500	5	30	0.72	**<0.001**	10	20	−0.05	0.700				
	30	20	0.05	0.200	25	30	0.64	**<0.001**	30	20	−0.02	0.500				
	50	20	−0.05	0.800					50	20	0.42	**0.001**				
Mg	10	20	−0.05	0.800	5	30	0.44	**<0.001**	10	20	0.14	0.060				
	30	20	−0.04	0.600	25	30	0.43	**<0.001**	30	20	0.28	**0.010**				
	50	20	−0.02	0.500					50	20	0.66	**<0.001**				
Fe	10	20	−0.02	0.400	5	30	0.60	**<0.001**	10	20	−0.02	0.500				
	30	20	0.05	0.200	25	30	0.74	**<0.001**	30	20	0.09	0.110				
	50	20	0.70	**<0.001**					50	20	−0.05	0.734				
S	10	20	0.05	0.200	5	30	0.77	**<0.001**	10	20	0.01	0.280				
	30	20	−0.05	0.800	25	30	0.57	**<0.001**	30	20	−0.02	0.449				
	50	20	−0.01	0.400					50	20	0.10	0.091				

† SMC, soil moisture content; Temp, temperature.

‡ Statistically significant p values at the level 0.05 are in bold.

follow extractable pool sizes across all SMC levels (Table 2). The Ca and Mg supply rates were more responsive to changes in exchangeable pools at higher SMC (50% for Ca and 30–50% for Mg); while exchangeable pools were poor predictors of supply rates for these nutrients under drier conditions. The KCl-extractable NH_4–N, mineralizable N (measured as NH_4 in anaerobic incubation), and total N were poor predictors of inorganic N supply rates. Correlations of nutrient supply rates vs. nutrient pools stratified by temperature yielded similar results as stratification by SMC and are not presented here.

The PCA of the lab supply rates across six temperature and two SMC levels for the 10 soils ($N = 60$) reduced dimensionality of the lab data set to two significant PCs ($p < 0.001$). PC1, explaining 49% of total variance, was associated with SMC and most of the metals (Mn, Fe, Al) and macronutrients (S, Ca, P, Mg, NH_4) while PC2, explaining 15% of variance, was associated with inorganic N (NO_3). The numerical outputs of the PCA and data visualization (not shown) confirmed that incubation temperature (5 vs. 25°C) did not influence soil nutrient supply rates, as convex hulls for both temperatures overlapped at each SMC level. The latter caused a significant separation of the data along one axis (PC1), supporting the strong influence of SMC on nutrient supply rates. Moreover, the 30% SMC level appeared to be a broad category spanning the majority of the PC1 moisture gradient and overlapping with both 10 and 50% SMC, which represented smaller discrete spaces. Consequently, lab PRS nutrients supply rates at 30% SMC ($N = 20$) were used to test against field PRS data for the 10 sites (Table 3). We generally found positive relationship between lab and field nutrient supply rates with correlations statistically significant for all macronutrients (N, except NH_4; P; K; Ca; Mg; S).

In addition, we performed a PCA on the lab supply rates for two temperature at 30% SMC ($N = 20$). PC1, explaining 36% of total variance, was associated with soil P, S, K. and Al, representing a P-K-S gradient (tightly associated with soil acidity). PC2, explaining 32% of variance, was associated most significantly with inorganic N and NO_3, and also with Ca and Mg, and representing mainly a nitrogen supply gradient. The numerical outputs and PCA visualization showed lab supply rates broadly separated by ecosystem type (data not shown).

DISCUSSION AND CONCLUSIONS

Our PCA analyses showed that the a priori selection of the subset of 10 soil samples adequately represented the broad environmental, edaphic, and ecosystem gradient presented in the field. Across this data set, regression analysis supported by multivariate statistics (PCA) revealed the importance of SMC over temperature on nutrient supply rates determined through PRS probes. These results were consistent with lab assays conducted by Johnson et al. (2005) and field observations by Verburg et al. (2009) for inorganic N in tallgrass prairie. Similarly to the Johnson experiment, KCl-extractable soil N was a poor predictor for inorganic N (NH_4, NO_3 and NH_4+NO_3) supply rates. This is not surprising, as extractions are static snapshots that represent a single condition in time and space, whereas N availability is temporally and spatially variable (i.e., hot spot and hot moments [Johnson et al., 2010]). Furthermore, results for inorganic N (both NH_4–N and NO_3–N) may also be affected by short-term storage of samples and by potential turnover of organic N during that time (Van Miegroet, 1995). The lack of agreement between net N mineralization and PRS data for inorganic N is more puzzling as both are dynamic indicators of N turnover and were performed on the same soil samples. The role of nutrient pool size on measured supply rates was not unequivocal. This suggests that for some nutrients (e.g., N, K, Fe, and S) other conditions may be critically limiting (e.g., SMC for Ca and Mg) or may control relationship between nutrient abundance (general presence) and availability (presence in solution), such microbial mineralization-immobilization (for N, S), chelation (for Fe), precipitation (Ca, S), or biological competition (for N [Johnson et al., 2010]).

The agreement between the lab assays and the field measurements indicated that the environmental variability across a complex landscape in the field (e.g., different local topography, soil properties, and vegetation cover) and the differences in nutrient supply that can result from these differences were well captured under more controlled and convenient lab conditions. Field assays can seldom be totally synchronized, and if significant SMC differences emerge as a result of unequal burial time, nutrient supply rates may consequently differ. Drohan et al. (2005) also found that lengthening burial times in the field beyond 1 mo may cause desorption and readsorption of nutrients, further confounding the PRS results. By using laboratory assays, we can avoid technical and logistic difficulties of obtaining supply rates from wide-scale landscape environments and remote areas, we can determine nutrient supply rates over a relatively short time period following field campaigns, and we can limit confounding local factors, such as plant and microbial competition and hotspots sensu Johnson et al. (2010, 2011).

A post hoc PCA of the lab PRS data indicate that the different ecosystems, represented by the 10 samples (Table 1), were well distributed and clearly separated in the nutrient gradient space (PC1: P, K, S; PC2: inorganic N) (not shown). This represents a

Table 3. Summary of regressions of lab on field PRS probes macronutrient supply rates for 10 different soil types.

Supply rate	N	Adj. R^2	p	Equation
NH_4–N	20	0.01	0.377	$y = -0.0041x + 0.3091$
NO_3–N	20	0.75	**<0.001**†	$y = 1.0408x^{0.9661}$
Inorg. N, NH_4+NO_3	20	0.72	**<0.001**	$y = 0.1134x^2 + 0.0118x + 2.0484$
PO_4–P	20	0.41	**0.002**	$y = 0.6636x - 0.0622$
K	20	0.88	**<0.001**	$y = -0.0244x^2 + 0.6076x + 0.8636$
Ca	20	0.16	**0.040**	$y = 3E\text{-}06x^2 - 0.0095x + 37.204$
Mg	20	0.62	**<0.001**	$y = -4E\text{-}06x^2 + 0.0056x + 3.7028$
S	20	0.37	**0.002**	$y = 0.3091x^2 - 0.6196x + 1.8369$

† Statistically significant p values at the level 0.05 are in bold.

true difference in soil fertility and site quality among the sample sites, as relatively acidic and less fertile ecosystems (subalpine fir, Douglas-fir, nonforested, and rocky-quartzite) are clearly separated from more alkaline and fertile ecosystems (aspen and curlleaf mahogany) (Kusbach, 2010; Kusbach et al., 2012). Thus, our lab PRS results were able to discern environmental and vegetation differences in the landscape.

Additional work is needed to extend and test the results on larger data set, for example, for more nonforested ecosystems and more extreme soils such as on willow wetlands, subalpine tall-forb meadows, or sagebrush steppe. Besides the spatial scale of soils, the range of lab conditions (temperature, moisture) could be also expanded below 5 and above 25°C.

From our lab experiments we conclude that at the study sites temperature was not an important control of biologically or geochemically mediated nutrient supply rates. Among the factors investigated, SMC came out as the strongest driver of nutrient supply rates. Even large nutrient pools were insufficient to provide significant supply rates at lower SMC. Nutrient pools per se exerted a limited influence on nutrient supply rates, except at SMC levels sufficient for nutrient movement through diffusion. The PRS probes use in the lab can serve as a fast, practical, economical, and reliable substitute for the field use in semiarid mountainous environments such as those encountered in the central Rocky Mountains.

ACKNOWLEDGMENTS

This research was supported in part by the Utah State University Ecology Center, Western Ag Innovations Inc., and the Utah Agricultural Experiment Station and approved as journal paper no. 8445. We thank anonymous reviewers for invaluable help in improving the paper.

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