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Temporal dynamics of soil spatial heterogeneity in sagebrush-wheatgrass steppe during a growing season

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Abstract

Variability in five soil resources essential for plant growth (NH_4^+, NO_3^-, P, K and soil moisture) was quantified using univariate, multivariate and geostatistical techniques in a sagebrush-grass steppe ecosystem at three times (early April, June and August) during the 1994 growing season. Samples were collected every meter in a 10 × 10-m 'macrogrid', every 20 cm within nested 1 × 1-m 'minigrids', and every 3 cm within additionally nested 15 × 15-cm 'microgrids'. Strong autocorrelation for all variables in the three sample periods was only found over distances less than 2 m, indicating that patches of high internal uniformity in this soil were smaller than 2 m during the growing season. Differences in semivariograms between sample periods were most pronounced for NO_3^-, NH_4^+ and soil moisture, variables that we consider to primarily limit plant growth in this system. The distance over which sample points were autocorrelated for NO_3^-, NH_4^+ and soil moisture increased from April to June. In contrast P and K, which are relatively more abundant at the study site, exhibited relatively constant semivariance patterns over the three sample periods.

Weak correlation was found between samples collected in the three sample periods for N and soil moisture indicating that the spatial pattern of these limiting resources changed between sample periods. However, P and K had highly significant correlations ($p < 0.00001$) among sample periods, indicating that the distributional patterns of these relatively more abundant resources remained rather constant. There were strong negative correlations between P and K and distance from the base of shrubs for all sample times ($p < 0.001$), indicating an increase in P and K close to shrubs. Similar strong negative correlations were not found between distance from the shrubs and levels of NH_4^+, NO_3^-, or soil moisture, nor for any soil variable and distance from perennial tussock grasses. Changes in patterns of nutrient and soil moisture variability within a growing season suggest that not only must plants acquire soil resources that vary in time and space, but that they may also have to adjust to different scales of resource patchiness during the season.

Introduction

Heterogeneity in soil properties has been suggested as a contributor to coexistence of plant species (Grime, 1979; Palmer, 1992) and also is thought to affect the composition of plant communities (Tilman, 1988). Differences in the spatial and temporal distribution of nutrient transformation and consumption processes result in soil patches of differing concentrations, and the resistance to diffusion and mass flow between regions of high and low concentration contributes to maintenance of patches (Stark, 1994). Interactions between nutrient pool size and transport rates of nutrients in the soil have been hypothesized to be a significant factor in the coexistence of species (Huston and DeAngeles, 1994).

Heterogeneity in the soil has been described in scales ranging from the landscape level to the neighborhoods of a few individual plants. Assessments of such soil heterogeneity have been conducted at scales of tens of meters and extending to whole landscapes (Stark, 1994), where spatial variability in soil characteristics has been related to community composition and ecosystem structure (see e.g. Milne, 1992; Palmer, 1992; Urban et al., 1987). Recently, attention has been directed to describing heterogeneity in the soil at the scale of individual plant neighborhoods. Geostatistical procedures (Burgess and Webster, 1980; Rossi et al., 1992) have been employed by Halvorson et al. (1995), Jackson and Caldwell (1993a, b) and Smith et al. (1994) to quantify the extent of patches and variability of soil nutrients at scales of decimeters around individual and among groups of plants in shrub-steppe vegetation. In some cases this includes descriptions of nutrient enrichment in the immediate proximity of larger shrubs and tussock grasses, sometimes called 'islands of fertility'. These analyses were conducted only once in the growing season, during periods of active plant growth.

The nutrient status of a soil patch is affected by interactions of a variety of factors including plant cover (Chariey and West, 1975; Hook et al., 1991; Vinton and Burke, 1995), plant species composition (Jackson and Caldwell, 1993b; Vinton and Burke, 1995), microbial activity (Smith et al., 1994), and soil temperature and moisture content (Stark, 1994). Since factors having the largest influence on soil nutrients may vary over the growing season, nutrient pool size of soil patches may change depending on which factors are most significant at a particular time (Stark, 1994). In addition, the dynamics of pool size may be different for nutrients limiting plant growth or microbial activity than for those that are not limiting.

In this study we quantify variability in five soil resources essential for plant growth in substantial quantities, NH_4^+, NO_3^-, P, K and soil moisture, in a sagebrush-wheatgrass steppe ecosystem at three times (early April, June and August) during the 1994 growing season. During this season, soil moisture was high in April, but no appreciable precipitation occurred from the April sample period through the August sample period. In this steppe ecosystem, N and soil moisture are considered limiting to plant growth (Caldwell, 1985; Dobrowolski et al., 1990). Available P is often quite low in Great Basin soils owing largely to the calcareous soils (Caldwell et al., 1985); however at this site, perhaps because of the noncalcareous nature of the soil, both available P and K are relatively more abundant than N or soil moisture (see e.g. Jackson and Caldwell, 1992) and are likely less limiting to plant growth. A nested sampling scheme was used to assess concentrations of these resources in grids with points separated by 3 cm, 20 cm and 1 m. Geostatistics were used to aid in assessing patch extent and the association with individual plants. Correlation analysis was used to assess changes in patch nutrient concentrations over the course of the growing season.

Materials and methods

The study site was located on a nearly level lacustrine bench formed in ancient Lake Bonneville 8 km northeast of Preston, Idaho (42° 9′ N, 111° 50′ W, 1500 m elev.). The study area was covered by a mixture of big sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle) and crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult.) that had not been grazed for at least 10 years. The sagebrush were approximately 30 years old and covered approximately 37% of the ground, while the perennial wheatgrass occurred in scattered tussocks covering 13% of the ground. Sagebrush averaged 100 cm in height, and 70 cm in diameter. In April, patches of the low-statured and shallow-rooted bulbous bluegrass (*Poa bulbosa* L.) were scattered in the open soil between the bases of sagebrush and wheatgrass, but by June the plants were already senescent. Only a few scattered individuals of other herbaceous plant species were found within the site. Formed from noncalcareous lacustrine deposits of high terraces of ancient Lake Bonneville, soil at the site was Parleys silt loam to a depth over 150 cm (unpublished soil survey, U.S. Natural Resource Conservation Service, Preston, Idaho, USA), containing minimal rock fragment and characterized by moderate permeability and high water-holding capacity (Chugg et al., 1968). The soil pH at the site ranged from 5.8 to 7.2. The level aspect of this site precluded significant uneven moisture accumulation within the site, and this, combined with fine and uniformly textured soils, limited the potential for resource heterogeneity owing primarily to topography and different parent soils.

Samples were collected in April (early in growing season), June (peak of growing season) and August (late in growing season). A 10 × 10-m 'macrogrid' was established near the center of a 100 × 50 m tract of sagebrush-wheatgrass vegetation. One-meter grid lines were marked with stakes and suspended string. Samples were collected from the center of each 1 × 1-m cell (100 total). At each sampling period, three 1 × 1-m subplots within the macrogrid were randomly selected without replacement for sampling. Grid lines were established within each of these 'minigrids' at 20-m intervals and samples were collected from the center of each 20 × 20-cm cell (25 total). A 15 × 15-cm 'microgrid' was selected within each minigrid in a location midway between the base of a sagebrush trunk and a wheatgrass tussock. Samples were taken in a 5 × 5 matrix, centered at 3 cm distances between sampling points (25 total).

Samples were collected after first removing the uppermost one-cm layer of debris and major Poa root layer. Then a 2.8-cm-diameter steel tube was driven into the soil to a depth of 15 cm. The resultant soil sample was removed from the corer and immediately sieved (2-mm mesh), then an aliquot was added to a preweighed centrifuge tube containing 2 *M* KCl (soil:solution ratio = 2.5 g: 25 mL. Samples were mechanically shaken for 30 minutes before centrifuging. The remaining soil sample was stored in another sample tube for subsequent air drying at 70 °C for 48 h. In addition, all identifiable root material sieved from the sample was carefully removed from the screen surface and placed in a glass vial for drying. Root mass and volatile organic matter (VOM) were estimated by dry ashing the dried root and soil samples, respectively, at 550 °C for 12 h, and subtracting ash mass from total dry mass.

The 2-*M* KCl samples were refrigerated until processed (no longer than 72 h). The KCl-extractable NO_3^- and NH_4^+ were determined with a LaChat flow-injection autoanalyzer (LaChat Chemical, Mequon, Wisconsin, USA). Moisture content was determined gravimetrically, and nitrate and ammonium analysis results were adjusted to reflect soil dry mass rather than wet mass. Sodium-bicarbonate-extractable P and K (soil:solution ratio = 1.25 g : 25 mL extractant) were determined with colorimetry (Murphy and Riley, 1962; Sims and Haby, 1971) and flame emission spectrophotometry (Hamm et al., 1970). Samples were mechanically shaken for 30 minutes prior to filtering. The K was not analyzed in samples collected in April.

Geostatistical semivariograms were calculated using measurements of NH_4^+, NO_3^-, P, K and soil moisture in soil samples; data were logarithmically transformed as distributions of nutrients and soil moisture were positively skewed (Welbster and Oliver, 1990). Analyses were conducted using the program GS^+ (Gamma Design Software, Plainwell, MI). Minimum pair distance used in semivariogram calculation was 3 cm and the maximum was approximately 8 m. To facilitate comparisons of spatial parameters between sample periods, semivariograms were standardized by dividing the semivariance by the sample variance (Isaaks and Srivastava, 1989). Evidence of anisotropy (directional) in calculated semivariograms was minimal, and analyses were conducted using isotropic semivariance (assumes no directional difference in semivariance). Plotted semivariograms were fit with the spherical function (Webster and Burgess, 1984), a modified quadratic function which assumes that sample points will not be autocorrelated beyond some distance. Points were assumed to not be autocorrelated when semivariance was equal to the sample variance (i.e. standardized semivariance = 1.0; Halvorson et al., 1994). Spatial dependence for each variable was calculated using the nugget variance, C_o, (y intercept of semivariogrann) and sill (plateau of semivariogram) equal to $C + C_o$, where C is structural variance. Spatial dependence is defined as the ratio of structural variance to total variance ($C/[(C+C_o])$, and relates small-scale patch variability to large-scale site variability.

Correlations were calculated to quantify correspondence between variables and to assess temporal changes in resource patches. Spearman rank-correlation coefficients were used because of skewed distributions in nutrients and soil moisture. Minimum significance of $p = 0.001$ was set for consideration of significant correlations because of multiple comparisons within correlation matrices (conservative Bonferroni adjustment).

Spatial variation in combined nutrient availability (NH_4^+, NO_3^-, P and K) was assessed using the non-parametric index proposed by Jackson and Caldwell (1993b). All samples of each nutrient during each sample period were ranked in ascending order. Semivariograms were then calculated by sample period using the sum of ranks for each nutrient for each sample. Semivariograms generated for the April sample period were calculated without K, as this nutrient was not analyzed at that time. Anisotropy was minimal for these semivariograms.

Spatial relationships of nutrients and soil moisture were related to plant position within the three 1 × 1 m subplots sampled each month. Spearman rank-correlation coefficients were calculated between nutrient concentration and distance from the center of the base of the nearest sagebrush or wheatgrass tussock for each of the 25 sample cores. Nutrient values from each 1 × 1-m miniplot were normalized (mean = 0.0, sd = 1.0) and combined by sample period to calculate correlations with distance to plants. Significant correlations ($p < 0.001$) were used to indicate nutrient accumulation or depletion in the vicinity of plants. Spearman rank-correlation coefficients were also calculated between

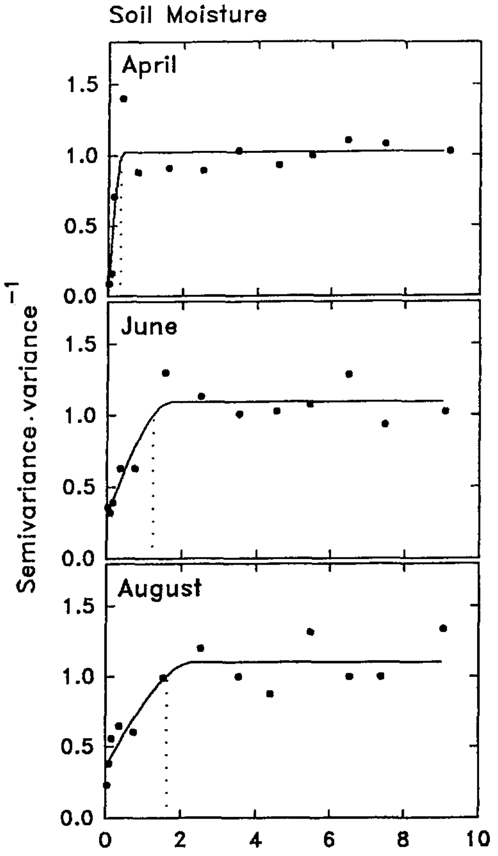

Figure 1. Standardized semivariogram of soil moisture at three sample periods. Standardized semivariance was calculated by dividing semivariance by sample variance. Sample values were logarithmically-transformed prior to semivariance and variance calculation. Dotted line indicates where standardized semivariance equaled sample variance.

Table 1. Parameters for spherical model for semivariograms shown in Figures 1, 2, 3 and 4. Nugget variance or y-intercept (C_0), and sill or curve plateau ($C+C_0$) are shown. The degree of spatial dependence ($C/[C+C_0]$) is the ratio of relative structural variance to relative population variance. K was not analyzed in April samples. Soil moisture variable is indicated as 'H_2O'

	C_0	$C+C_0$	Spatial dependence (%)
April			
H_2O	0.001	1.022	99.9
NH_4^+	0.030	1.157	97.4
NO_3^-	0.271	1.022	73.5
P	0.209	1.055	80.2
Nutr. index	0.297	1.138	73.9
June			
H_2O	0.298	1.090	72.7
NH_4^+	0.524	1.111	52.8
NO_3^-	0.373	1.060	64.8
P	0.266	1.050	74.7
K	0.268	1.000	73.1
Nutr. index	0.442	1.079	59.0
August			
H_2O	0.362	1.103	67.2
NH_4^+	0.951	1.068	11.0
NO_3^-	0.607	1.057	42.6
P	0.058	1.043	94.4
K	0.031	1.024	97.0
Nutr. index	0.267	1.018	73.8

root density and nutrient concentrations and distance from plant base for samples collected in the minigrids.

Results

Isotropic semivariances calculated for four nutrients and soil moisture for the three sample periods are shown in Figures 1, 2 and 3. Strong autocorrelation for all variables in the three sample periods was only found over distances of less than 2 m, indicating that patches of high internal uniformity in this soil were smaller than 2 m during the growing season. Differences in semivariograms between sample periods were most pronounced for variables that we consider to primarily limit plant growth in this sagebrush-wheatgrass system. The distance over which sample points were autocorrelated for soil moisture increased from the April through the August sampling periods (Figure 1). Similarly, the distance over which sample points were autocorrelated for NH_4^+ and NO_3^- increased from April to June. But different patterns for the two ions were observed for August (Figure 2). For NO_3^-, the semivariogram for August samples remained nearly the same as in June, while almost no spatial autocorrelation was found for NH_4^+ in August even for samples at the 3-cm minimum sample interval.

In contrast, P and K which are relatively more abundant at this site, exhibited relatively constant semivariance patterns in the three sample periods (Figure 3). Slightly less autocorrelation for P in August may have occurred, but the change was less than that observed for N or soil moisture. Also, the distance of strong autocorrelation of 0.3 to 0.9 m was generally less than that for N or soil moisture, particularly during June.

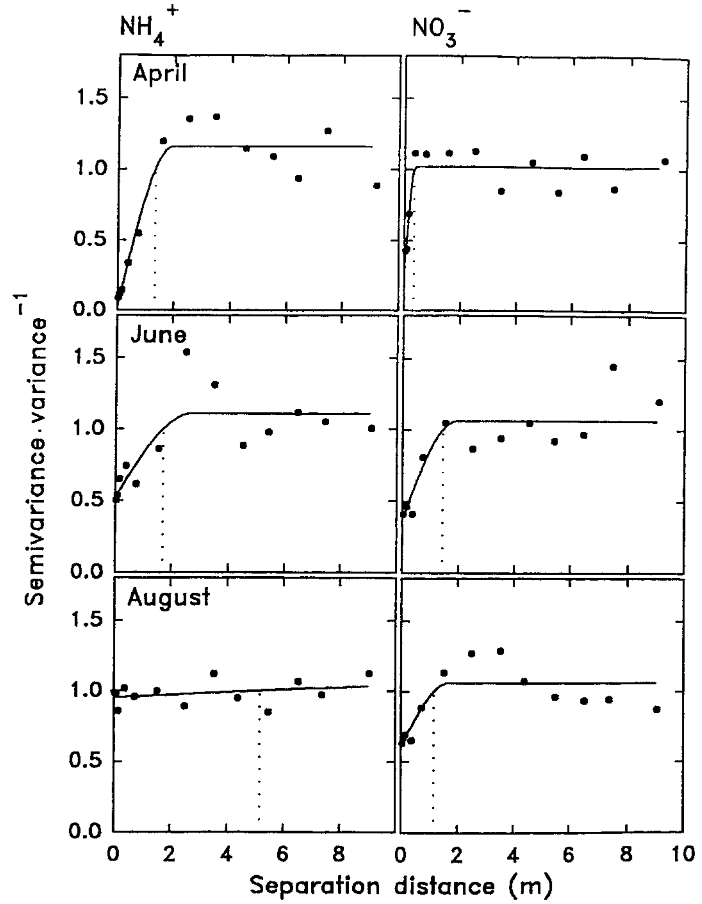

Figure 2. Standardized semivariogram of NH_4^+ and NO_3^- at three sample periods. Standardized semivariance was calculated by dividing semivariance by sample variance. Sample values were logarithmically-transformed prior to semivariance and variance calculation. Dotted line indicates where standardized semivariance equalled sample variance.

Temporal patterns of spatial dependence of N and soil moisture also differed from P and K. Soil moisture and N had highest spatial dependence in April and lowest in August, while P and K had highest spatial dependence in August, with lower values in April and June (Table 1). Nugget variances were particularly high for NH_4^+ and NO_3^- in August, indicating patches with high internal variability in nutrient concentrations. Very low nugget variances for soil moisture and NH_4^+ in April, and for P and K in August suggest patches of high internal uniformity relative to variability across the large sampling grid.

Semivariograms for the nonparametric nutrient index showed spatial autocorrelation of samples separated by up to 2.4 m in June; but only 1.0 m and 0.4 m in April and August, respectively (Figure 4). This pattern was different than patterns observed for individual nutrients (Figures 2 and 3). The period of greatest spatial autocorrelation corresponds with the peak growing period in June. Spatial dependence was lowest in June when nugget variance was highest, while spatial dependence and nugget variance in April and August were nearly identical (Table 1).

Spatial autocorrelation was minimal for nutrients and soil moisture at distances > 1.0 m as semivariance was within 90% of the sample variance (Figures 1, 2 and 3). This suggests that samples collected in the 10 × 10 'macrogrid' at 1-m intervals could represent the variability in resource patches within the study site. Means and sample variability (expressed as coefficient of variation) were calculated for each variable for the three sample periods (Table 2). Soil concentrations of limiting resources showed significant differences ($p < 0.05$) between at least two sample periods. Soil moisture declined from April to August with the largest decline between April and June. Variability among samples was greatest in June and August. Concentrations of both N variables declined between April and

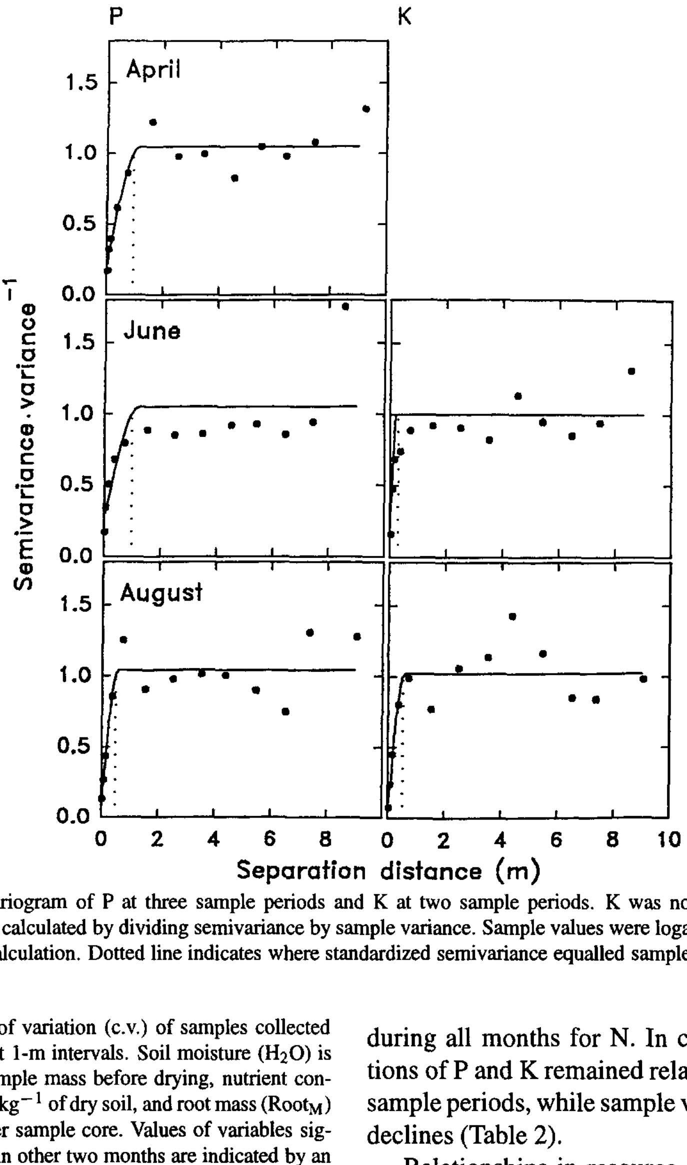

Figure 3. Standardized semivariogram of P at three sample periods and K at two sample periods. K was not analyzed in April samples. Standardized semivariance was calculated by dividing semivariance by sample variance. Sample values were logarithmically-transformed prior to semivariance and variance calculation. Dotted line indicates where standardized semivariance equalled sample variance.

Table 2. Mean and coefficient of variation (c.v.) of samples collected from 10 × 10-m 'macrogrid' at 1-m intervals. Soil moisture (H_2O) is expressed as percent of soil sample mass before drying, nutrient concentrations are expressed as mg kg^{-1} of dry soil, and root mass ($Root_M$) is expressed as g dry weight per sample core. Values of variables significantly different than values in other two months are indicated by an asterisk (ANOVA, $p< 0.05$, LSD multiple comparisons, data logarithmically transformed). K was not analyzed in April samples

	April		June		August	
	Mean	C.V.	Mean	C.V.	Mean	C.V.
H_2O	13.3*	9.3	4.3	18.8	3.0	14.7
NH_4^+	2.35	31.5	0.84*	41.7	2.54	31.1
NO_3^-	1.15	38.3	0.76*	47.4	1.08	47.2
P	21.4	39.1	18.9	34.0	19.6	27.7
K	–	–	407	27.8	397	23.4
$Root_M$	0.09*	60.9	0.29*	53.1	0.24*	92.6

June, but returned in August to levels similar to April. Sample variability (coefficient of variation) was high during all months for N. In contrast, soil concentrations of P and K remained relatively constant between sample periods, while sample variability showed slight declines (Table 2).

Relationships in resource concentrations between sample periods for individual locations in the 10 × 10-m 'macrogrid' were assessed using Spearman rank-correlation. Since June and August samples within the large grid were collected within approximately 10 cm of samples collected in April, high correlation among samples collected in different periods would indicate stability in the spatial distribution. (The distances between successive samples for the macrogrid of < 10 cm are within the zone of high autocorrelation for samplings conducted at any of the time periods). In contrast, minimal correlation would indicate changes in spatial distribution between months. As with semivariance, N and soil moisture showed different patterns than P and K. Minimal correlation was found

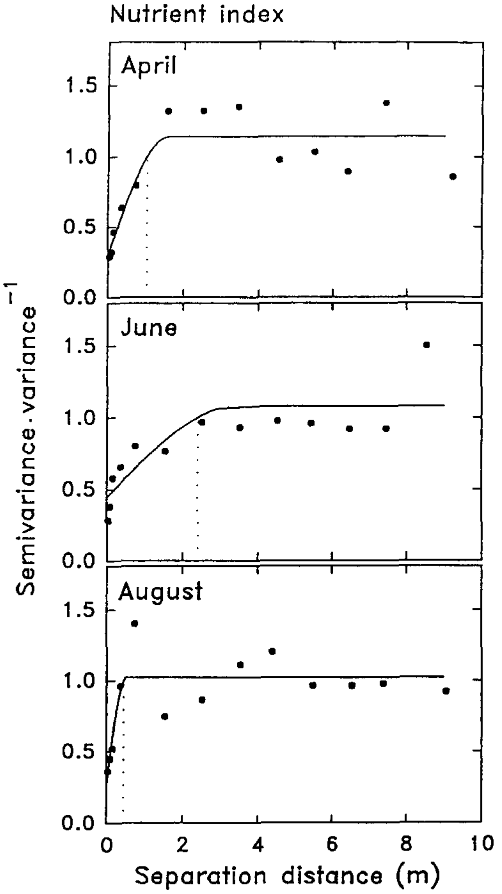

Figure 4. Standardized semivariogram of nutrient index at three sample periods. Standardized semivariance was calculated by dividing semivariance by sample variance. Sample values were logarithmically-transformed prior to semivariance and variance calculation. Dotted line indicates where standardized semivariance equalled sample variance. Nutrient index is sum of ranked sample values for NH_4^+, NO_3^-, P and K. Nutrient index for April was calculated without K, which was not analyzed in samples in April.

Table 3. Spearman rank-correlations between samples collected in the three sample periods on the 10 × 10-m 'macrogrid'. Samples each month at a grid location were collected approximately 10 cm from previous samples. K was not analyzed in April samples. Soil moisture variable is indicated as 'H_2O'

H_2O			
	April	June	August
April	1.00		
June	0.10	1.00	
August	0.16	0.09	1.00
NH_4^+			
	April	June	August
April	1.00		
June	0.23*	1.00	
August	−0.04	0.16	1.00
NO_3^-			
	April	June	August
April	1.00		
June	−0.01	1.00	
August	−0.08	0.21*	1.00
P			
	April	June	August
April	1.00		
June	0.69***	1.00	
August	0.61***	0.58***	1.00
K			
	June	August	
June	1.00		
August	0.65***	1.00	

*$p < 0.05$.
*** $p < 0.00001$.

between samples collected in the three sample periods for N and soil moisture, while P and K had highly significant correlations among sample periods (Table 3). This indicates that the spatial pattern of these limiting resources changed between sample periods, while distributional patterns of the relatively more abundant P and K remained rather constant.

Correlations were also calculated among variables within each sample period for the 10 × 10-m 'macrogrid' (Table 4). Highly significant correlations were found only between concentrations of P and K for samples from June and August (K was not analyzed in the April samples). Less significant correlations were found between NH_4^+ and NO_3^- in April and August samples, and no correlation was found in June samples. Correlations were also calculated between these variables and dry mass of roots in sample cores, VOM, and pH for the 'macrogrids' for each sample period. Significant correlations ($p < 0.001$) were found only between soil moisture and VOM for April and June, K and VOM and pH in June and August, and P and VOM in August.

There were strong negative Spearman rank-correlations ($p < 0.001$) between P and K and distance from the base of shrubs for all sample times (Table 5). Negative correlations indicated that concentrations decreased with distance away from the shrub base. Similar strong correlations with distance from the sagebrush base were not found for NH_4^+, NO_3^-, or

Table 4. Spearman rank-correlations between variables for samples collected in three sample periods on the 10 × 10-m 'macrogrid'. Correlations were calculated for variables measured in the same sample cores. K was not analyzed in April samples. Soil moisture variable is indicated as 'H_2O'

April

	H_2O	NH_4^+	NO_3^-	P
H_2O	1.00			
NH_4^+	0.20*	1.00		
NO_3^-	0.24*	0.38**	1.00	
P	0.35**	0.28*	0.15	1.00

June

	H_2O	NH_4^+	NO_3^-	P	K
H_2O	1.00				
NH_4^+	–0.40**	1.00			
NO_3^-	0.23*	–0.05	1.00		
P	–0.12	0.30*	–0.22*	1.00	
K	0.06	0.25*	–0.28*	0.70***	1.00

August

	H_2O	NH_4^+	NO_3^-	P	K
H_2O	1.00				
NH_4^+	–0.10	1.00			
NO_3^-	–0.28*	0.48**	1.00		
P	0.24*	0.05	–0.30*	1.00	
K	0.31	0.23*	–0.18	0.67***	1.00

* $p < 0.05$.
** $p < 0.001$.
*** $p < 0.00001$.

soil moisture, nor for any variable and distance from wheatgrass tussocks. In June, near the peak period of plant growth and presumably the period of greatest water and nutrient uptake, all variables were negatively correlated (but not all significantly) with distance from sagebrush plants indicating that plant distribution may have some effect on distribution of all four nutrients and soil moisture during this period of active growth.

Root mass was also negatively correlated with distance from sagebrush shrubs although with low significance levels (Table 5). In general, root mass was weakly but positively correlated with soil nutrients (except NO_3^-) and soil moisture (Table 6). Correlations were highest between root mass and P and K.

Table 5. Spearman rank-correlations between distance of sample from center of base of nearest sagebrush or wheatgrass, and sample variables collected in three sample periods from the 1 × 1-m 'minigrids'. Variables from each minigrid were standardized $\mu = 0.0$, s.d. $= 1.0$ prior to combining by sample period. K was not analyzed in April samples. Soil moisture variable is indicated as 'H_2O', and root dry mass as '$Root_M$'

	April	June	August
Distance to nearest sagebrush			
H_2O	0.06	–0.26*	–0.25*
NH_4^+	–0.23*	–0.09	0.11
NO_3^-	–0.03	–0.23	0.01
P	–0.46**	–0.42**	–0.53***
K	- -	–0.62***	–0.60***
$Root_M$	–0.27*	–0.14	–0.36*
Distance to nearest wheatgrass			
H_2O	0.07	–0.27*	0.01
NH_4^+	0.09	–0.11	–0.11
NO_3^-	–0.05	0.06	–0.11
P	0.05	0.18	–0.30*
K	- -	0.15	–0.24*
$Root_M$	–0.01	–0.18	–0.13

* $p < 0.05$.
** $p < 0.001$.
*** $p < 0.00001$.

Table 6. Spearman rank-correlations between root dry mass ($Root_M$) and variables for samples collected in three sample periods on the 1 × 1-m 'minigrids'. Correlations were calculated for variables measured in the same sample cores. K was not analyzed in April samples. Soil moisture variable is indicated as 'H_2O'

	April $Root_M$	June $Root_M$	August $Root_M$
H_2O	–0.18	0.29*	0.15
NH_4^+	0.24*	0.36*	0.23
NO_3^-	–0.18	–0.05	–0.07
P	0.20	0.37*	0.25*
K	–	0.36*	0.46**

* $p < 0.05$.
** $p < 0.001$.

Discussion

Soil moisture and concentrations of soil nutrients were quite variable within the research plot (macrogrid), even within the close proximity of individual plants. Variability in sample values was great enough that some of the highest and lowest measured nutrient concentrations occurred within the extent of individual sagebrush plant root systems. The spatial extent of variability was comparable to that found by Halvorson et al. (1994) and Jackson and Caldwell (1993a, b) in similar sagebrush steppe systems.

Temporal variability in the spatial soil heterogeneity was also found to be significant through the growing season. Gross et al. (1995) found differences in the degree of spatial variation of nitrogen between three successional communities in southwestern Michigan, but discernible temporal changes in spatial variation of nutrients and soil moisture, as indicated by our results, can apparently occur much faster, even within a single growing season.

Temporal changes in patterns of spatial variability of soil resources was greater for resources (N and soil moisture) we consider to be most limiting to plant growth at this site than for P and K. The rather similar degree of spatial variability of P and K during the growing season is consistent with our interpretation that these ions at this site are relatively abundant for sagebrush steppelands, and probably do not limit plant growth at this site. Large differences in the spatial variability of N between sample periods suggest that soil pools of N are highly dynamic. The lack of significant temporal correlation in concentrations of NH_4^+ and NO_3^- is also consistent with the existence of highly dynamic N pools. Stark (1994) indicates that several factors regulate N production and consumption, and that temporal differences in these factors greatly influence pool sizes. Perhaps differences in plant uptake rates and microbial activity, as affected by temperature and soil moisture, influenced the dynamics of N pools at this site. Low concentrations of NH_4^+ and NO_3^-, measured in the June samples, suggests that plants may have had the largest effect on changes on pool sizes of N, as most plant growth occurs between early April and late June in this steppe system. While plant uptake at this time of year may have been responsible for small pool sizes, it did not seem to have a pronounced effect on spatial heterogeneity of NO_3^- and NH_4^+. This is based on the rather weak correlations between concentrations of these ions, and distance from the base of sagebrush and tussock grass plants. Greater nitrogen pool sizes in August suggest that plant uptake rates were less than rates of microbial production which has been reported in other systems (Pavidson et al., 1993).

Soil moisture, the other limiting resource measured, declined during the course of the study, with the largest decline between the first two sample periods. The overall decline was consistent with transpirational and evaporational water loss that was not replenished by measurable precipitation during the study. Significant correlation in soil moisture at the same locations in the study plot between sample periods was not found. Plant shading of the soil surface, differential root activity or hydraulic lift (see Caldwell et al., 1991) may have contributed to this temporal variation. In June and August, soil moisture exhibited a weak inverse correlation with distance from the plant base suggesting effects of hydraulic lift in supplying moisture to the upper soil layers near the plant base and shading in reducing evaporation from the soil surface.

The nonparametric nutrient index proposed by Jackson and Caldwell (1993b) showed the greatest change in spatial variability among sample periods. In April, there was a moderate range of autocorrelation which extended to over 2 m in June. By August, this autocorrelation range was very small. This seasonal pattern in the nutrient index suggests that plant uptake of nutrients, which would be greatest in June, intermediate in April and least in August, may be a significant contributor to the extent of autocorrelation. In August, when uptake activity is typically much lower due to limited water availability in the upper soil layers, the range of autocorrelation in the nutrient index was very low, perhaps because other processes, such as microbial transformations which can work on much smaller spatial scales (Stark, 1994), were dominating, leading to much smaller patch sizes.

Soil nutrient concentrations were found to be related to the positions of sagebrush plants but not of wheatgrass tussocks. Concentrations of P and K were found to be greater closer to base of sagebrush shrubs during all three sample periods. Higher concentrations of P and K near sagebrush shrubs may relate to recycled leaf and root litter that accumulates near the plant and perhaps the entrapment of windblown debris. Persistence in the distribution of P may also be sustained by its immobility in the soil (Nye and Tinker, 1977). Similar 'islands of fertility' have been observed in steppe systems (Charley and West, 1975; Hook et al., 1991; Schlesinger et al., 1990), and such influences on soil nutrients have been found in sagebrush-wheatgrass systems similar to our study site (Halvorson et al., 1994; Jackson and Caldwell, 1993b). Vinton and Burke (1995) suggest that discontinuous plant canopy cover is an important contributor to soil nutrient variability.

While concentrations of P and K were inversely correlated with distance from the plant base for all three sample periods, concentrations of NH_4^+ and NO_3^- did not show consistent patterns with location throughout the growing season. Only a very weak inverse correlation occurred between nitrogen and distance to sagebrush plants in April and June as found by Halverson et al. (1994) for similar sagebrush-steppe lands in March. This suggests that plants did not have a consistent influence on soil nitrogen distributions throughout the growing season at this site.

Influence on nutrient and soil moisture distributions by wheatgrass tussocks may have been less than for sagebrush shrubs due to their smaller size. Jackson and Caldwell (1993b) found higher concentrations of P and K near tussocks of *Pseudorogneria spicata* in a similar sagebrush-tussockgrass system, but the sagebrush were much smaller and likely much less influential on nutrient distributions. As in our study, Jackson and Caldwell (1993b) did not find obvious relationships between plant locations and soil nitrogen pools.

Although plant modification of soil nutrient distributions is known from earlier studies, our study indicates that plants, interfacing with other favors affecting soil resource production and consumption, may differentially affect the patterns of spatial resource variability within a single growing season. The greatest changes in these patterns was found with resources considered to be most limiting at this site and with an index of nutrient availability. These changes in patterns of nutrient and soil moisture variability within a growing season indicate that not only must plants acquire soil resources that vary in time and space, but that they must also adjust to different scales of resource patchiness during the season.

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