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Geostatistical patterns of soil heterogeneity around individual perennial plants

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Summary

1 Univariate, multivariate, and geostatistical techniques were used to quantify the scale and degree of soil variability around individual perennial sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and bluebunch wheatgrass (*Pseudoroegneria spicata* ssp. *spicata*) plants. This variability was then compared to that found across the larger sagebrush-steppe site. Samples were taken every metre in a 10-m × 12-m grid and every 12.5 cm in nine nested 0.5-m × 0.5-m grids containing at least one *Artemisia* shrub or *Pseudoroegneria* tussock (362 total samples). The 11 soil properties measured were organic matter, pH, water content, live root mass, microbial respiration, net N mineralization, nitrification potential, and soil-extractable ammonium, nitrate, phosphate, and potassium.

2 There was considerable biological variation in many of the properties measured. Soil organic matter varied from 1.3% to 7.4% within the 10-m × 12-m area and pH varied by as much as 1.3 pH units among samples less than 50 cm apart. Samples showing strong negative N mineralization (N immobilization) were only 12.5 cm from samples showing strong positive N mineralization.

3 Spearman rank-correlation coefficients between pairs of the 11 soil parameters showed a number of strong, positive associations between some variables (e.g. phosphate and potassium, $r_s = 0.64$), but not others (e.g. ammonium and organic matter, $r_s = 0.013$).

4 Semivariograms for soil organic matter and pH showed strong spatial autocorrelation at distances of less than 1 m, and both showed a high spatial dependence of *c.* 90%. A combined index of soil fertility (incorporating information on soil ammonium, nitrate, phosphate, and potassium) also showed strong autocorrelation at scales of less than 1 metre. None of the microbial processes analysed (net N mineralization, nitrification potential, or microbial respiration) showed any significant autocorrelation, even at the finest measurement scale of 12.5 cm.

5 Kriged (interpolated) contour plots of soil organic matter, phosphate, and potassium showed strong spatial patterning associated with the tussock grasses, but less consistent patterning for the sagebrush plants. From the degree and scale of variability seen in this study and previously, we conclude that root plasticity and active foraging in a heterogeneous soil environment are likely to be important to the nutrient balance of many plants.

Keywords: kriging, nitrogen mineralization, nutrient availability, patchiness, *Pseudoroegneria* tussocks, sagebrush-steppe, spatial scale, semivariograms

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Introduction

Researchers in agricultural systems have recognized the problems associated with soil variability since at least the beginning of the century (e.g. Waynick & Sharp 1919; Harris 1920). The emphasis on pooling multiple soil samples for a 'representative' cross-section of an agricultural field is one practical result of addressing such variability (Ferrari & Vermeulen 1955). Investigations of heterogeneity in natural systems have also showed substantial variability, even at scales of less than a metre (Snaydon 1962;

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Frankland *et al.* 1963). Downes & Beckwith (1951), for example, found soil pH to vary by a full pH unit within *c.* 1 m^2 of apparently uniform soil.

Environmental heterogeneity has had an important influence on the development of both experimental design and statistics in general. Such models as randomized-block, Latin-square, and split-plot designs were created to minimize the effect of environmental variability on the outcome of crop trials. These and other forms of analysis of variance suffer from the requirement that all samples be statistically independent or free from autocorrelation, an unrealistic assumption for many field studies. A relatively new class of statistics called geostatistics (Matheron 1963) was developed to specifically address the problem of autocorrelation among data. The semivariogram, a geostatistic that stratifies the variance in a data set by at least one spatial or temporal dimension, is a useful tool for identifying both the structure of variability for that dimension and for quantifying the scale of autocorrelation (Rossi *et al.* 1992). Geostatistical techniques were developed in the mining industry (Matheron 1963; Journel & Huijbregts 1978) and have been used extensively in the soil sciences for over a decade (e.g. Burgess & Webster 1980). Recently, geostatistical techniques have begun to be applied in an ecological context (Robertson *et al.* 1988; Lechowicz & Bell 1991; Jackson & Caldwell 1993).

Numerous researchers have proposed a positive correlation between environmental variability and species richness (e.g. Simpson 1964). Although plants can be quite plastic in responding to resource variability (e.g. Fitter 1982; Campbell & Grime 1989; Jackson *et al.* 1990), little is known of the actual heterogeneity in soil resources that an individual plant encounters and induces in the field. In this study, we quantify the scale and degree of soil variability around individual perennial plants in the field, and compare this variability with that found across a larger sagebrush-steppe site. To accomplish this goal, we used a nested sampling scheme, with samples taken every metre in a 10-m x 12-m grid and every 12.5 cm in 0.5-m x 0.5-m grids. The nested 0.5-m x 0.5-m grids contained at least one native perennial mountain sagebrush plant, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle, or bluebunch wheatgrass plant, *Pseudoroegneria spicata* (Pursh) A Löve ssp. *spicata*. The soil properties measured were soil organic matter, pH, water content, live root mass, microbial respiration, net nitrogen mineralization, nitrification potential, and soil-extractable ammonium, nitrate, phosphate and potassium. We applied univariate, multivariate, and geostatistical techniques to the data, emphasizing the degree and scale of variability around the individual perennial plants. We calculated geostatistical semivariograms for each soil property and then used those semivariograms to generate contour plots of the various soil properties.

Materials and methods

The research was conducted in the spring of 1991 at a native sagebrush-steppe site 30 km south of Logan, Utah on silt loam formed from noncalcareous alluvial material (USDA 1974). Typical annual precipitation is 430–500 mm (USDA 1974), the altitude is 1575 m a.s.l., and the site is essentially flat.

As well as *Artemisia tridentata* ssp. *vaseyana* and *Pseudoroegneria spicata* ssp. *spicata*, species of *Balsamorhiza*, *Zigadenus*, *Viola*, *Poa* and *Lomatium* occur. *Artemisia* plants at the site tend to be relatively small, usually < 0.5 m tall with a fairly sparse canopy, but growth-ring analysis showed several to be between 15 and 20 years of age. Inter- and intraspecific neighbours of *Artemisia* and *Pseudoroegneria* are sometimes closely spaced, in some cases within 0.5 m. The site experiences light, irregular grazing by cattle in the fall of some years, and mule deer are frequently seen browsing in the winter or spring. Pocket-gopher (*Thomomys talpoides*) activity, ant mounds, and narrow cracks in the soil (up to 30 cm in depth) are all apparent sources of heterogeneity at the soil surface.

In the spring of 1991, we established a 10-m x 12-m grid at the site, with points sampled every metre (143 samples). Within this grid, we also sampled at a finer scale of 12.5 cm within nine nested 0.5-m x 0.5-m grids (225 fine-scale samples, a total of 362 samples for the entire experiment). Each of these smaller grids contained at least one *Artemisia* or *Pseudoroegneria* plant (six grids with a target *Artemisia*, three with a target *Pseudoroegneria*). Replicate cores 4 cm in diameter and 10 cm deep were taken at each sampling point within two days in early May.

Soil organic matter was determined colorimetrically with potassium dichromate (Sims & Haby 1971). Soil pH was determined on a saturated soil paste of air-dried soil passed through a 2-mm sieve. Gravimetric water content was determined by drying *c.* 20 g soil samples to constant mass at 105°C. The mass of live roots in single 4-cm-diameter, 10-cm-deep cores was determined by first separating the roots from the soil (hydropneumatic root elutriator, Gillison Variety Fabrication Inc.) and then oven-drying and weighing the roots. Soil phosphate and potassium were extracted with 0.5 mol l^{-1} $NaHCO_3$ (Olsen & Sommers 1982). For soil ammonium and nitrate analyses, 10 to 20 g samples of mixed soil were placed in 100 ml of 2 mol l^{-1} KCl in the field, cooled and taken to the lab, shaken for 1 h, filtered through Whatman no. 1 filters previously rinsed with KCl, and then tested by continuous-flow analysis using a Lachat autoanalyser. Microbial respiration, nitrification potential, and net nitrogen mineralization were

determined from aerobic incubations in 1-litre glass jars. Prior to incubation, a soil subsample from each of the 362 sampling points was sieved (2-mm sieve) and water content, NH_4^+, and NO_3^- concentrations were measured as before. A second 15–20-g subsample was placed in a glass jar after adjustment to a uniform water content. After 10 days storage at 25°C, a gas sample was removed by syringe through a septum and the CO_2 concentration was measured in an infrared gas analyser (linear calibration of $r^2 > 0.99$ for the CO_2 concentrations encountered). The postincubation soil NH_4^+ and NO_3^- concentrations were then determined as before. Nitrification potential is the difference between post- and preincubation NO_3^- concentrations; net N mineralization is the difference between postincubation and preincubation (NH_4^+ + NO_3^-) concentrations.

Univariate statistics and the correlation matrix for the soil parameters were calculated with SYSTAT modules STATS and CORR. Spearman rank-correlation coefficients were used for the correlation matrix because several variables were positively skewed. A minimum level of significance for these coefficients was set at $P = 0.001$ (a conservative Bonferroni adjustment) because of the multiple comparisons made in the matrix.

Geostatistical semivariograms were calculated with the US Environmental Protection Agency program 'Geo-EAS' using all 362 points for each soil parameter. The minimum pair distance used was 12.5 cm and the maximum was *c.* 7.5 m (roughly half the maximum distance available from the data). Each semivariogram lag class had at least 350 pairs of points and over 40 000 pairs were used for each semivariogram. There was no obvious anisotropy (directionality) to any of the semivariograms, but the data for microbial respiration, root mass, soil ammonium, and soil nitrate were logarithmically transformed prior to analysis because their distributions were positively skewed (Webster & Oliver 1990). We also applied rank transformations (Conover & Iman 1981) to generate a novel summary semivariogram that combines information from all four of the soil nutrients sampled (NH_4^+, NO_3^-, P, and K). The 362 observations for a given nutrient were ranked in ascending order and then summed with the ranks for the other three nutrients at the same grid position. This provides a relative estimate of combined nutrient availability and allows us to examine the spatial autocorrelation of nutrient patches in the soil. A semivariogram was then calculated from this summary of N, P and K availability. Semivariograms for the four nutrients individually can be found in Jackson & Caldwell (1993). The least-squares fit for each semivariogram was calculated with the SYSTAT NONLIN module from among linear, spherical, and exponential models (Isaaks & Srivastava 1989). Ordinary block kriging and generation of contour plots was performed with the program GS+ (Gamma Design Software) using the five nearest neighbours and a distance of 10 mm between block centres; kriging is a form of weighted interpolation with the weights based on the structure of the semivariogram (Isaaks & Srivastava 1989).

Results

Variability for the seven non-nutrient soil parameters across the 10-m x 12-m sampling area was quite high (Table 1, Fig. 1) and comparable to the variability observed for the soil nutrients phosphate, potassium, ammonium and nitrate (Jackson & Caldwell 1993). Microbial respiration varied from 49.6 to 1810 mg CO_2 kg^{-1} soil with a coefficient of variation (CV) of 64.9% (Table 1). Root mass varied by well over two orders of magnitude, from 0.013 g to 2.63 g (Fig. 1). Soil organic matter, though not expected to vary by orders of magnitude, showed considerable variabil-

Table 1 Selected properties of soil samples taken in 4 cm diam. x 10 cm deep soil cores at a native sagebrush-steppe field site. All soil terms are expressed on a dry-mass basis. The aerobic incubations for microbial respiration, nitrification potential, and net N mineralization were maintained for 10 days at 25°C. Values for root mass are expressed per core. There are 362 samples for each property, with two missing values for both nitrification potential and net N mineralization and five missing values for microbial respiration.

Factor	Units	Mean	Median	SD	CV(%)
Soil organic matter	(%), or dg kg^{-1} soil	2.68	2.55	0.72	26.9
pH	unitless	6.3	6.3	0.22	3.6
Gravimetric H_2O content	kg H_2O kg^{-1} soil	0.29	0.28	0.037	13.1
Root mass	g	0.29	0.23	0.27	92.2
Microbial respiration (CO_2 production)	mg CO_2 kg^{-1} soil	263	229	170	64.9
Nitrification potential (net NO_3^- production)	mg N kg^{-1} soil	14.4	13.3	8.14	56.4
Net N mineralization (NH_4^+ and NO_3^- production)	mg N kg^{-1} soil	10.3	10.2	6.27	60.9
Soil ammonium	mg N kg^{-1} soil	3.48	2.15	13.4	386
Soil nitrate	mg N kg^{-1} soil	1.30	1.11	1.53	117
Soil phosphate	mg P kg^{-1} soil	19.1	17.0	7.61	39.8
Soil potassium	mg K kg^{-1} soil	315	287	108	34.3

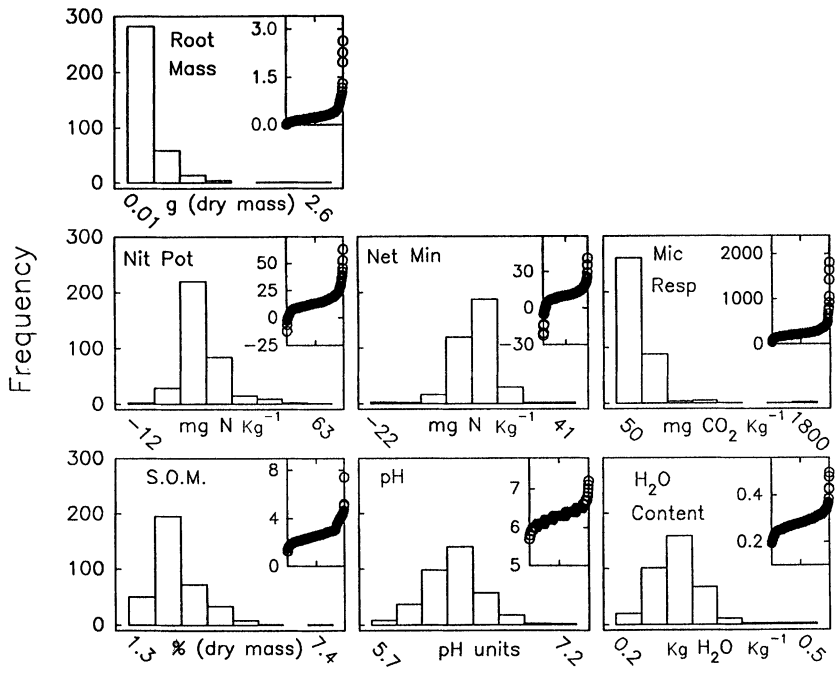

Fig. 1 Histograms for each of seven soil parameters, with the insets containing the values of the 362 soil samples comprising each histogram ranked in ascending order for that parameter. The *x*-axis label for each histogram is the unit of measurement for the property and its lowest and highest value in the data set. The *y*-axis label of each inset is the unit of measurement for the property. A 10-m x 12-m grid was established in a native sagebrush-steppe with soil properties sampled every metre. In addition, nine nested 0.5-m x 0.5-m grids contained six *Artemisia* and three *Pseudoroegneria* plants with soil sampled every 12.5 cm. Each of the nine smaller grids contained 25 samples and there were 362 total samples in the experiment. The panel in the upper row presents results for live root mass, the panels in the middle row present net nitrification potential, net N mineralization, and microbial respiration, and the panels in the lower row present soil organic matter, soil pH, and soil water content. A more complete description of the units and properties can be found in Table 1.

ity; values ranged from 1.3% to 5.0% (dry-mass basis) with one extreme value at 7.4% confirmed by reanalysis of a second subsample. Soil pH varied by 1.5 pH units and, in several cases, by more than one pH unit within a given 0.5-m x 0.5-m sampling area.

The correlation matrix for the 11 soil parameters (Table 2) showed a number of strong, positive associations between such variables as soil phosphate and potassium (r_s = 0.64), soil organic matter and potassium (r_s = 0.54), and, not surprisingly, nitrification potential and net N mineralization (r_s = 0.86). There was also a notable lack of correlation between some pairs of variables, such as organic matter and both ammonium (r_s = 0.13) and nitrate (r_s = 0.07). Even the significant relationship between ammonium and nitrate was much lower than expected (r_s = 0.38). The only soil factors significantly correlated with root mass were soil K, organic matter, and H_2O content, but these correlation coefficients were quite weak (r_s = 0.24, 0.20 and 0.19, respectively). Parametric Pearson correlation coefficients for the complete data set, and with selected extreme values deleted for some variables, both showed similar patterns of significance as in Table 2, but the parametric correlations were generally stronger than their nonparametric counterparts.

Semivariograms for soil organic matter and pH showed increasingly strong autocorrelation at distances of less than a metre (Fig. 2, fitted model parameters in Table 3). Beyond that distance the semivariograms were essentially flat, indicating the region where classical assumptions of statistical independence may be justified. The structural variance or degree of spatial dependence for each of the seven variables was calculated from the *y*-intercept or nugget value (C_0) of each semivariogram and the *y*-value at which each semivariogram becomes a plateau or sill (C), (Table 3: structural variance = $(C - C_0)/C$). Both soil organic matter and pH showed a high degree of spatial dependence (*c.* 90%, Fig 2), as the *y*-intercept or nugget for each semivariogram was *c.* 10% of the sill. The summary semivariogram for nutrient availability (a nonparametric index combining information on soil ammonium, nitrate, phosphate and potassium) showed detectable autocorrelation at < 1 m (Fig. 2), indicating correlations among nutrient availabilities and implying that nutrient patches in this soil may be < 1 m. Its degree of spatial dependence was moderately high at 63%. Soil water content showed much weaker spatial autocorrelation (Fig 2), with a degree of spatial dependence of only 34%. Finally, the three microbially driven variables (microbial respiration, net N mineralization, and nitrification potential) and live root mass showed essentially no spatial patterning, their semivariograms being linear with apparent slopes slightly greater than zero (Fig. 2).

Table 2 Nonparametric Spearman rank-correlation coefficients for the eleven soil parameters (in descending order—soil ammonium, nitrate, phosphate, potassium, organic matter, pH, water content, root mass, microbial respiration, net N mineralization, and nitrification potential). Because of the multiple comparisons made between variables, a minimum level of significance was chosen at $P = 0.001$ (a conservative Bonferroni adjustment)

	NH_4	NO_3	P	K	SOM	pH	H_2O	Root mass	Micr resp	Net min	Nit Pot
NH_4	1.0										
NO_3	0.38*	1.0									
P	0.24*	–0.01	1.0								
K	0.15	0.10	0.64*	1.0							
SOM	0.13	0.07	0.46*	0.54*	1.0						
pH	–0.03	–0.15	0.35*	0.45*	0.39*	1.0					
H_2O	0.10	0.17*	0.22*	0.29*	0.32*	0.09	1.0				
Root mass	–0.05	–0.04	0.09	0.24*	0.20*	0.06	0.19*	1.0			
Micr resp	0.06	0.00	0.32*	0.25*	0.16	0.16	0.37*	0.14	1.0		
Net min	0.05	0.07	0.04	0.03	0.10	–0.15	0.18*	0.03	0.05	1.0	
Nit Pot	0.14	0.13	0.10	0.11	0.12	–0.10	0.24*	0.07	0.15	0.86*	1.0

*$P < 0.001$

Since plant species might potentially affect the patterns of soil variability observed, semivariograms for the eleven soil properties were recalculated to examine any effect of plant species. First, the 75 data points from the three small grids around *Pseudoroegneria* tussocks were deleted and semivariograms were calculated on all the remaining data; second, the 150 points from the six small *Artemisia* grids were deleted and semivariograms recalculated. Plant species apparently only affected the semivariograms for soil nitrate and microbial respiration, where variability was always lower around *Pseudoroegneria* tussocks than around *Artemisia* shrubs (Fig. 3). The scale of autocorrelation (or range) for soil nitrate also appeared to be slightly

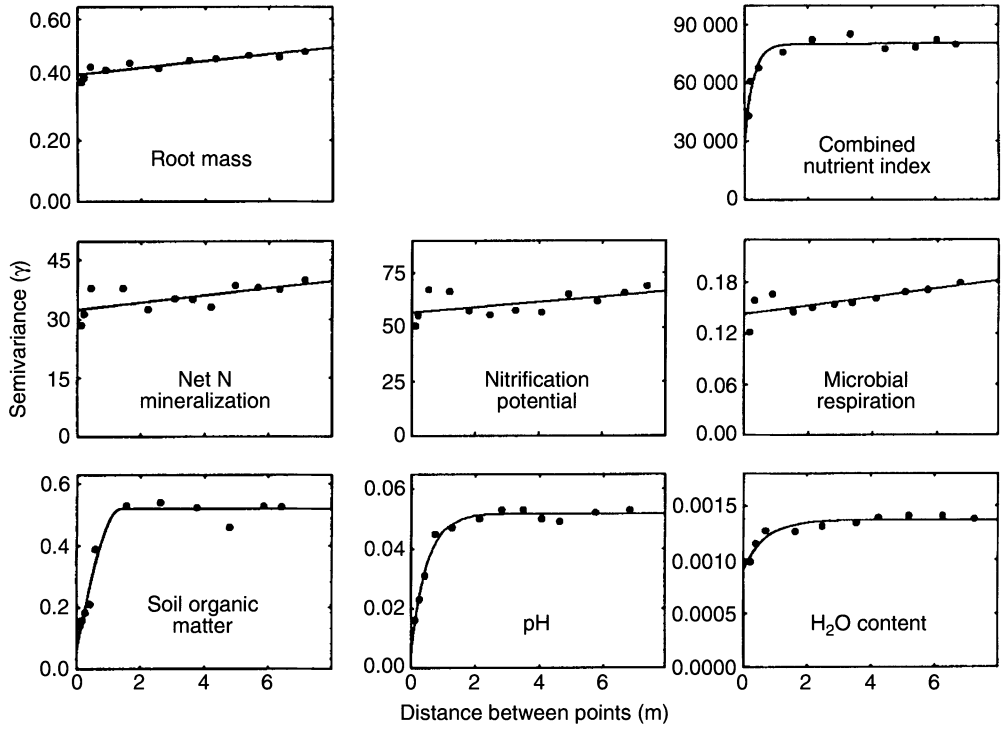

Fig. 2 Semivariograms of eight soil properties (soil organic matter, pH, water content, net N mineralization, nitrification potential, microbial respiration, root mass, and a nutrient index) based on 362 samples from the 120-m^2 field area. The semivariogram in the upper right, titled 'nutrient index', is a nonparametric index of nutrient availability that combines equally-weighted information on soil ammonium, nitrate, phosphate, and potassium (see Methods). Semivariograms stratify calculated variances by the distance (lag) separating each pair of points. The minimum and maximum pair distances used in the calculations were 12.5 cm and 7.5 m, and over 40 000 calculations were incorporated into each graph. The units for each semivariogram are the square of the units presented in Table 1, except for the nutrient index, which is unitless, and microbial respiration and root mass, which where ln-transformed prior to semivariogram analysis due to positive skewness in the data (Fig. 1). Parameter values for the solid-line models of each semivariogram may be found in Table 3.

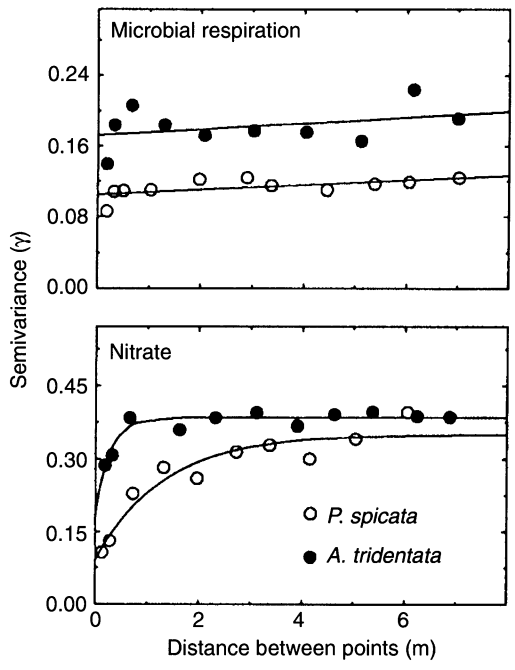

Fig. 3 Separate semivariograms for soil nitrate and microbial respiration with the small-grid data subdivided by plant species. Semivariograms were calculated on the 143 points that comprise the 10-m x 12-m grid plus the samples from either the three 0.5-m x 0.5-m grids around *Pseudoroegneria* tussocks (open symbols) or the six 0.5-m x 0.5-m grids around *Artemisia* shrubs (filled symbols).

greater around *Pseudoroegneria* tussocks compared with *Artemisia* shrubs (Fig. 3).

Interpolated (or kriged) 0.5-m x 0.5-m contour plots containing individual tussock grasses showed strong spatial patterning of soil organic matter and soil-extractable phosphate and potassium, with higher amounts near tussocks (Fig. 4). Patterns of soil ammonium and nitrate were not so consistently coupled with tussock location (kriged data not presented). Although Fig. 4 only shows data from one of the small tussock-containing grids, similar soil patterns were found in the other two grids containing grasses. Kriged soil properties from 0.5-m x 0.5-m grids containing sagebrush plants did not appear to be coupled to the location of the shrub centre or canopy (Fig. 5); none of the eleven soil properties measured showed consistent patterning associated with the location of the shrubs.

Discussion

There was a high degree of soil variability observed in the 0.25-m^2 areas around individual plants. For two of the sagebrush plants and one of the tussock grasses, samples showing strong negative net N mineralization (N immobilization) were separated by only 12.5 cm from samples showing strong positive N mineralization. Microbial respiration around the nine plants varied by a mean (± SEM) factor of 5 ± 1.0 and the mean range of soil organic matter around each plant (max. – min. within each set of 25 samples) was 1.6%. Soil pH varied by as much as 1.3 pH units in samples separated by less than 0.5 m. Documenting such variability around individual plants is quite important because species can differ profoundly in their ability to exploit variable soil resources (Grime *et al.* 1986; Jackson & Caldwell 1989). Also, the outcome of competition between

Table 3 Model parameters for the solid lines fitted through each semivariogram in Figure 2 and the four soil-nutrient semivariograms from Jackson and Caldwell (1993). The nugget is the y-intercept of the graph, the sill is the semivariogram value (y value) where each graph becomes a plateau (approximately equal to the traditional sample variance), the range is the distance (x value) where the plateau begins, and the degree of spatial dependence ($(C–C_0)/C$) is the ratio of structural to population variance. See footnotes for explanations of the various models and parameters. Values for soil ammonium, nitrate, microbial respiration, and root mass were ln-transformed prior to semivariogram analysis due to positive skewness in the data.

Variate	Model	Nugget (C_0)	Sill (C)	Range (m)	Spatial dependence (%)
Organic matter	Spherical*	0.060	0.519	1.35	88
pH	Exponential†	0.0040	0.0518	1.44	92
H_2O content	Exponential	0.00091	0.00137	2.06	34
Root mass	Linear‡	0.418	0.500	7.50	—
Micr. resp.	Linear	0.143	0.180	7.50	—
Net N mineral.	Linear	32.5	39.3	7.50	—
Nitrif. potential	Linear	57.1	65.9	7.50	—
Nutrient index	Exponential	29600	80400	0.82	63
Soil ammonium	Spherical	0.209	0.386	0.99	46
Soil nitrate	Exponential	0.170	0.317	1.07	46
Soil phosphate	Spherical	12.6	61.9	1.48	80
Soil potassium	Spherical	960	13300	1.39	93

* For $h \leq$ range, $\gamma(h) = C_0 + (((C–C_0)(1.5\ h/\text{range})) – (0.5((h/\text{range})^3)))$
$h \geq$ range, $\gamma(h) = C$

† $\gamma(h) = C_0 + ((C–C_0)(1-\exp(–3h/\text{range})))$; the range for the exponential model is defined as the distance at which the semivariogram value is 95% of $(C–C_0)$.

‡ $\gamma(h) = C_0 + (hC/7.5)$; the range for the linear model is arbitrarily set to be the maximum lag used in the analysis (7.5 m) and the sill (C) is the semivariogram value at that maximum lag.

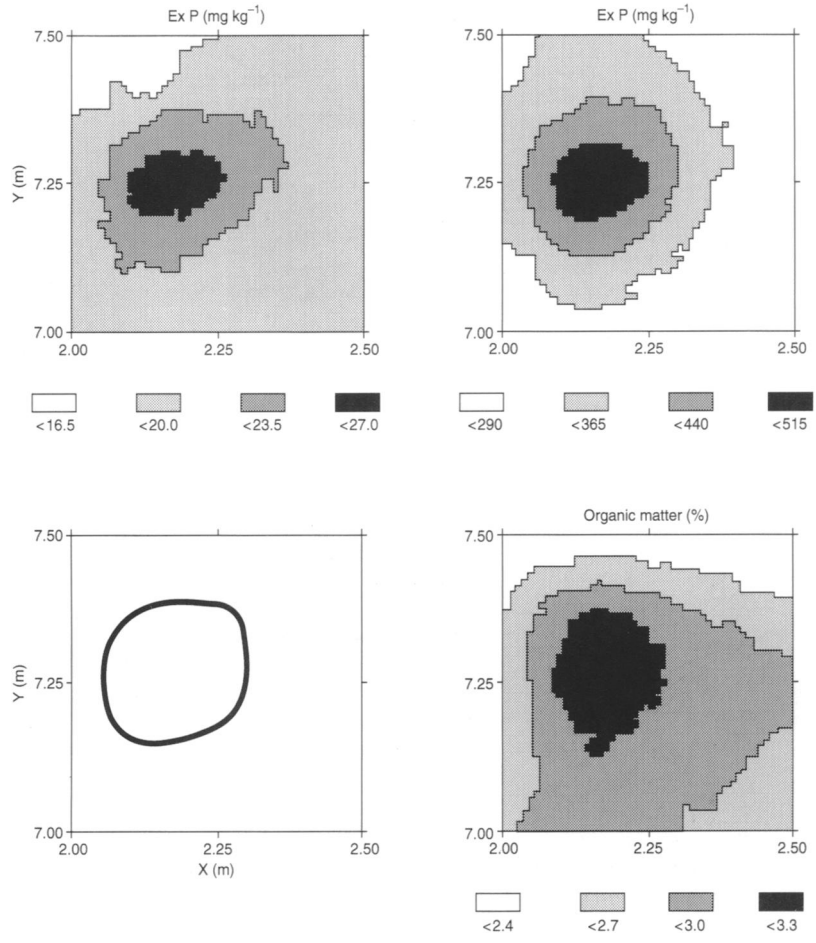

Fig. 4 Kriged (interpolated) soil contour plots for soil organic matter (% dry mass) and soil-extractable phosphate and potassium (mg kg^{-1}) in a 0.5-m x 0.5-m area around one of three *Pseudoroegneria* tussocks sampled in the experiment. The graph in the lower left represents the approximate location of the tussock (dark line) and the *x*- and *y*-axis of each graph represent the Cartesian coordinates of the 0.5-m x 0.5-m plot contained in the 10-m x 12-m sampling area.

individuals could theoretically be different if the same quantity of resource were presented in homogeneous and heterogeneous fashions. Questions of resource capture, a plant's associated costs, and subsequent effects on plant interactions may at times force us to specifically incorporate heterogeneity at a scale relevant to the individual plant.

Extractable levels of nitrate, ammonium, and phosphate at our site were quite low relative to agricultural soils (Barber 1984), and both N and P may limit growth at the site. If we assume that all or most of the extractable NO_3^- came from the soil solution, we can estimate solution NO_3^- from each extractable NO_3^- value and associated water content. Our approximate median for soil solution NO_3^- was 4 mg NO_3^-–N l^{-1} (or roughly 300 μmol l^{-1}). The range was 0.4–100 mg l^{-1}, with most of the values between 0.8 and 30 mg l^{-1}. These values are quite low relative to Reisenauer (1964), who found less than 5 % of 879 NO_3^- samples from agricultural soils to be below 25 mg NO_3^-–N l^{-1}. Since a less concentrated KCl extractant yielded somewhat lower NO_3^- values for our soil (data not presented), the actual values of soil solution NO_3^- at our site are probably even smaller.

It has been suggested for decades that soil variability increases with the area measured (e.g. Beckett & Webster 1971; Palmer 1990). However, in the absence of large-scale gradients in topography, soil depth, parent material, etc., our overall field variability may not actually be much greater than what we found, since 'within-field' variance often does not vary much with the size of the field (Beckett & Webster 1971). Smith *et al.* (1952) (cited in Beckett & Webster 1971) found little variability between grass yields in 0.03- and 0.4-ha plots. Ferrari & Vermeulen (1955) showed that pooled soil samples from fields 0.33- to 2.5-ha in size also had similar coefficients of variation.

Six of the soil parameters examined (soil organic matter, pH, phosphate, potassium, ammonium, and nitrate) showed strong spatial patterning at scales of less than a metre (Fig. 2; figure 2 in Jackson & Caldwell 1993). When additional semivariograms for these variables were calculated with samples from only the larger field grid (the 143 samples at 1-m spacings), all six of these semivariograms were completely flat, further emphasizing their lack of autocorrelation at scales greater than a metre. None of the three microbial processes we studied (nitrification potential, net N mineralization, and microbial respiration) showed any significant autocorrelation, even at the finest scales of 10–50 cm. Apparently our

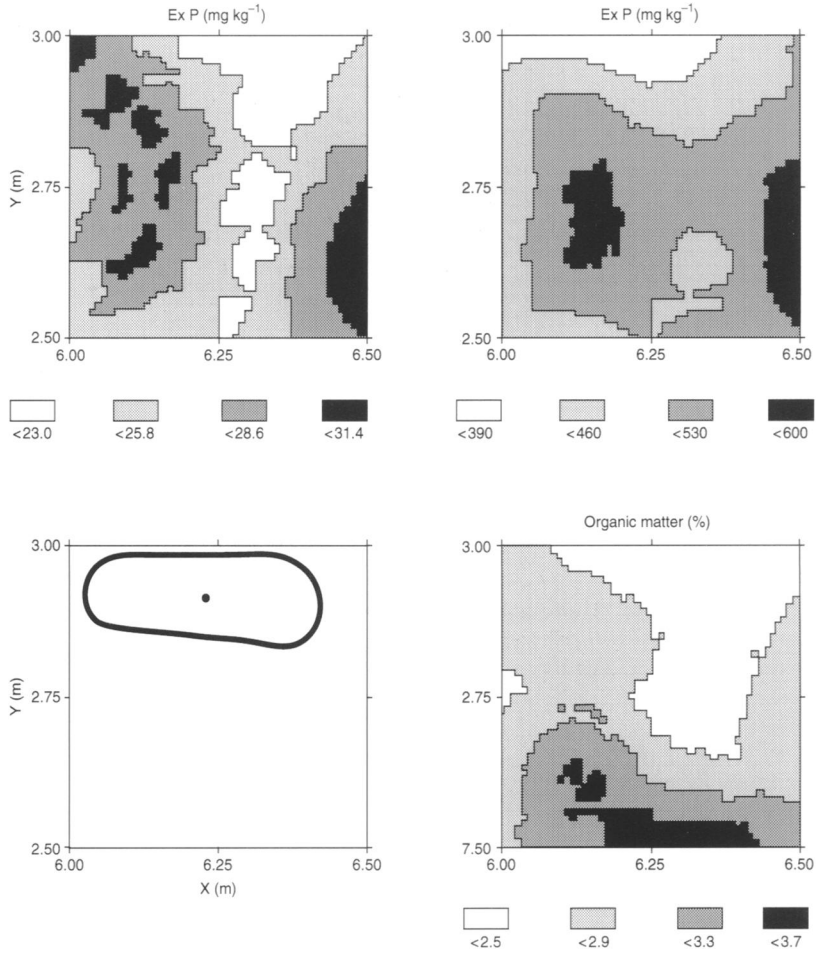

Fig. 5 Kriged (interpolated) soil contour plots for soil organic matter (% dry mass) and soil-extractable phosphate and potassium (mg kg^{-1}) in a 0.5-m x 0.5-m area around one of six *Artemisia* shrubs sampled in the experiment. The graph in the lower left represents the approximate location of the shrub canopy (dark line) and the location of the shrub stem (black dot); the *x*- and *y*-axis of each graph represent the Cartesian coordinates of the 0.5-m x 0.5-m plot contained in the 10-m x 12-m sampling area.

smallest scale of measurement was simply too coarse for these three variables to capture substantial spatial structure (Allen & Hoekstra 1991), though this might not be the case at other sites. Although Robertson *et al.* (1988) found essentially no spatial pattern for microbial respiration between scales of 1 m (their smallest scale) and 50 m in a Michigan old field, they did find significant patterning in N mineralization and nitrification at scales from 1 to *c.* 20 m, which they attributed, at least in part, to topographical features and accompanying gradients in water availability. Any site that contained strong patterns in such factors as parent material, topography, or aspect might be expected to show patterning of soil properties consistent with the scale of such factors.

Individual plants have been shown to influence soil properties in various ecosystems, including forest trees (Zinke 1962; Boerner & Koslowsky 1989), dune grasslands (Gibson 1988), and semi-desert shrubs and tussock grasses (Charley & West 1975; Schlesinger *et al.* 1990; Hook *et al.* 1991). Most of these studies have examined large, widely spaced individuals, comparing soil properties at one point directly under the plant canopy with a second point in canopy interspaces. Although such 'islands of fertility' were evident around the *Pseudoroegneria* tussocks in our study (Fig. 4), they were not as apparent with the *Artemisia* shrubs (Fig. 5), perhaps because of the relatively short stature and sparse open canopies of the shrubs, as well as apparently greater pocket gopher activity near the shrubs compared with tussock grasses. Gophers may disturb existing soil patterns that might otherwise form around undisturbed plants. Soil from gopher mounds has been shown in at least one study to have lower total N and P than in undisturbed surface areas, probably as a result of deeper, less fertile soil being moved to the surface (Koide *et al.* 1987).

In this paper and in Jackson & Caldwell (1993) we analysed the degree and scale of soil variability from scales of *c.* 10 cm to 10 m at a native sagebrush-steppe field site. Although our results show large variability both around individual plants and across the field site, the observed scale of that variability is, in our opinion, the most significant result. The three microbial processes (net N mineralization, nitrification potential, and microbial respiration) showed no apparent autocorrelation even at the finest scale measured of 12.5 cm. Soil organic matter and pH (this study) and soil ammonium, nitrate, phosphate,

and potassium (Jackson & Caldwell 1993) all demonstrated apparent autocorrelation only at spatial scales of less than a metre or so. These results imply that an individual shrub or tussock grass, which would likely have roots more than a metre apart, should encounter as much variation in soil properties in its individual rooting zone as found across the entire field plot. From the degree and scale of soil variability seen in these two studies, we conclude that root plasticity and active foraging in a heterogeneous soil environment are likely to be important to the nutrient balance of many plants.

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