

Notes and Comments

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THE SCALE OF NUTRIENT HETEROGENEITY AROUND INDIVIDUAL PLANTS AND ITS QUANTIFICATION WITH GEOSTATISTICS

R. B. Jackson^{1,2} and M. M. Caldwell¹

Heterogeneity in the soil is regularly invoked as important for competitive interactions among plants (Chapin 1980), but surprisingly few attempts have been made to examine in situ soil heterogeneity in the context of individual plants (Snaydon 1962). Variability around individuals is of fundamental importance because current theories of plant competition (e.g., Grace and Tilman 1990) differ in their treatments of heterogeneity and scale. Although quantifying scale has been historically problematic, statistical advances of recent decades (Matheron 1963, Burgess and Webster 1980) now provide tools for ecologists to specifically address scale and heterogeneity in their experiments (Robertson et al. 1988, Rossi et al. 1992).

In this study we use geostatistical techniques to quantify the scale and variability of soil nutrients at distances from 10 cm to 10 m in the field, with emphasis on the variability around individual perennial plants. The study area is 30 km south of Logan, Utah in a native sagebrush steppe (41°29' N, 111°47' W, 1575 m elevation); the soil is a silt loam formed from noncalcareous alluvial material. Average soil organic matter and pH are $\approx 2.7\%$ (dry mass basis) and 6.3%, respectively. Prevalent at the site are the native shrub *Artemisia tridentata* (Rydb.) Beetle and the native tussock grass *Pseudoroegneria spicata* (Pursh) A. Löve., both common Great Basin perennials. The sagebrush (*Artemisia*) plants tend to be relatively small (usually < 0.5 m tall with a fairly sparse canopy) for this species, but growth ring analysis of five plants showed several to be between 15 and 20 yr old. Neighbors of mature plants are sometimes closely spaced, in some cases within 0.5 m. Other plant genera present include *Balsamorhiza*, *Zigadenus*, *Viola*, *Poa*, and *Lomatium*.

¹ Department of Range Science and the Ecology Center, Utah State University, Logan, Utah 84322-5230 USA. Address for correspondence.

² Department of Mathematics and Statistics, Utah State University, Logan, Utah 84322-3900 USA.

Plants at the site experience some browsing by mule deer. Substantial small-scale variation in the soil surface was apparent due to ant and gopher activity and narrow cracks (as much as 30 cm in depth), probably arising seasonally from wetting and drying of the soil.

We established a 10 × 12 m grid in the spring of 1991 with points sampled every metre (143 samples). Within this grid we also centered 0.5 × 0.5 m grids around six *Artemisia* and three *Pseudoroegneria* plants, sampling at a second scale of 12.5 cm between adjacent points (25 samples around each plant, 225 total sam-

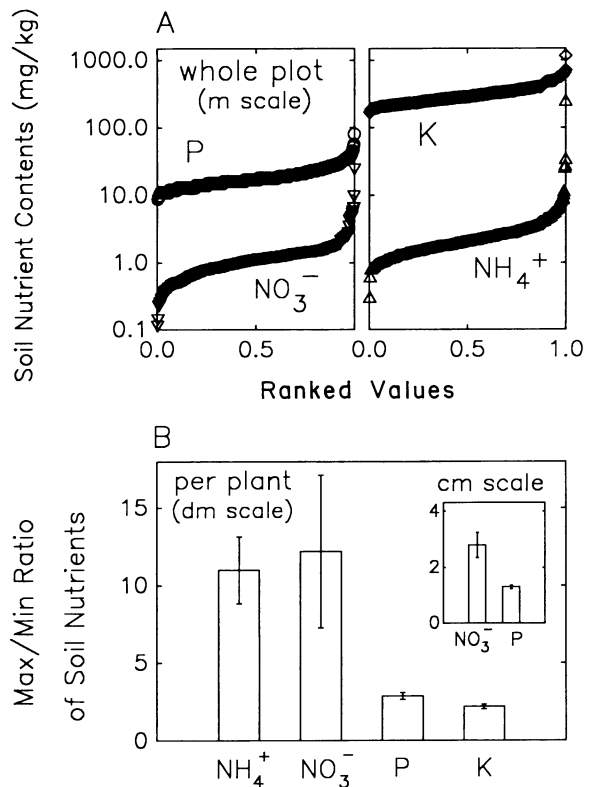


FIG. 1. The values of all 362 soil samples (NH_4^+ , NO_3^- , P, and K) ranked in ascending order for each nutrient (A) and the average ratio of maximum to minimum soil NH_4^+ , NO_3^- , P, and K (mean, ± 1 SE shown by line width) in 0.25 m² areas around nine perennial plants (B). A 10 × 12 m grid was established in a native sagebrush steppe with soil nutrients sampled every metre. In addition, nested 0.5 × 0.5 m grids were centered on six *Artemisia tridentata* and three *Pseudoroegneria spicata* 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. In a separate sampling, pairs of soil samples 3 cm apart were taken in the rooting zone of 20 individual plants. The average ratio of NO_3^- values for each pair was more than twice the average P ratio even at distances of only 3 cm (B, inset).

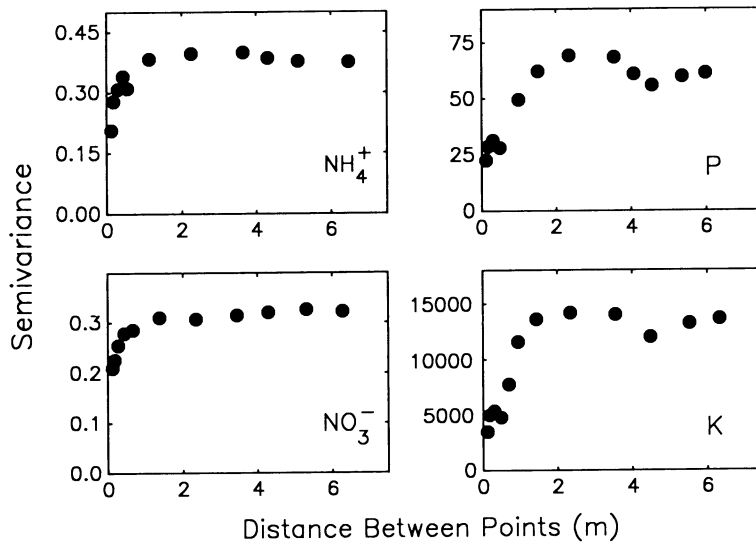


FIG. 2. Variograms of soil NH_4^+ , NO_3^- , P, and K in the 120-m² field plot. Variograms stratify calculated variances by the distance (lag) separating each pair of points. The minimum and maximum pair distances used in the calculations were 12.5 cm and 7 m, and over 40 000 calculations are used in each graph. The units for each nutrient were mg/kg soil; because the distributions of NH_4^+ and NO_3^- were positively skewed their values were ln-transformed prior to analysis. Variograms for each nutrient show increasing autocorrelation at scales of <1 m, but substantial variability remains even at 12.5 cm.

ples at the finer scale). Cores of 4 cm diameter and 10 cm depth were taken at each point, and all 362 sample points were cored in 2 d in early May. The soil from each position was well mixed, and a subsample for NH_4^+ and NO_3^- analysis was immediately placed in 2 mol/L KCl. NH_4^+ and NO_3^- extracts were filtered through number 1 Whatman filters previously rinsed with KCl and were tested by continuous flow analysis using a Lachat autoanalyzer; H_2PO_4^- and K^+ were measured colorimetrically in extracts of 0.5 mol/L NaHCO_3 (Olsen and Sommers 1982). Field samples analyzed strictly for sampling variability (four replicate samples at one position) had coefficients of variation <10% for each nutrient.

Geostatistical variograms stratify calculated variances by the distance (or lag) between pairs of points (Isaaks and Srivastava 1989). What emerges is a representation of spatial autocorrelation, points closer together often having lower variances than points farther apart. Variograms for extractable NH_4^+ , NO_3^- , P, and K were calculated with the EPA program Geo-EAS, using a minimum pair distance of 12.5 cm and a maximum of ≈ 7 m (<50% of the largest distance). Because of the nested structure of the data, variogram lag intervals were specified to be shorter for lag distances of <0.75 m, to more clearly present the results at these finer scales. Each variogram lag class had at least 250 pairs of points, and over 40 000 pairs were used for each variogram. There was no evidence of anisotropy in the data, but because the distributions of NH_4^+ and NO_3^- were positively skewed their values were log nor-

mally transformed prior to analysis (Webster and Oliver 1990).

Nutrient heterogeneity at the site was quite high, with both NH_4^+ and NO_3^- varying by 2–3 orders of magnitude and P and K close to one order of magnitude within the 10×12 m area (Fig. 1A, data for each nutrient plotted in ascending order). Replicate cores taken at all points for assays of soil-solution ammonium and nitrate (data not presented) corroborated the more extreme values seen in the ranges of these two nutrients (Fig. 1A). The mean values across the plot for soil phosphate and potassium concentrations were 19 and 315 mg/kg, and the median values for ammonium and nitrate were 2.2 and 1.1 mg/kg (the median is a more robust measure of central tendency for skewed distributions). Within the 0.5×0.5 m subplots, NH_4^+ and NO_3^- varied by an average factor of 11 and 12, respectively, with smaller average variation for P and K (Fig. 1B). Variograms for each of the four nutrients demonstrated increasing autocorrelation, but only at spatial scales of <1 m (Fig. 2). Beyond this scale each variogram is essentially flat, indicating the region where classical assumptions of statistical independence may be justified. This important result implies that an individual plant with roots a metre or so apart encounters the same degree of soil variability as found across the entire field plot. The variograms also mirror the greater small-scale heterogeneity in N, since the variance at the y axis (nugget) appears proportionally higher for either form of N than for P or K (Fig. 2).

At a second site we measured NO_3^- and P in 20 separate sets of paired 100-mg soil samples (3 cm between the two samples) in the shared rooting zones of *Artemisia* and *Pseudoroegneria* plants (data not included in the variograms). Nitrate varied by an average factor of 2.8 for each pair while P only varied by an average factor of 1.3 ($P < .01$ by paired t test, Fig. 1B inset). One might expect greater heterogeneity for N at small scales since NH_4^+ and NO_3^- are more susceptible to localized microbial transformations and immobilization than P or K.

Despite the potential importance of soil heterogeneity, few studies have addressed the variability associated with individual plants. Studies with large, widely spaced perennials have tended to compare soil nutrients under plant canopies with those in canopy interspaces (e.g., Charley and West 1975, Burke et al. 1989) and have sometimes identified "islands of fertility" apparently induced by the plants themselves. Though plants may sometimes induce patterning in soil properties, individuals may also respond to heterogeneity caused by abiotic and other biotic sources. Visible surface features at our site included ant and gopher activity and deep cracks in the soil. Such local variation in potential water-flow pathways may, for example, contribute to small-scale variation in nutrient availability, though water may also potentially smooth existing soil heterogeneity.

Plants possess a suite of potential mechanisms for exploiting soil heterogeneity, including root proliferation, changes in nutrient uptake kinetics, and changes in the frequency of mycorrhizal infection (Drew and Saker 1975, Jackson et al. 1990). These traits vary among species (Jackson and Caldwell 1989, Campbell et al. 1991) and may be important in explaining competitive effectiveness. Identifying the structure and range of soil variability and incorporating this information into stochastic soil models is one mechanism for testing the importance of plant responses to small-scale heterogeneity. We believe the explicit modelling of heterogeneity in natural and agricultural systems will yield substantial insight into competitive dynamics among plants.

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