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Spatial heterogeneity of soil respiration and related properties at the plant scale

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Abstract

Geostatistical techniques were used to quantify the scale and degree of soil heterogeneity in 2 m^2 plots around 9-year-old poplar trees and within a wheat field. Samples were taken during two years, on an unaligned grid, for analysis of soil respiration, C and N content, available P, gravimetric moisture, pH, nitrification potential, and root biomass. Kriged maps of soil respiration, moisture, and C content showed strong spatial structure associated with poplar trees but not with wheat rows. All soil properties showed higher autocorrelation in June than in April. Isopleth patchiness for all variates was less in June. This was associated with lower respiration rates due to lower litter decomposition. From the degree and scale of heterogeneity seen in this study, we conclude that the main causes of soil heterogeneity at this scale (2 m^2) are likely to be found at micro scales controlled in part by plant root and plant residue patterns. These must be understood in the evaluation of ecosystem processes.

Introduction

Soil respiration accounts for about 25% of global CO_2 evolution (Bouwmann and Germon, 1998), but is difficult to quantify because it is one of the most variable parameters in soils (Aiken et al., 1991). Coefficients of variation for soil respiration range from 35% in grasslands (Pol-van Dasselaar et al., 1998) to 150% in corn and soybean fields (Cambardella et al., 1994). Much of that heterogeneity occurs over short distances (Heilmann and Beese, 1992; Robertson et al., 1997). Soil respiration is the sum of root and microbial respiration, with root respiration contributing 20 to 50% of the total CO_2 (Ben-Asher et al., 1994; Paul and Clark, 1996). Non-root respiration is an indicator of the microbial activity that regulates nutrient dynamics and soil organic matter (SOM) turnover.

Information about the spatial and temporal distribution of soil respiration is useful for: (1) understanding nutrient and SOM dynamics in ecosystems, (2) assessing the contribution of soil respiration to the global CO_2 budgets, and (3) guiding sampling-design decisions for both research and site–specific farming applications. Soil processes produce a complex series of related gradients of nutrient availability, moisture, and oxygen supply. These location and scale-dependent gradients function over a number of scales, from individual enzyme reactions through microbial cells to plant scale and landscape effects.

Different processes operate at various scales to create a pattern of nested variability (Robertson and Gross, 1994). The measurement scale needs to be chosen to match the phenomena studied. The spatial and temporal distribution of soil respiration is defined by the overlapping distributions of substrates, soil physical conditions, soil organisms, and temperature and moisture conditions. Since these are often found in restricted areas, microbially mediated processes such as denitrification (Parkin, 1993), are often found in 'hot spots' only a few square centimeters in size (Heil-

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mann and Beese, 1992; Morris, 1999; Parkin, 1993). Geostatistics are useful for describing these spatially structured phenomena. Classical parametric statistics cannot be used to evaluate autocorrelated data without violating the central assumption of sample independence. Yet virtually all environmental samples are autocorrelated: samples taken from locations close to each other tend to be more similar than samples taken farther apart. Geostatistics provides a means for defining this autocorrelation and for using the knowledge about its strength and scale to interpolate the value of the variates at unsampled locations.

The central tool in geostatistics is the semivariance statistic, which is defined as:

$$2\gamma(h) = E[(Z_x - Z_{x+h})^2]$$

where $\gamma(h)$ is the semivariance for all locations separated by the distance interval h, and $E(\bullet)$ is the expectation of the squared difference between variate Z at location x and $x + h$. Graphing the semivariance values across all separation distances provides the semivariogram, which summarizes both the degree of autocorrelation present and the geographic range over which it is significant. For a spatially dependent variate, the semivariogram should theoretically increase asymptotically from the origin. The asymptote is equivalent to the sample variance past the range of autocorrelation. Where no autocorrelation occurs at the scales examined, the semivariogram does not rise from the origin but exhibits what geostatisticans call a pure nugget effect, that is a value equivalent to the sample variance at all separation distances. Various fitting procedures are used to estimate the semivariogram parameters from the experimental semivariogram (Cressie, 1993). The semivariogram parameters can also be estimated by jackknife kriging (Lamorey and Jacobson, 1995). This procedure uses a non-linear fitting routine to optimize the semivariogram parameters by minimizing the sum of the kriging variances.

When spatial dependence is present, the semivariogram can be used in kriging algorithms to weight the samples used for interpolating a value for an unknown location. In kriging, neighboring samples within the range of spatial dependence are assigned weights based on their distance from the unknown point and the degree of autocorrelation present. See Goovaerts (1999) or other geostatistical reviews for a complete description of the kriging system.

Geostatistics has been used to describe spatial variability at the landscape scale (Amador et al., 1997; Kluitenberg et al., 1997; Meredieu et al., 1996) and recent studies have shown that spatial dependence at scales relevant to individual plants can explain a large proportion of the sample variance within individual fields (Gross et al., 1995; Robertson et al., 1993; Schlesinger et al., 1996). Selles et al. (1999) used semivariograms to show the close association between chemical and biological measures of N-supplying power to develop a soil test for this soil parameter. The objective of this study is to investigate the spatial and temporal variability of soil respiration and its controls at the plant scale to provide more efficient sampling and better conceptual data interpretation.

Methods

Sampling

Our study sites were located at the W.K. Kellogg Biological Station (KBS) Long-term Ecological Research (LTER) site in southwest Michigan, USA (85° 24′ W longitude, 42° 24′ N latitude). KBS is located in the southern Great Lakes region of the USA on a pitted outwash plain of the morainic system left by the last retreat of the Wisconsin glacier. Soils are either fine-loamy or coarse loamy, mixed, mesic Hapludalfs (Whiteside et al., 1959). Mean annual temperature is 9 °C. Mean precipitation is 920 mm annually, spread evenly throughout the year; potential evapotranspiration exceeds precipitation in summer months.

Nine-year-old poplar and winter wheat plots in a maize, soybean, wheat rotation (3 reps) were sampled twice between early April and late June 1998. The poplar plots were also sampled during August and September 1997. In each plot, we took 60 soil cores, 1.5 cm diameter by 7 cm in depth, from a 1 × 2 m area within the poplar plots and from a 1.2 × 1.7 m area within the wheat plots. There was a tree in the middle of each sampling plot in the poplar plots and 8 or 10 wheat rows in each wheat plot. Cardboard stencils were used to determine the location of 48 sample points. The remaining sample points were placed adjacent to a randomly selected set of 12 of the 48 points. Steel tubes (1.5 cm diameter, 20 cm depth) were used to sample the soil at each location. We also collected samples (30 samples from each of three plots) from the 0–7 cm, 7–14 cm and 14–21 cm layer in 1 m^2 wheat plots during July. Soil cores for each grid were sampled within one hour (one grid per day). The tubes were closed at each end by a rubber septa and immediately transported to the laboratory for analysis.

Analyses

Carbon dioxide was determined by injecting 0.5 ml of head space gas into an Infrared-Absorbtion-Gas-Analyzer (EGA Carbon Dioxide Analyzer, ADC Hoddesdon, England). Measurements were made at 0, 3, and 5 hours after closing the tubes. Respiration was calculated by fitting a zero order model to the sample points. Soil moisture was calculated from mass loss on drying at 60 °C for 48 h. Root weights were determined by sieving the dried soil samples through a 2-mm sieve and hand-picking and weighing visible root fragments. Total C and N were determined by dry combustion using a C/N-analyzer (Carlo-Erba NA 1500 NCS, Milano, Italy).

Nitrification potentials were measured using a soil-slurry method (Hart et al., 1994). Nitrate analysis was performed using the Quick Chem method (12-107-04-1-A Revision 86) on a LACHAT-instrument (Lachat Instruments, Milwaukee, WI). Phosphorus was extracted using Bray P1 solution (Recommended Chemical Soil Test Procedures for the North Central Region 1998). Color development was measured by a Brinkmann PC800 Fiberoptic Probe Colorimeter.

Some CO_2 could have originated from physically trapped gas released due to the soil disturbance during sampling. We tested this possibility by: (1) flushing some closed tubes prior to incubation with CO_2-free air and (2) evacuating and refilling tubes with laboratory air. If less CO_2 was produced in the flushed tubes than in the control tubes (normal assay) this would indicate release of physically trapped CO_2 during normal sampling.

Statistical analyses

Geostatistical analysis (Goovaerts, 1998) such as semivariogram model fitting and mapping was performed using GS+ (Gamma Design, 1995). We estimated the semivariogram by the equation:

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{x=1}^{n} (z_x - z_{x+h})^2$$

where $n(h)$ is the number of lag pairs at distance interval h, and z is the value of the parameter at location x and $x + h$. To estimate the semivariograms, the replicate plots were combined by placing them on the same coordinate system, offsetting them by 10 m and restricting the search radius for the semivariogram calculation to less than 2 m. In this manner all of the short distance pairs were used for the semivariogram estimation. Non-normal data were log-transformed to stabilize the variance, and normality tests were recalculated using the transformed data.

Table 1. Comparison of the heterogeneity of soil properties with depth

		0–7 cm		14–21 cm	
		Mean	CV (%)	Mean	CV (%)
CO_2-C	$\mu g\ g^{-1}\ h^{-1}$	1.06	64	0.38	63
Moisture	$g\ kg^{-1}$	104.3	17	58.9	25
Carbon	$g\ kg^{-1}$	8.42	13	8.11	21
Nitrogen	$g\ kg^{-1}$	0.83	9.6	0.84	19
Root weight	$g\ kg^{-1}$	16	187	21	300

Measurements were performed in the wheat plots during June 1998 (average of 3 grids with 30 samples each).

Backtransformations followed Krige (1981) prior to mapping. Semivariograms for all variables were fitted to a spherical, exponential or linear model by a least squares technique (Gamma Design, 1995). Several semivariograms were also modeled by jackknife optimization (Lamorey and Jacobson, 1995) to check the semivariogram parameters estimated by the least squares technique. While jacknifing does not provide the assurance that the semivariogram model is correct, it can be used to flag an incorrect model. Maps were interpolated using ordinary block kriging at a block size of 5 cm. When severe drift was detected a plane was fitted through the data, and semivariogram modeling and kriging estimation were performed on the residuals. To separate the nugget effect due to analysis error from the nugget effect due to microscale variability, we followed the procedure outlined by Goovaerts and Chiang (1993). Briefly, the cross-semivariograms are examined for the presence of a large nugget effect, which would indicate that the variability is mainly due to microscale variability that is common to the two variables. A small nugget effect in the cross-semivariogram would indicate that measurement errors contribute to the microscale variability. Cross-semivariograms were calculated using the gamv program of the gslib library (Deutsch and Journel, 1998).

Results

Parameters and coefficient of variation

Tubes flushed with CO_2-free air did not exhibit lower respiration rates than control tubes (2.2 vs. 1.7 μg

Table 2. Soil respiration, root weight, total C and N content of samples taken in a 0–7 cm depth (average of 3 grids with 60 samples each) in April and June. Available P, pH and nitrification potential (average of 3 grids with 30 samples each) in June

			April		June	
			Mean	CV (%)	Mean	CV (%)
Poplar	CO_2-C	$\mu g\ g^{-1} h^{-1}$	1.41	37	1.18	36
	Roots	$g\ g^{-1}$	0.006	83	0.008	38
	Carbon	$g\ kg^{-1}$	12.34	20	14.52	28
	Nitrogen	$g\ kg^{-1}$	1.02	19	1.23	54
	pH [a]				7.32	7
	Avail. P	$mg\ kg^{-1}$			43.42	50
	NPEA [b]	$mg\ NO_3\ kg^{-1}\ h^{-1}$			0.25	52
Wheat	CO_2-C	$\mu g\ g^{-1} h^{-1}$	0.97	57	1.10	64
	Roots	$g\ g^{-1}$	0.001	100	0.002	250
	Carbon	$g\ kg^{-1}$	10.12	8	7.83	12
	Nitrogen	$g\ kg^{-1}$	1.0	10	0.7	9
	pH				7.09	8
	Avail. P	$mg\ kg^{-1}$			34.16	84
	NPEA	$mg\ NO_3\ kg^{-1}\ h^{-1}$			0.63	22

[a] pH in water (1:1).
[b] Nitrification Potential determined with Nitrification Potential Enzyme Assay (NPEA).

$g^{-1}\ h^{-1}$ CO_2-C). We concluded that trapped CO_2 did not affect our measured respiration rates. In the wheat plots sampled in June (Table 1), the CO_2 evolved from the surface (0–7 cm) soil (1.06 μg C $g^{-1}\ h^{-1}$) was three times that at the lower 14–21 cm depth (0.38 μg C $g^{-1}\ h^{-1}$), which had a lower moisture content. The values for C and N content as well as root weight of these cultivated plots did not change significantly ($p > 0.05$) with depth. Most soil respiration studies are conducted for longer periods than our study. We calculated the rate from a zero order linear function over 5 hours. Test incubations for longer periods showed that the established rate stayed constant for at least 48 h.

Soil surface respiration from the poplar plots was higher in April than in June; the reverse was true in the wheat plots (Table 2). Total C and N content of the surface samples did not change significantly between the April and the June samples, but were higher in the poplar than in the wheat soil. Average soil respiration was higher in the poplar (1.29 μg $g^{-1}\ h^{-1}$) than in the wheat plots (1.03 μg $g^{-1}\ h^{-1}$). Soil respiration in April ranged from 0.50 to 3.22 μg g^{-1} soil h^{-1} CO_2-C (SD = 0.53) in poplar and from 0.30 to 3.40 μg g^{-1} soil h^{-1} CO_2-C in wheat (SD = 0.55). Carbon and N were more consistent in the wheat plots than the poplar, reflecting the mixing action of tillage (Table 2). Phosphorus content was slightly but not significantly

Table 3. Correlation coefficients for the poplar (top) and wheat (bottom) plots. The upper triangular area contains the April correlations, the lower area the June correlations

Poplar	CO_2	Root weight	Moisture	Nitrogen	Carbon
CO_2		0.549*	0.563*	0.477*	0.614*
Root weight	0.441*		0.380	0.314	0.398
Moisture	0.401*	0.118		0.553*	0.682*
Nitrogen	0.192	0.113	0.092		0.890*
Carbon	0.185	0.146	0.062	0.950*	
Wheat					
CO_2		0.712*	0.566*	0.236*	0.200
Root weight	0.553*		0.528*	0.169	0.103
Moisture	0.648*	0.467*		0.412*	0.379
Nitrogen	0.030	0.230	0.150		0.657*
Carbon	0.088	0.170	0.049	0.708*	

*Significant for $p < 0.05$, $n = 180$.

higher in the poplar than in the wheat plots, while the average nitrification potential was over twice as high in the wheat (0.63 mg NO_3-N $kg^{-1}\ h^{-1}$) than in the poplar plots (0.25 mg NO_3-N $kg^{-1}\ h^{-1}$).

The soil biotic parameters showed a great deal of heterogeneity (Table 2) over the 2 m^2 plots. Roots did not exploit all of the soil volume evenly. The coefficient of variation (CV) for root weight was 38–83% in the poplar and 100–250% in the wheat plots. Soil respiration was next most variable (CV of 36% for poplar and 57 to 64% for wheat). Total C was more variable in the poplar (CV $\cong$ 20–28%) than in the wheat plots (CV $\cong$ 8–12%) reflecting the mixing effect of tillage in the wheat. In both ecosystems, the coefficient of variation for C was higher in the June sample than in the April sample. Total N was more variable in the poplar (CV $\cong$ 20–55%) than the wheat plots (CV $\cong$ 8–10%). The variability in the nitrification potential (NPEA) was higher in the poplar than in the wheat, although the average rate was higher in the wheat plots. Phosphorous concentrations were more variable in the wheat (CV $\cong$ 84%) than in the poplar plots (CV $\cong$ 50%). The variability in the pH was similar on both plots.

Correlations

We found the highest correlations between N and C (r = 0.89) in the poplar plots (Table 3), followed by the correlations between moisture and C content as well as between soil respiration and moisture. In wheat, the correlation between soil respiration and root weight was highest (r = 0.71), while the correlation between N and C content as well as between respiration and

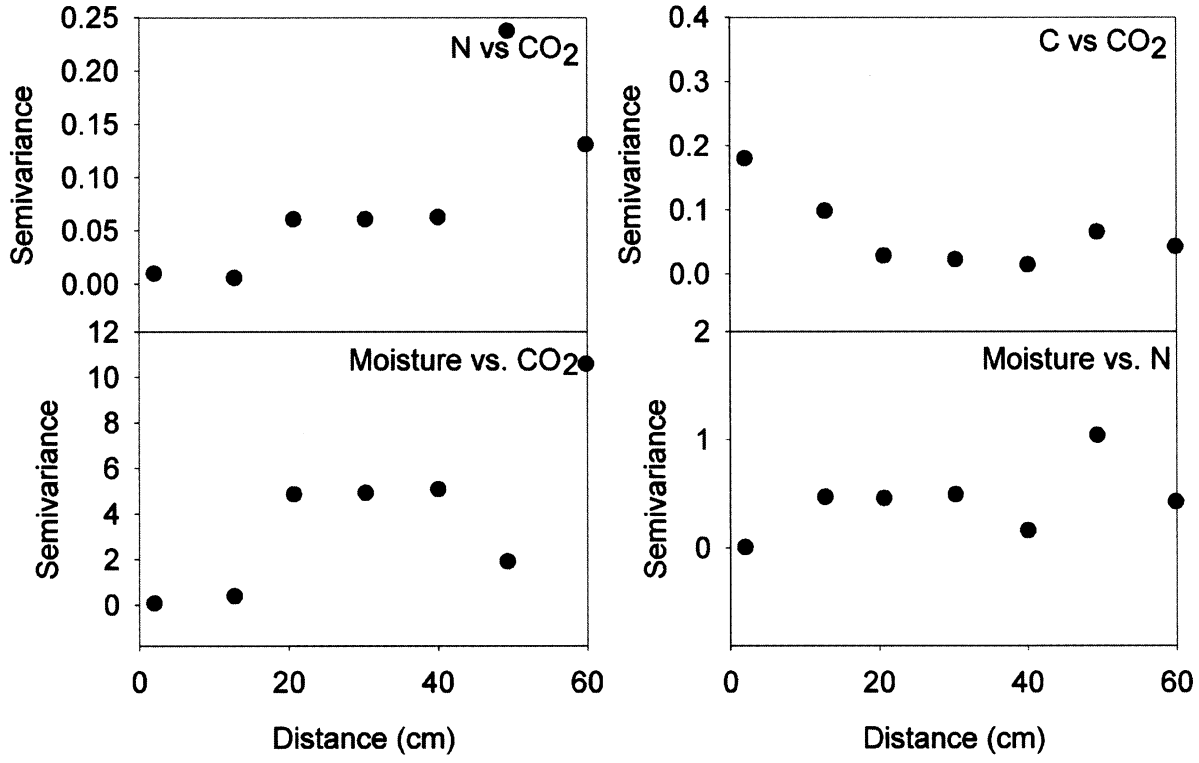

Figure 1. Sample cross-semivarograms for the poplar site in April.

moisture were lower (Table 3). No significant correlations were found between root weights vs. total C or N. The correlation between moisture vs. C or N was stronger in April than in June. The correlations also changed with the crop. Carbon and soil respiration were highly correlated in the poplar plots, but not in the wheat plots. The high correlation between C and soil respiration is probably a result of the correlation between C and moisture retention. Consequently, the lack of significant correlation between soil respiration and C in the wheat plots could reflect lower SOM, or higher transpiration in the wheat plots. The highest correlation was found for soil respiration and root weight in wheat during April. This could be due to respiration of the excised roots. This correlation is also reflected in the difference between rows and inter-rows for the root weight in the wheat plots (data not shown). Map similarities (Figure 1) between soil variables also reflects these correlations.

Semivariograms

The range of autocorrelation for N in the poplar plots was much longer in June (198 cm) than in April (45 cm). Moisture, which failed to reach a sill in the April sample, had a range of 35 cm in June. The root data was log-transformed to yield a more symmetrical distribution. The range of autocorrelation for the roots was 19 cm in April vs. 85 cm in June. The structural variance for CO_2, C and N varied between 59% and 84% of the total variance. The variance was less structured in the wheat plots. CO_2 was autocorrelated to 9 cm in April and 26 cm in June. At both sampling dates, C was unstructured at the ranges measured, while N had a range longer than the plot size. Moisture was autocorrelated to 140 cm in April and failed to reach a sill within the sampling area in June. Root weights were uncorrelated in April, but autocorrelated within 15 cm in June when the structural variance was 100% of the total variance. The ranges of autocorrelation for respiration in wheat increased from 29 cm at the surface to 74 cm in the 14–21 cm depth. Approximately 80% of the variance was structured at the July sample

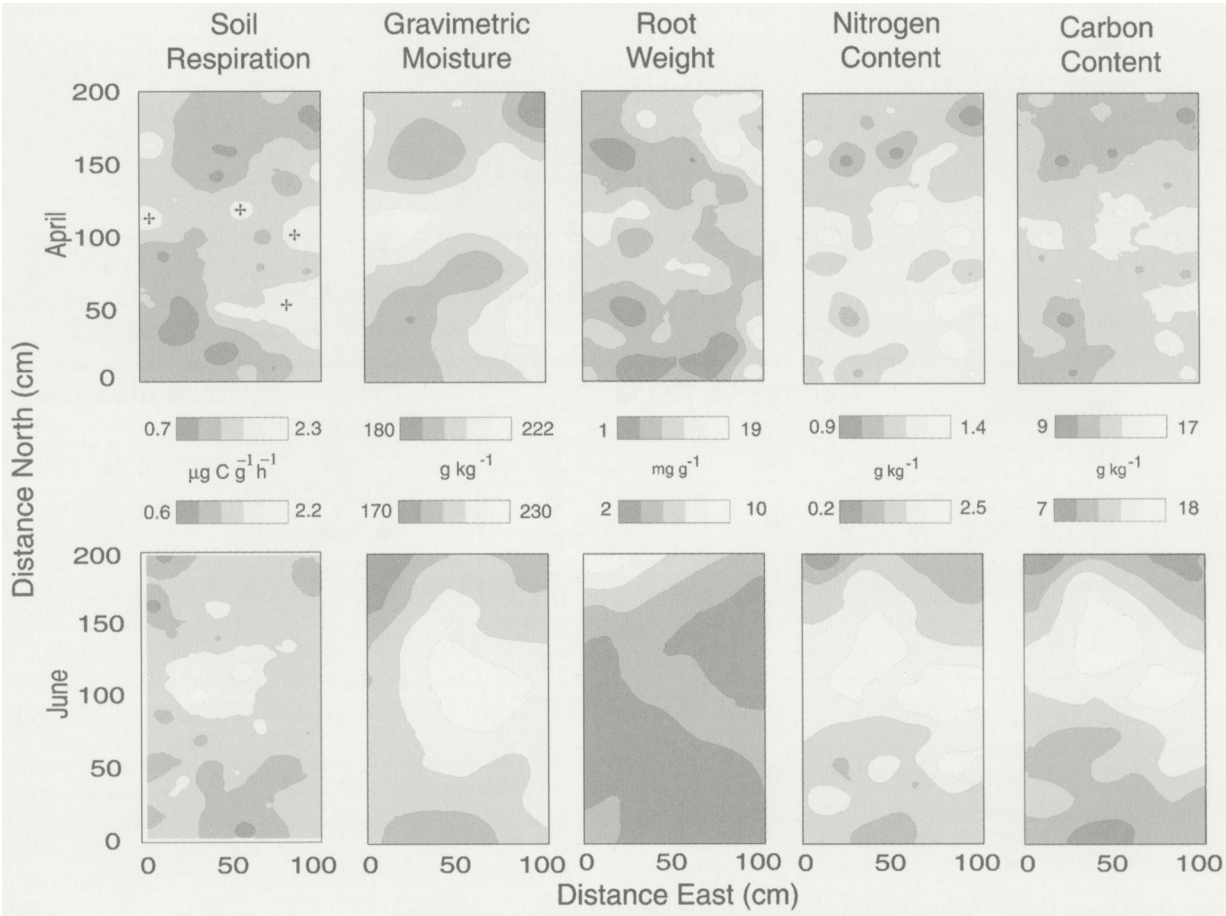

Figure 2. Isopleths for soil variables across a representative poplar grid for April and June: soil respiration, gravimetric moisture, root weight, N and C content. The poplar tree was located in the center of the plot. Crosses on the respiration map indicate the locations of earthworm-castings.

date. Nitrification had a range of 10 cm in the poplar plots and more than 74 cm in the wheat plots. In the poplar plots, 69% of the variance was structured while only 25% was structured in the wheat plots. The jackknife optimization produced similar ranges but smaller nugget effects than the least-squares fitting of the graphical semivariograms (Table 5). Estimates from the jackknife optimization appeared to be more sensitive to the input and starting parameters, reflecting the low number of points per plot. The graphical semivariogram fitting the replicate samples could be combined to yield one graph, while the jackknife optimization used each plot separately.

To better understand the small scale variability, we took 48 samples in a 14 × 14 cm-plot in the wheat. Figure 3 illustrates the small-scale variability of soil respiration. It shows a hot spot (2.5 μg CO_2 g^{-1} h^{-1}) in the lower left quadrant, surrounded by larger areas of low values (1 μg CO_2 g^{-1} h^{-1}). The difference between adjacent samples (1.5 cm diameter) was as much as 2 μg CO_2 g^{-1} h^{-1}. These large changes over short distances caused the behavior of the semivariogram at the closest lag distances to be extremely variable. To check that these differences were not caused by the disturbance of soil during tube insertion we sampled several grids by pushing both tubes (the tubes were taped together) into soil at the same time. Because the semivariance for the pairs did not depend on the manner of tube insertion, we believe that soil disturbance during sampling is not the cause of the high small-scale variability. The cross-semivarograms involving N, moisture and CO_2 tended to have a small nugget effect (Figure 1) while those between C and CO_2 and between total N and C (not shown) had a large nugget effect. This would suggest a common cause of microscale variability for total C and CO_2 and the total N and C.

Table 4. Fitted semivariogram parameters for the poplar and wheat plots in April and June and July

Sample	Parameter	Model	Nugget variance	Sill variance	Range (cm)	Structural variance (%)	r^2
				Poplar			
April	CO_2	Exp[c]	0.077	0.29	11.7	74	0.8
	C	Exp	0.017	0.066	24.9	73	0.9
	N	Exp	0.0001	0.0004	45.9	75	0.7
	Moisture	Lin[a]	1.102	1.513	>113		0.5
	Roots (log)	Exp	4E-6	5.5E-6	18.9	93	0.4
June	CO_2	Exp	0.288	0.949	6.0	70	0.7
	C	Exp	0.015	0.099	13.8	85	0.3
	N	Exp	0.016	0.039	198	59	0.8
	Moisture	Sph[d]	0.980	10.8	35.0	91	0.5
	Root (log)	Sph	0.80	1.1	85	27	0.6
				Wheat			
April	CO_2	Exp	0.050	0.204	9.0	75	0.4
	C	Nugget					
	N	Lin[a]	5E-5	7E-5	>154		0.001
	Moisture	Sph	0.295	0.591	139	50	0.9
	Root (log)	Nugget					
June	CO_2[b]	Exp	0.041	0.137	25.8	70	0.9
	C	Nugget					
	N	Lin[a]	2.9E-5	4.9E-5	>94		0.4
	Moisture	Nugget					
	Root	Sph	0	1.36E-5	15.2	100	0.5
				July CO_2			
	0–7 cm	Sph	0.16	0.907	28.9	82	1.0
	7–14 cm	Exp	0.071	0.244	45.3	71	1.0
	14–21 cm	Sph	0.289	1.559	74	82	0.6
				Nitrification			
	Poplar	Exp	0.004	0.013	9.6	69	0.9
	Wheat	Lin[a]	0.012	0.016	>74		0.005

[a] For linear models the equation is presented as semivariogram = Nugget + h((Sill-Nugget))/Range.
[b] Only used Rep 2 and 3 with values below 2.
[c] Exponential.
[d] Spherical.

Isopleths

Maps help to localize areas of high coincidence. Kriged isopleths for all variables show a patchy pattern with small, scattered, hot spots (Figures 2 and 5). Hot spots (the lightest areas on the maps) in soil respiration, as well as C (and to a lesser extent N) content in the April poplar samples occurred where earthworm casts were found at the time of sampling (Figure 2). High values for soil respiration, gravimetric moisture, C and N content were found in June close to the tree in the middle of the grid (Figure 2). Similar patterns were found the year before (Figure 5a). These patterns show spatial structure at the plant scale that might be due to the higher accumulation of litter around the tree trunks. Nitrification potential was highest next to the tree trunk and fell off gradually away from the tree (Figure 6). The wheat plot had higher overall nitrification potential with an average of 0.63 mg kg^{-1} h^{-1}, relative to 0.25 mg kg^{-1} h^{-1} in the poplar. This occurred as a few scattered high spots surrounded by a fairly even background.

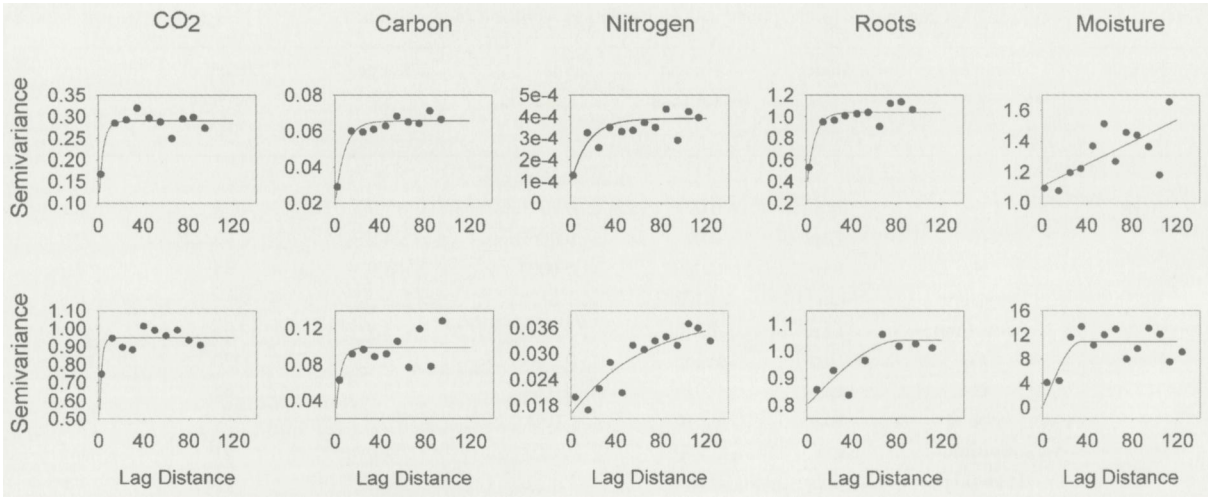

Figure 3. Semivariograms for soil respiration, moisture, root weight and total N and C content for the poplar plots in April (top) and June (bottom).

Table 5. Semivariogram parameters for the poplar samples in April as estimated by the jackknife optimization procedures

Variate	Nugget variance	Sill variance	Range (cm)
N	3.74E-7	0.0004	10.5
C	2.1E-11	0.066	14.1
CO_2	0.075	0.29	21.9

Discussion

Highly significant correlations between C and N content, soil respiration and moisture, and soil respiration and root biomass could help to model soil respiration and explain some of the reasons behind the extreme heterogeneity. There were fewer significant correlations in June than in April. In both treatments the correlation between moisture and N disappeared, indicating that organic matter helps control moisture by retention of water at lower moisture stresses (Grahammer et al., 1991). Loss of this relationship in June could be caused by the increased water capture by wheat roots (Thierron and Laudelout, 1996).The presence of short-range autocorrelation in soil nutrients has been demonstrated in a number of studies (Kluitenberg et al., 1997; Palmer, 1990; Schlesinger et al., 1996). The ranges of autocorrelation reported in different studies are dependent on the sample size, and sample intervals. The range of autocorrelation reported varies between 80 m for total organic N in an Iowa farm field (Cambardella et al., 1994), 20 m for nitrate and ammonium in an old field community in Michigan (Robertson et al., 1997) and less than 2 m for nitrate in a southern Quebec forest ecosystem (Lechowicz and Bell, 1991).

Microbially influenced nutrients such as N tend to have shorter ranges than some of the inorganic nutrients such as P and K (Morris, 1998; Robertson et al., 1993; Schlesinger et al., 1996). Since CO_2 does not accumulate appreciably in the soil, it is a direct measurement of the microbial activity at the microniche level. We therefore expect CO_2 to be more heterogeneous than the soil nutrients and have a fairly short spatial range. A range of 30 m has been reported for respiration in an old field ecosystem; however, the minimum sample distance used was 4.6 m (Robertson et al., 1988). In a later study, soil respiration was found to correlate at scales of less than 30 cm (Robertson et al., 1997). Our observed ranges of 9 to 25 cm for respiration in wheat and 6 to 11 cm for poplar are shorter than those reported for other nutrients but consistent with a previous study by Robertson et al. (1997).

Total C was reported to be auto-correlated at distances of less than 7.4 m in an uncultivated successional field at KBS (Robertson et al., 1993). This is more than 10 times the range observed in the poplar plots of this study. In the previous study, samples in the first lag class were separated by about 1.2 meters. When samples were taken at 5 m intervals, in an Iowa field, total C was auto-correlated to 109–129 m (Cambardella et al., 1994). Both studies used compositing to reduce the small-scale variability. Sampling at meter-

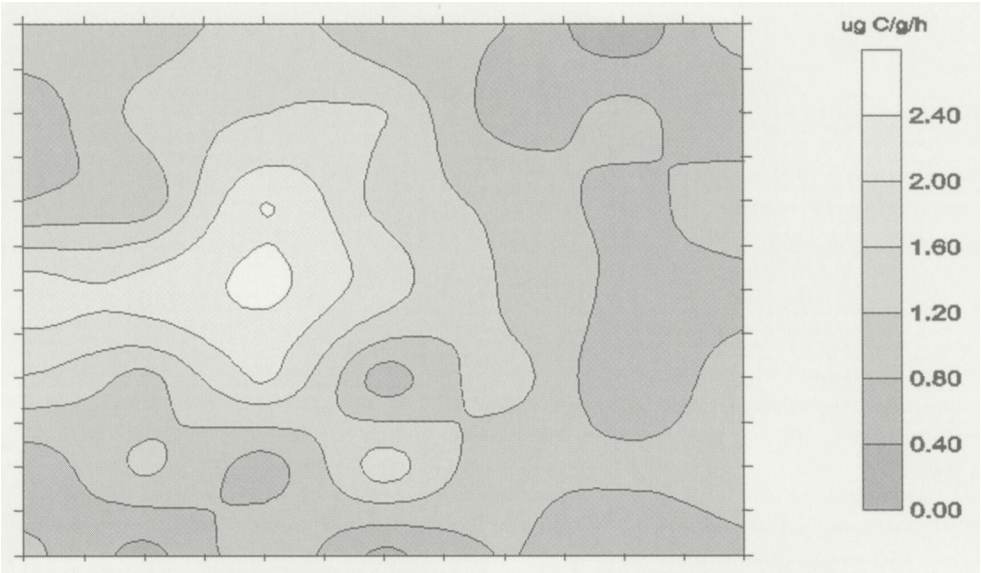

Figure 4. Isopleths for soil respiration measured in a 14 × 14 cm-plot in June 1998 in a wheat plot.

scale distances will not reveal sub-meter heterogeneity. We tried to measure the small-scale heterogeneity to reflect the actual microbial and plant root respiration. This resulted in large nugget variances for the variates even at lag distances of less than 1 meter. The 14×14 cm-plot contained several cases where samples with high and low soil respiration values occurred within 2 cm of each other (Figure 3). We also observed similar small-patch heterogeneity in the normal grids. Soil respiration varying on scales still smaller than those measured might explain the observed small-patch heterogeneity found in our study and that of Rochette et al. (1991). Patches of very high or low soil respiration – so called 'hot spots' – could have sizes smaller than our tube diameters (Morris, 1999). Thus we would get similar values for our coupled tubes when both tubes hit the inner area or the borderline of those 'hot spots.' These 'hot spots' are probably smaller than 7 cm^2 (Figure 3). We believe that most of the spatial variability of soil respiration occurs on this micro scale where soil aggregates, fine soil crevices, and groupings of microorganisms control the spatial heterogeneity of soil respiration at millimeter or smaller scales.

The patterns of microbially mediated nutrients such as mineralizable N can persist for several months when the microbial activity in the soil is reduced (Goovaerts and Chiang, 1993). Rapid changes can occur during the growing season (Table 2). Increased temperature and the availability of food results in increased variability of soil respiration, since the favorable living conditions for microbes are concentrated in 'hot-spots' (Parkin, 1993). Much of the particulate organic matter that is found within aggregates occurs in the 53 to 250 μm range. Since microbial growth on such substrates is probably a source of much of the soil respiration, a true understanding of the processes will require still more detailed sampling for microbial diversity studies. The plant, in effect, samples a soil volume equal to its root system. Therefore, larger composited samples can be used to interpret the processes at the plant and field site specific scale.

The results from the poplar plots showed that, when the favorable conditions decreased, the variability was reduced. The activity of decomposers working on the leaf litter from the previous fall in a moist environment resulted in soil activity in the poplar plots that was higher in April than in June. Areas of high soil respiration were noted to coincide with observed earthworm castings. These castings are produced by earthworms consuming and drawing leaf litter into their burrows (Laverack, 1963). By concentrating the leaf litter and producing earthworm casts, the earthworms are increasing the C content and other nutrients in an area that has been designated as the drilosphere (Beare et al., 1995). The amount of mineralizable organic matter, as measured by laboratory CO_2 evolution (Willson, 1998), shows a pattern of annual fluctuation that coincides with our observed changes in heterogeneity. Soil respiration was lower in June than in April, but it became more concentrated around the tree trunks in June. One explanation for this pattern

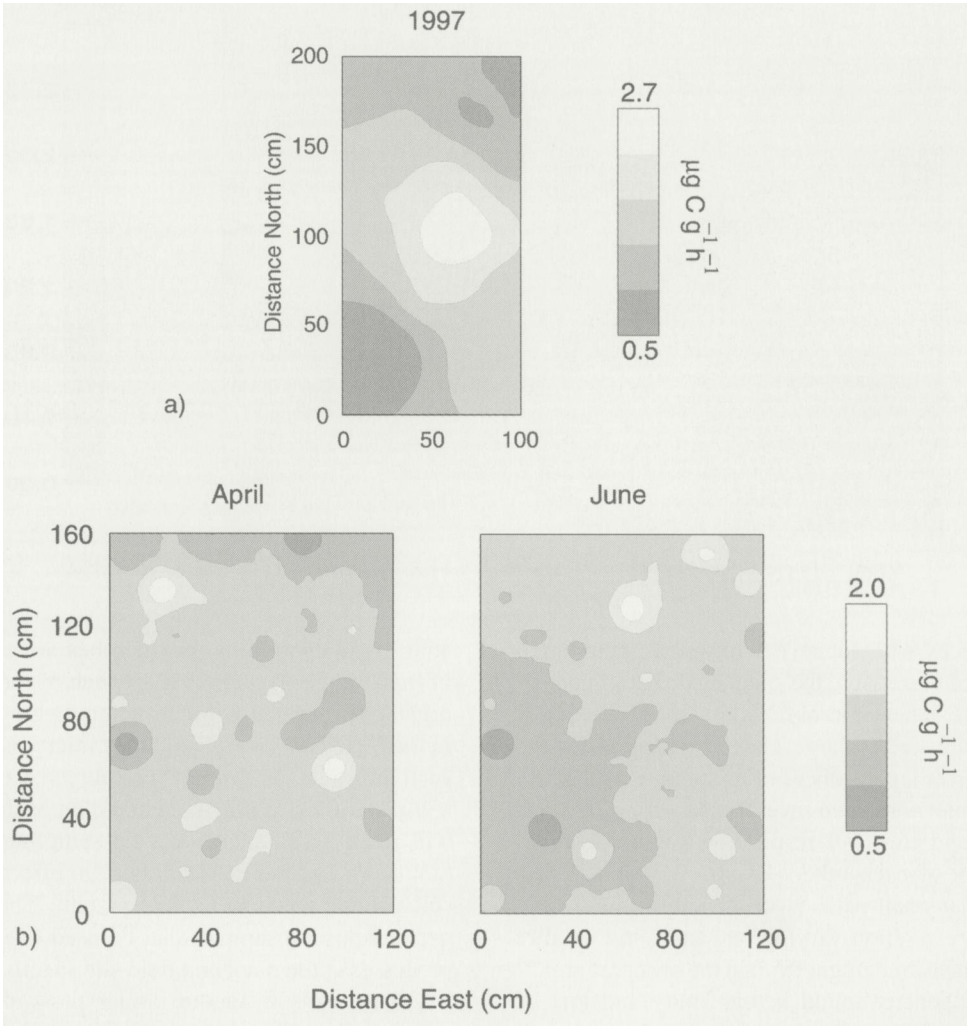

Figure 5. (A) Isopleth for soil respiration in poplar plots (August and September of 1997). (B) Soil respiration of one representative grid in wheat plots for April and June.

could be higher moisture close to the trunk as a result of stem flow. It could also be due to the release of plant-derived C. Moisture stress can also explain the pattern of variability in the wheat plots. In April the moisture was still distributed fairly uniformly but by June, the transpiration demands of the wheat had left only pockets of moisture in the soil.

The more structured variability observed in the deeper soil supports the hypothesis that the heterogeneity is due either to the non-uniform addition of organic material to the surface or the variations in moisture content. The soil moisture and organic material spread out while diffusing into the soil, resulting in smoother shifts between high and low soil respiration areas. Soil respiration, C and N content, moisture and nitrification potential vary at spatial scales smaller than the plant scale. The spatial patterns also change during the season in response to plant inputs, heterogeneous moisture withdrawal as well as microbial events such as decomposition of available substrates. To understand processes as well as microbial diversity it will be necessary to sample the microniches so that the processes involved are not masked. Knowledge of spatial heterogeneity of soil properties is essential for understanding soil fertility, especially as more site specific agriculture is practiced. It is equally important for the understanding of ecosystem processes, microbial diversity, microbial-soil organic matter interactions and global climate change.

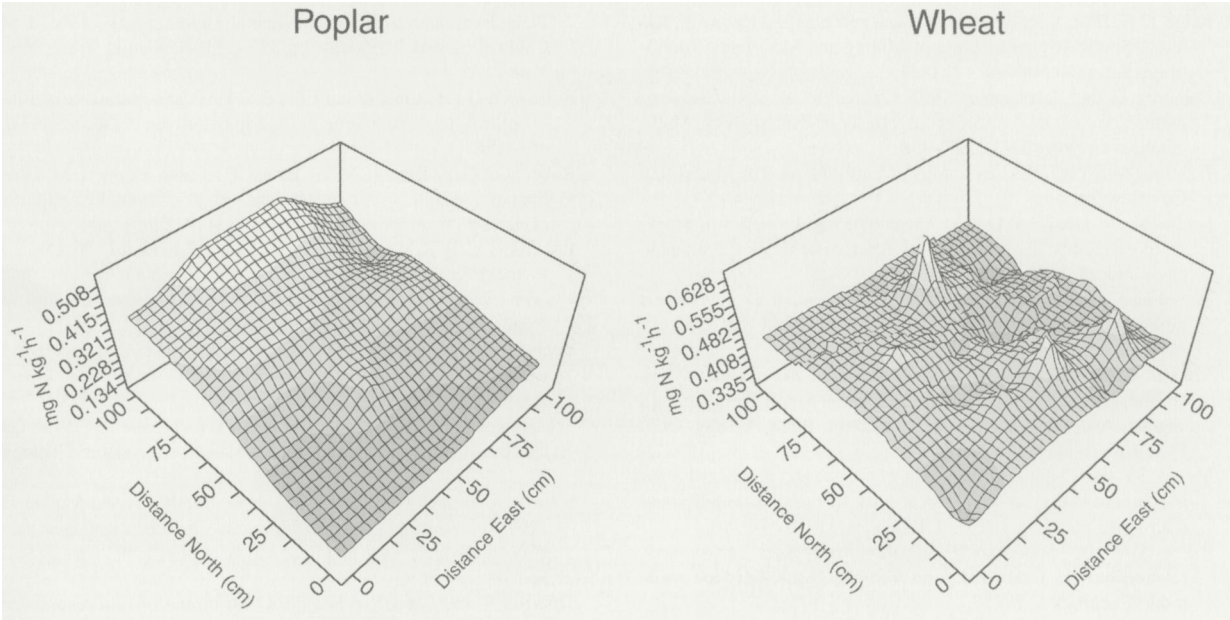

Figure 6. Isopleths for nitrification potential of one representative grid in poplar plots and in wheat plots. The tree location in the poplar plot is in the middle of the upper boundary.

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