Soil properties related to the spatial pattern of microbial biomass and respiration in agroecosystems

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Dupuis, E. M. and Whalen, J. K. 2007. **Soil properties related to the spatial pattern of microbial biomass and respiration in agroecosystems**. Can. J. Soil Sci. **87**: 479–484. Soil microorganisms exhibit a high degree of spatial variation, even in homogenously managed agroecosystems. The spatial pattern of microbial biomass and activity may be related to soil properties like hydrology, texture, organic matter and pH. This study took place in a 0.4-ha field with research plots under wheat and maize production. Soil microbial biomass, respiration and extractable nutrient levels were not generally affected by fertilizer treatments (inorganic NP fertilizer, poultry manure), relative to the unfertilized plots. This was probably due to soil heterogeneity; for instance, soil pH (1:2, soil:water) ranged from 5.8 to 7.2 across the field. Exploratory path analysis revealed that soil pH, dissolved organic carbon and total organic carbon concentrations were directly related to the spatial pattern in soil microbial biomass and respiration. This work demonstrates that path analysis could be used to identify independent soil variables and describe relationships between soil properties and microbial indicators in spatially heterogeneous agroecosystems.

Key words: Field variability, microbial biomass, mineral fertilizer, organic amendment, soil respiration, spatial dependence

Dupuis, E. M. et Whalen, J. K. 2007. **Propriétés du sol associées à la répartition de la biomasse unicellulaire dans l'espace et à la respiration dans les écosystèmes agricoles**. Can. J. Soil Sci. **87**: 479–484. La microflore du sol varie considérablement dans l'espace, même dans les écosystèmes agricoles gérés de façon homogène. Il se pourrait que la répartition spatiale de la biomasse unicellulaire et l'activité de la microflore soient liées à certaines propriétés du sol comme l'hydrologie, la granulométrie, la concentration de matière organique et le pH. Les auteurs ont effectué une étude dans un champ de 0,4 ha divisé en parcelles sur lesquelles étaient cultivés du blé ou du maïs. La biomasse unicellulaire, la respiration et la concentration d'éléments nutritifs extractibles ne sont généralement pas affectés par la fertilisation (engrais NP inorganique, fumier de volaille), comparativement aux parcelles non bonifiées. On le doit sans doute à l'hétérogénéité du sol. Ainsi, le pH du sol (1:2, sol:eau) variait de 5,8 à 7,2 dans le champ. L'analyse de dépendance préliminaire indique que le pH du sol, le carbone organique dissous et la concentration totale de carbone organique sont directement reliés à la répartition spatiale de la biomasse unicellulaire dans le sol et à la respiration. Ces résultats montrent qu'on pourrait se servir de l'analyse de dépendance pour identifier les variables indépendantes du sol et décrire les liens entre les propriétés du sol et les indicateurs microbiens dans les écosystèmes agricoles spatialement hétérogènes.

Mots clés: Variabilité au champ, biomasse unicellulaire, engrais minéral, amendement organique, respiration du sol, dépendance spatiale

Soil biological indicators may provide insight into soil functions such as nutrient cycling, resistance and resilience, and biodiversity (Doran and Parkin 1994; Schjønning et al. 2004). Soil microorganisms are appropriate biological indicators because they respond rapidly to changes in the soil environment induced by anthropogenic activities such as agricultural management (Sparling 1997; Doran and Zeiss 2000). However, previous land management and disturbances that create soil heterogeneity can exert a greater effect on soil microbial communities than current agricultural management (Cavigelli et al. 2005), making it difficult to distinguish how soil microorganisms are responding to recently adopted management practices versus the "noise" induced by environmental variation.

Soil microorganisms exhibit a high degree of spatial and temporal variation, even in homogenously managed agroecosystems (Parkin 1993; Ettema and Wardle 2002). The spatial patterns in soil microbial biomass and activity are related to abiotic factors like resource availability, soil properties, temperature and moisture regimes, as well as biotic factors such as synergism, competition, parasitism and predation (Ettema and Wardle 2002). Soil heterogeneity can lead to spatial dependence in soil microbial communities at multiple scales, ranging from the rhizosphere to 100 m or more (Ramette and Tiedje 2007). At the landscape level, there is much more unexplained variation in soil microbial properties than other soil properties (Oline and Grant 2002; Cavigelli et al. 2005). Previous work has found that variation in microbial biomass, microbial activity and microbial community structure can be partially explained by soil type and drainage class (Rogers and Tate 2001; Girvan et al. 2003), soil texture (Schutter et al. 2001), organic matter con-

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Abbreviations: **DOC**, dissolved organic carbon; **GFI**, goodness of fit index; **NFI**, normed fit index; **MBC**, microbial biomass carbon

tent and pH (Yanai et al. 2003). These soil properties are temporally stable, compared with other abiotic factors (resource availability, temperature and moisture) and biotic factors that affect soil microorganisms. They could therefore be used to explain and interpret soil microbial dynamics, to make predictions about the environmental heterogeneity in agroecosystems and permit researchers to devise sampling schemes that capture the breadth of variation in soil microbial properties within a study area (Bergstrom et al. 1998; Cavigelli et al. 2005).

Geostatistical analysis can be used to detect, estimate and map spatial variation, and it can be combined with correlation analysis to reveal associations between soil properties (Rossi et al. 1992). Using geostatistics, correlation and multiple regression analysis, Robertson et al. (1997) found that about 50% of the spatial variation in soil microbial biomass across a 48-ha site under soybean production was related to five variables (elevation, clay content, net nitrification, pH and sand content). Ramette and Tiedje (2007) used multiscale spatial analysis and derived partial regression coefficients to explain the variation in the population of *Burkhoderia ambifaria*, a free-living soil bacterium. They reported that spatial variation in this bacterial population was related to soil pH, NO_3-N concentration, clay content and sand content. The insight about spatial patterns that can be gained from correlation analysis or multiple regression analysis is obscured when interdependent variables are included in the analysis (e.g., clay content and sand content are negatively correlated).

Path analysis could be used to identify independent variables and represent the relationships between soil variables and microorganisms in a spatially heterogeneous milieu. This technique is based on structural equation modelling that partitions correlation (hypothesized causal effects) into direct and indirect effects, so the relative importance of each hypothesized causal effect can be clarified and the strength of the relationship determined (Hatcher 1994; Shipley 2000). Path analysis begins with a conceptual model that specifies theoretical relationships among variables. Although it cannot prove a mechanistic hypothesis, path analysis can confirm or refute the plausibility of the conceptual model and identify statistically significant relationships. Path analysis could suggest a set of independent (i.e., not intercorrelated) soil physico-chemical and biological properties, and represent the conceptual relationships between these properties. This information could then be used to select a limited number of soil physical, chemical and biological indicators for soil quality assessment. Identifying independent soil properties may facilitate the process of scoring and integrating indicators into a simple index, like the computer-based Soil Management Assessment Framework (Andrews et al. 2004).

The objective of this study was to use exploratory path analysis to identify soil properties related to soil microbial biomass and respiration in agroecosystems.

MATERIALS AND METHODS

The experimental site was located at the Macdonald Research Farm of McGill University, Sainte-Anne-de-Bellevue, Québec (45°3′N 74°11′W). Mean monthly temperatures range from –10.3ºC in January to 20.9ºC in July, and the mean annual precipitation is approximately 970 mm (Environment Canada 2004). The soil was a mixed, frigid Typic Endoaquent, classified as a Chicot sandy-loam, containing 580 g kg^{-1} of sand and 120 g kg^{-1} of clay with 24.5 g organic C kg^{-1}, 1.98 g total N kg^{-1} and pH (H_2O) of 6.3. The site was used as a recreational soccer playing field for more than a decade, but was plowed and planted to soybean in 2003, the year before this experiment began.

In May 2004, adjacent 0.2 ha areas at the site were tilled with a disk harrow (10 cm depth). The field experiment was a randomized complete block design with nine fertilizer treatments, replicated in four blocks, giving 36 plots in each area. The plot size was 5 m long by 3 m wide, and there was a 6-m cultivated border between the experimental areas and surrounding agricultural land. Fertilizer treatments were broadcast by hand on the day of seeding and incorporated by harrowing (10-cm depth) before crops were planted.

Wheat (*Triticum aestivum* L. 'Messier') was planted on May 20 at a rate of 3 700 000 seeds ha^{-1} using a direct seeder (20-cm row spacing). There were 12 rows of wheat in each experimental plot. Fertilizer treatments applied to wheat plots included a control (no N or P fertilizers applied), four inorganic fertilizer treatments (calcium ammonium nitrate plus triple superphosphate) and four poultry manure treatments. Plots amended with inorganic fertilizers received a uniform application of 20 kg P_2O_5 ha^{-1} and N rates of 60, 90, 120 and 180 kg N ha^{-1}. The recommended N application rate for wheat grown in the study region is 90 kg N ha^{-1} [Centre de référence en agriculture et agroalimentaire du Québec (CRAAQ 2003)]. Fresh poultry manure (from a broiler facility) was applied at rates equivalent to 60, 90, 120 and 180 kg N ha^{-1}, based on the N mineralization expected from poultry manure during the growing season in Québec (CRAAQ 2003).

Maize (*Zea mays* L. 'Mycogen 2K350') treated with the fungicides Maxim and Captan was planted on May 26 at a rate of 75 000 seeds ha^{-1} using a direct seeder (75 cm row spacing), which gave four rows of maize per plot. Fertilizer treatments included a control (no N or P fertilizers applied), four inorganic fertilizer treatments (calcium ammonium nitrate plus triple superphosphate) and four poultry manure treatments. Plots amended with inorganic fertilizers received a uniform application of 30 kg P_2O_5 ha^{-1} and N rates of 90, 120, 180 and 240 kg N ha^{-1}. The recommended N application rate for maize grown in the study region is 120 kg N ha^{-1} (CRAAQ 2003). Fresh poultry manure was also applied at rates equivalent to 90, 120, 180 and 240 kg N ha^{-1}, based on the N mineralization expected from poultry manure during the growing season in Quebec (CRAAQ 2003). No additional fertilizers or pesticides were applied to the wheat or maize plots during the growing season, and weeds were removed by hand or mowed as necessary.

Soil Sampling and Chemical Analysis

Soil was sampled following harvest (2004 Aug. 30 for wheat plots, 2004 Oct. 25 for maize plots). Soil samples (0–15 cm depth) were composites of three subsamples dug

from each plot with a shovel (~500 g per subsample), mixed and sieved (< 6 mm mesh) in the field. A portion of each sample was oven-dried (60°C for 48 h) and sieved (< 2 mm), then analysed for soil pH (1:2 soil:water) and Mehlich-3 extractable P and Al (Tran and Simard 1993). A finely-ground (< 0.25 mm) subsample was analyzed for total organic C and total N (Carlo Erba NC Soils Analyzer, Milan, Italy). The remaining soil was immediately placed in a polyethylene bag and stored in a walk-in refrigerator (0°C) until analysis (~ 6 mo for wheat soils and ~ 4 mo for maize soils).

Soil Respiration and Microbial Biomass

Soil pre-incubation is recommended when samples have been stored at cold temperatures, to avoid the initial flush in CO_2 production that occurs after disturbances like re-warming or mixing (Jenkinson and Powlson 1976; Forster 1995). We placed 213.5 g (dry weight basis) of field-moist soil into 500 mL mason jars at a bulk density of 1.0 g cm^{-3}, moistened the soil to 27% water-filled pore space and incubated it in a Conviron controlled climate chamber at 15°C and 80% humidity for 1 wk. Then, the jars were sealed with lids fitted with rubber septa and returned to the incubation chamber for 24 h. The headspace gases were sampled and stored in contaminant-free vacutainers until CO_2-C concentrations was measured on a gas chromatograph (Hewlett Packard 5890 Series II, Palo Alto, CA). Soil respiration (mg CO_2-C kg^{-1} soil dry weight) was calculated using equations from Christian and Cranston (1997).

Following pre-incubation and CO_2 measurements, lids were removed and soils were returned to the controlled climate incubator (15°C, 80% humidity) for 2 d to permit equilibration of soil and atmospheric gas concentrations. After homogenizing the soil, about 10 g of soil was extracted with 0.5 M K_2SO_4 (1:4 soil: extractant) following chloroform fumigation (Voroney et al. 1993). Unfumigated soil was also extracted with 0.5 M K_2SO_4 (1:4 soil: extractant) and analysed for mineral N (NH_4-N and NO_3-N) with a Lachat Quick-Chem flow injection autoanalyzer (Lachat Instruments, Milwaukee, WI). Fumigated and unfumigated K_2SO_4 extracts were digested with an alkaline persulfate solution (Cabrera and Beare 1993) and the NO_3-N in persulfate digests was evaluated with the autoanalyzer. Microbial biomass nitrogen (MBN) was the difference in NO_3-N concentration of fumigated and unfumigated samples, divided by an efficiency factor (K_{EN} = 0.54) (Joergensen and Mueller 1996). Dissolved organic nitrogen was the difference in NO_3-N concentration of the digest and the mineral N (NO_3-N + NH_4-N) concentration in the original unfumigated extract (Cabrera and Beare 1993). Dissolved organic carbon (DOC) in fumigated and unfumigated soil extracts was determined with a Shimadzu TOC-V carbon analyzer (Shimadzu Corporation, Kyoto, Japan). Microbial biomass carbon (MBC) was the difference in DOC concentration of fumigated and unfumigated extracts, divided by an efficiency factor (K_{EC} = 0.45) (Joergensen 1996).

Statistical Analysis

Prior to analysis, the data were tested for normality using the Kolmogorov-Smirnov test and were $\log_e$- or square-root-transformed when required to adjust for normality and stabilize variance. The dataset was analysed as an augmented factorial (2 fertilizer sources × 4 N rates plus an untreated control) using the PROC GLM function of SAS statistical software (SAS System 9.1, SAS Institute Inc., Cary, NC). The sources of variance associated with the treatments (control versus fertilizer treatments) and nested within the fertilizer treatments (2 × 4 factorial structure) were evaluated using the approach outlined by Piepho et al. (2006).

Exploratory path analysis was used to determine the causal relationships between soil properties, microbial biomass and respiration. The correlation matrix for path analysis was generated using a normalized dataset (pooled data from wheat and maize agroecosystems, n = 72) with the PROC CORR function of SAS. To avoid multicollinearity, we removed predictor variables with a variance inflation factor greater than 3. Path coefficients, their significance level and the fit of the structural model were calculated using the CALIS procedure in SAS. The path coefficients correspond to the standardized partial regression coefficients. We used the Goodness of Fit Index (GFI), the Normed Fit Index (NFI) and the χ^2 statistic as indices of the model fit. When GFI and NFI are greater than 0.9 and the χ^2 statistic is non-significant, the predicted covariance matrix is considered to be in good agreement with the observed covariance structure in the data (Hatcher 1994; Schumacker and Lomax 2004).

RESULTS AND DISCUSSION

Soil microbial biomass, respiration and most soil properties were similar in control and fertilized plots in the wheat and maize agroecosystems (Tables 1 and 2). There were some differences associated with the N rate applied and the fertilizer source x N rate interaction, but the only consistent result in wheat and corn agroecosystems was that plots receiving a greater N rate had more mineral N after harvest (Tables 1 and 2). Generally, row-cropped agroecosystems receiving animal manure are expected to have more MBC and greater microbial activity than those that are unfertilized or receive inorganic fertilizers (Wander et al. 1995; Bossio et al. 1998; Murphy et al. 2003) because animal manure supplies readily mineralizable substrates that stimulate microbial growth and respiration (Fauci and Dick 1994; Marschner et al. 2003). The lack of consistent response among the fertilizer treatments was probably due to the short-term nature of this study, in that plots received a single fertilizer application in the season that samples were collected and microbial communities analyzed.

Another reason for the lack of response to fertilizer treatments was the considerable soil heterogeneity across the 0.4-ha field site. For example, soil pH ranged from 6.0 to 6.9 (median soil pH = 6.3) in the wheat agroecosystems, and was between 5.8 and 7.2 (median soil pH = 6.5) in the corn agroecosystems. This led us to consider exploratory path analysis as a means of identifying the soil properties that directly and indirectly affected microbial biomass and respiration.

We did not find an acceptable model for MBC alone, but the MBC concentration was a significant component of the

Table 1. Soil microbial biomass, respiration and selected soil properties in a wheat agroecosystem receiving poultry manure and inorganic fertilizer amendments. Values are the mean (± standard errors) $n = 4$

Fertilizer source	N rate (kg N ha^{-1})		MBC[z] (mg kg^{-1})	CO_2-C (mg kg^{-1} d^{-1})	SOC[z] (g kg^{-1})	DOC[z] (mg kg^{-1})	pH	P/Al ratio[a] (%)	Mineral N[z] (mg kg^{-1})
Manure	60		509 (91)	5.18 (0.68)	26.4 (0.5)	115 (1.1)	6.4 (0.1)	16.5 (0.8)	6.82 (1.5)
Manure	90		534 (70)	6.03 (0.37)	27.5 (2.3)	120 (0.59)	6.2 (0.1)	19.5 (1.2)	6.98 (0.71)
Manure	120		663 (129)	6.27 (0.63)	29.0 (1.3)	119 (4.9)	6.3 (0.1)	22.0 (1.6)	8.03 (0.61)
Manure	180		740 (43)	6.34 (1.3)	30.2 (3.2)	122 (2.7)	6.7 (0.1)	26.3 (2.2)	8.91 (0.86)
Inorganic	60		594 (104)	6.93 (1.7)	28.6 (2.0)	106 (1.8)	6.3 (0.1)	17.1 (0.8)	6.43 (0.75)
Inorganic	90		449 (55)	5.04 (0.7)	27.5 (2.2)	110 (8.1)	6.3 (0.1)	19.1 (0.4)	7.38 (1.3)
Inorganic	120		433 (44)	6.48 (1.6)	26.3 (1.1)	112 (3.4)	6.3 (0.1)	17.0 (1.2)	8.60 (1.5)
Inorganic	180		594 (63)	5.66 (0.59)	30.8 (1.6)	112 (1.6)	6.1 (0.1)	19.0 (3.0)	10.3 (2.2)
Control	0		488 (86)	4.78 (0.32)	27.1 (0.5)	107 (3.3)	6.3 (0.1)	16.6 (1.6)	6.29 (0.63)
Source of variation		d.f.[y]							
Block		3	***	NS	NS	NS	NS	NS	**
Control versus fertilized		1	NS	NS	NS	NS	NS	NS	NS
N rate		3	**	NS	NS	NS	NS	**	*
Fertilizer source × N rate		4	**	NS	NS	*	**	*	NS

[z]MBC = microbial biomass C; SOC = soil organic C; DOC = dissolved organic C; P/Al ratio = Mehlich-3 extractable P/Mehlich-3 extractable Al; Mineral N = NH_4-N + NO_3-N.
[y]d.f., degrees of freedom.
*, **, *** Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively; NS, not significant.

Table 2. Soil microbial biomass, respiration and selected soil properties in a corn agroecosystem receiving poultry manure and inorganic fertilizer amendments. Values are the mean (± standard errors) $n = 4$

Fertilizer source	N rate (kg N ha^{-1})		MBC[z] (mg kg^{-1})	CO_2-C (mg kg^{-1} d^{-1})	SOC[z] (g kg^{-1})	DOC[z] (mg kg^{-1})	pH	P/Al ratio[z] (%)	Mineral N[z] (mg kg^{-1})
Manure	90		436 (27)	3.41 (0.68)	32.6 (2.6)	164 (23)	6.7 (0.2)	28.9 (5.0)	10.9 (0.92)
Manure	120		403 (48)	3.95 (0.52)	32.3 (3.8)	159 (7.3)	6.7 (0.2)	32.6 (8.3)	10.7 (1.4)
Manure	180		432 (58)	6.40 (0.47)	32.5 (0.90)	207 (28)	6.5 (0.1)	29.7 (4.5)	21.3 (6.5)
Manure	240		451 (70)	6.09 (0.99)	33.0 (3.9)	179 (8.9)	6.4 (0.2)	31.5 (5.8)	21.0 (6.8)
Inorganic	90		382 (64)	3.57 (0.42)	32.0 (4.5)	153 (13)	6.7 (0.1)	28.0 (8.5)	10.1 (1.9)
Inorganic	120		356 (51)	3.14 (0.24)	32.6 (1.8)	156 (10)	6.5 (0.2)	30.0 (3.2)	17.7 (2.5)
Inorganic	180		303 (68)	3.52 (0.50)	33.1 (3.7)	162 (7.5)	6.4 (0.2)	33.0 (7.3)	29.0 (6.6)
Inorganic	240		301 (58)	4.18 (0.72)	34.0 (1.7)	151 (11)	5.9 (0.1)	21.7 (3.2)	37.7 (6.3)
Control	0		436 (55)	3.16 (0.64)	33.9 (3.3)	148 (12)	6.6 (0.2)	25.8 (3.1)	6.01 (1.7)
Source of variation		d.f.[y]							
Block		3	**	**	NS	NS	NS	NS	NS
Control versus fertilized		1	NS	NS	NS	NS	NS	NS	**
N rate		3	NS	**	NS	NS	*	NS	**
Fertilizer source × N rate		4	NS	**	NS	NS	NS	NS	NS

[z]MBC = microbial biomass C; SOC = soil organic C; DOC = dissolved organic C; P/Al ratio = Mehlich-3 extractable P/Mehlich-3 extractable Al; Mineral N = NH_4-N + NO_3-N.
[y]d.f., degrees of freedom.
*, ** Significant at $P < 0.05$ and $P < 0.01$, Respectively; NS, not significant.

Table 3. Direct and indirect effects of soil variables, and simple correlation coefficients between soil properties and soil respiration in wheat and maize agroecosystems (pooled dataset, $n = 72$). The direct effects (standardized partial regression coefficients) and correlation coefficients were not significant (NS) or significant at $^{+}$ $P < 0.1$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$

	Soil respiration (mg CO_2-C kg^{-1} d^{-1})		
Variable[z]	Direct effect	Indirect effect	Correlation coefficient (r)
pH	–0.47 ***	0.12	–0.40 ***
DOC	0.17 NS	–0.25	–0.30 **
MBC	0.44 ***	NA[y]	0.27 *
SOC	–0.22 +	NA	–0.32 **

[z]DOC = dissolved organic C; MBC = microbial biomass C; SOC = soil organic C
[y]NA = not applicable

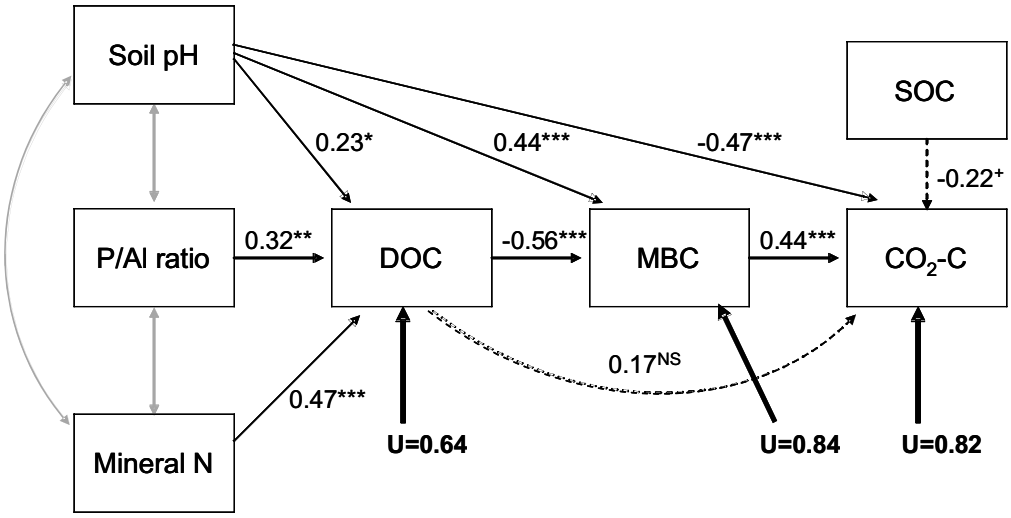

Fig. 1. Exploratory path model describing hypothesized causal relationships between soil parameters and soil respiration (CO_2-C). Soil parameters include: P/Al ratio = Mehlich-3 extractable P/Mehlich-3 extractable Al; mineral N = NH_4-N + NO_3-N concentration; DOC = dissolved organic C; MBC = microbial biomass C; SOC = soil organic C. Single-headed arrows indicate a hypothesized direct causal relationship and double-headed arrows indicate unanalysed correlations. For each effect path, standardized path coefficients are given (significant at $^+$ $P < 0.1$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$, or non-significant, NS). Marginally significant or non-significant paths coefficients are indicated with a dotted line. The residual variables (U) indicate the contribution of all unmeasured or unknown factors to the response variables.

best fit model for soil respiration (GFI = 0.9474, NFI = 0.9382 and nonsignificant χ^2, $P = 0.056$), described in Table 3. Path analysis permits us to partition correlation when variables are intercorrelated, and can be diagrammed to show relationships between independent, intermediary and dependent variables. Direct effects are indicated by single-headed arrows and correlations are indicated by double-headed arrows in the path diagram (Fig. 1). Indirect effects occurred when an independent variable was linked to a dependent variable through one or more intermediary variables.

The direct effects of soil pH (r = –0.47, $P < 0.001$) and MBC (r = 0.44, $P < 0.001$) on respiration were greater than would be predicted from the correlation analysis alone (Table 2). Although DOC was negatively correlated with respiration (r = –0.30, $P < 0.01$), there was a negligible direct effect on respiration ($r = 0.17$, NS) (Table 2). This suggests that the effect of DOC on respiration is mostly indirect and probably occurs through the MBC pool (Fig. 1). One possibility is that the consumption of DOC increased the size of the MBC pool as well as soil respiration, but this hypothesized mechanism remains to be confirmed. We also found a significant negative correlation ($r = –0.32$, $P < 0.01$) between the SOC pool and respiration, but path analysis revealed a marginally significant ($P < 0.1$) direct effect of SOC on respiration, and no relationship between SOC and other soil properties. This implies that the variance associated with SOC comes from soil variables not included in the path analysis.

In summary, we suggest small-scale variation in soil respiration at this 0.4-ha field site was controlled principally by soil pH. The MBC, DOC and SOC concentrations also explain part of the variation in soil respiration, while variance in the MBC pool was directly affected by soil pH and the DOC concentration. Finally, variance in the DOC pool was directly affected by soil pH, the mineral N (NH_4-N + NO_3-N) concentration and the P/Al ratio, a general indicator of soil fertility. With path analysis, we identified and proposed relationships between soil properties and biological indicators (microbial biomass and respiration), but more work is needed to understand the interactions and explain the mechanisms underlying these relationships. In the context of soil quality assessment, path analysis could be a valuable tool for describing relationships between soil physical, chemical and biological indicators in heterogeneous environments.

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